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ACIDIFICATION AND TERRESTRIAL BIRDS

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A report to the Department of the Environment, Transport
and the Regions: Project Number EPG 1/3/135

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EXECUTIVE SUMMARY

1. The UK Government has recently signed up to the 1999 UN ECE Protocol to Abate Acidification, Eutrophication and Ground-level Ozone under the Convention on Long- Range Transboundary Air Pollution. A more stringent strategy for EU countries, the National Emissions Ceilings Directive, is under development. While much is known about impacts of acidification on aquatic ecosystems in the UK, there is a real need for robust indicators that integrate the effects on terrestrial ecosystems. They should be able to measure the impact of abatement strategies and be readily understood by the general public.

2. Acidification reduces calcium availability in aquatic and terrestrial ecosystems, resulting in decreased productivity and reduced population sizes of some bird species. This project assesses the potential use of birds as cost-effective bio-indicators that integrate the effects of acidification within terrestrial ecosystems. It combines information from uniquely detailed historical data sets for bird distribution, abundance and productivity with those for acid deposition and critical loads. It investigates the extent of past and present effects of acidification on terrestrial birds and investigates whether the data sets can form the basis of a cost-effective bio-monitor of terrestrial acidification. It concentrates on those relationships that show adverse effects of acidification because these will provide the best potential candidates as bio-monitors of acidification abatement.

3. Acidification data used in the analysis:
   (a) UK Critical Loads. These were supplied by the Centre for Ecology and Hydrology. The critical loads define the sensitivity of the land to acid deposition of both Sulphur and Nitrogen species. Critical loads for all ecosystems combined for each 10-km square were used in the analysis to incorporate a measure of acid sensitivity in conjunction with accumulated exceedance (see below).
   (b) UK Deposition of Sulphur and Nitrogen. Deposition fields, including backcasts where required, were produced by the HARM model (University of Edinburgh) on a 10-km scale for 1955, 1970, 1983 and 1990. The lack of a reliable spatially disaggregated historical emissions inventory for oxidised or reduced Nitrogen in the UK limited the search for correlations between bird data and deposition, constraining it to the use of Sulphur deposition only.
   (c) UK 'Exceedance Ratio'. Accumulated exceedances (AE) of critical loads for all ecosystems combined were calculated on a 10-km scale by the Centre for Ecology and Hydrology for 1955, 1970, 1983 and 1990 using the HARM modelled deposition fields. It was considered reasonable to use the combination of the historical N deposition together with the more reliable historical S deposition to calculate historical changes in AE. A unit of AE in a sensitive area might be expected to be more damaging than a unit of AE in a less sensitive area. Thus after exploring a number of methods of using the exceedance data in the analysis, the ratio of the AE: 5% CLSMAX was calculated and used in the final analysis.

4. Bird data used in the analysis:
   Distribution data was taken from the two Breeding Bird Atlases, the first in 1968-72 and the second in 1988-91. The second atlas contains more detailed information concerning frequency of occurrence. Data used consist of:
   (a) the frequency of occurrence of species in 10-km squares in the 1988-91 atlas; and
   (b) the presence/absence of species in 10-km squares in both atlas periods. This latter data set was used to determine the number of 10-km squares experiencing losses (local extinction) and gains (local colonisation) between the two periods.
   Data on reproductive performance was analysed with respect to acidification and other environmental variables. Six measures of reproductive performance were considered: lay date, clutch size, brood size, partial brood loss, clutch failure rate and brood failure rate.

5. In the analyses of bird distribution and breeding performance, regression models were initially constructed that contained just environmental variables (e.g. geographical and habitat variables). We then tested whether Sulphur deposition and exceedance ratio made any significant additional

contributions to the models, thereby attempting to control for any confounding environmental factors.

6. The hypothesis that anthropogenic acidification has had a detrimental effect on bird species distributions in Britain was tested by analysing three ornithological data sets in relation to (1) Sulphur deposition and (2) exceedance ratio:
   (a) frequency of species occurrence in 1988-91 (a measure of relative abundance in 10-km squares);
   (b) species loss in 10-km squares between 1968-72 and 1988-91 (change in presence/absence in 10-km squares);
   (c) species gain in 10-km squares between 1968-72 and 1988-91.

   Nine species were selected for analysis that were invertebrate feeders and that had shown a change in range of at least 10% between the two atlas surveys. The species represented a range of ecological requirements.

7. Species distributions were significantly affected by a range of variables including latitude, altitude and habitat type. Significant additional contributions of either Sulphur deposition (SDep)or exceedance ratio (ER) were identified for all of the species selected for analysis, thus supporting the hypothesis of a detrimental effect of acidification on distribution:
   (a) Occurrence in 1988-91 was less likely in 10-km squares with greater acidification for Redshank (SDep), Dipper (SDep), Stonechat (ER), and Lesser Whitethroat (ER).
   (b) Species extinction between 1968-72 and 1988-91 was less likely for Lapwing (SDep & ER), Redshank (SDep), Dipper (SDep), Redstart (SDep) and Ring Ouzel (SDep) in 10-km squares showing a decrease in acidification.
   (c) Species colonisation over the same period was more likely for Little Ringed Plover (SDep) and Lesser Whitethroat (SDep) in 10-km squares showing a decrease in acidification.

8. In addition to relationships showing an apparently detrimental effect of acidification, there were a number that showed apparently beneficial relationships, e.g. where species occurrence was linked to areas where exceedance ratio was high. We tabulated the numbers of relationships showing significant detrimental and apparently beneficial effects on species distributions from all analyses involving combined habitat and acidification variables. For exceedance ratio, 4 relationships showed a detrimental effect, 9 a beneficial effect and 13 were not significant or inconclusive due to significant interaction terms. For Sulphur deposition, the respective figures were 13, 5 and 8. Thus there is little general evidence that exceedance ratio affects species in the expected direction, but Sulphur deposition appears to be more consistently detrimental with respect to species distribution.

9. There was no evidence that species richness in 1988-91 was lower in acidified areas, but richness of resident insectivorous, migrant insectivorous and resident omnivorous passerines increased significantly in 10-km squares that had experienced the greatest decreases in acidification.

10. Forecast reductions in acidification over the next decade were available: (1) the REFERENCE scenario, and (2) the WGS31B scenario, upon which the Gothenburg Protocol is based. These forecasts were used to predict changes in species range by 2010 from the models derived for Sulphur deposition, the most consistent predictor. Lapwing, Little Ringed Plover and Lesser Whitethroat showed the greatest predicted changes, with increases in range of 13%, 13% and 9% respectively, compared to 1990, under the WGS31b scenario. These species were most sensitive and therefore likely to be the best candidates for bio-monitors of acidification. Species richness was predicted to change by only an average of 1 species per 10-km square under the same scenario. Although the REFERENCE scenario produced results 20-40% smaller than the WGS31B scenario, the standard deviations were relatively large and the absolute sizes of the differences in predicted changes were relatively small, the most extreme being 5% (for Lapwing).

11. There were a number of species that showed distinct geographic regions of high sensitivity to acidification. However, there were no areas that were consistently the most sensitive across

species. Given the specific nature of the models for each species or species group and the lack of consistent spatial trends, it is difficult to identify regions where there is high sensitivity to changes in acidification across a range of species. Any consideration of areas in which birds are particularly sensitive to acidification within a monitoring framework would have to be undertaken on a species-by-species basis.

12. The effects of acidification, as measured by critical load exceedance and acid deposition, were analysed with respect to reproductive performance for four invertebrate-feeding passerines, Dipper *Cinclus cinclus*, Song Thrush *Turdus philomelos*, Ring Ouzel *T. torquartus* and Great Tit *Parus major*.

13. Measures of breeding performance were significantly affected by a range of variables including latitude, longitude and altitude. These significant predictors were included in the models before the addition of acidification variables. The majority of relationships between aspects of breeding performance and acidification were curvilinear in nature.

14. These regression models were used to predict effects of reductions in acidification forecast for 2010 under the WGS31B scenario on breeding performance. Predicted decreases in breeding performance were more common than increases (7 versus 3) but the latter were greater in magnitude. Brood survival rates in Dipper and Ring Ouzel were predicted to increase by 23% and 13% respectively compared with 1990 rates and Song Thrush clutch survival was predicted to increase by 7% under a scenario of reduced acid deposition by the end of the decade. Although the predictions under the REFERENCE scenario were smaller in magnitude than for the WGS31B scenario, the associated standard deviations were relatively large compared to the absolute size of the differences.

15. Overall, in both the investigation of bird distributions and breeding performance, detrimental impacts were more frequently detected using Sulphur deposition data than those based on exceedance ratio. Furthermore, species distribution was more sensitive to acidification than breeding performance. Thus the effects of Sulphur deposition on bird distributions are likely to form the most useful potential bio-monitors for acidification abatement strategies in the UK.

16. While breeding performance measured by the British Trust for Ornithology's Nest Record Scheme may prove to be a useful bio-monitor of acidification in the future, the species investigated here appeared not to be especially sensitive and further investigations are required to identify more sensitive species. It would be important to investigate the breeding performance of species showing significant relationships between distributions and acid deposition at a finer scale (i.e. intensive field studies).

17. The atlas data sets showed a number of apparently detrimental associations between Sulphur deposition and bird species distributions. This is despite the lack of sensitivity inherent in this presence/absence data set. It would be especially valuable to follow up these investigations by analysis of the BTO/JNCC/RSPB Breeding Bird Survey (BBS) and the Waterways Breeding Bird Survey (WBBS) data sets. This provides annually recorded, spatially referenced relative abundance data. Such data could be used to measure changes in presence/absence in 1-km survey squares, or they could be used to measure changes in relative abundance, which may be more sensitive to changes in acid deposition and might correlate with exceedance ratio. The BBS could provide a useful, frequently updated, system for tracking the responses of British bird populations identified in this study to reductions in Sulphur and Nitrogen emissions in the future.

18. Due to the slow recovery time of ecosystems to reductions in deposition, future monitoring of bird species sensitive to acid deposition may be more likely to indicate ecosystem recovery in the period starting in 1990, as opposed to the period from 1970 to 1990. The time delay between reductions in critical load exceedances and ecosystem recovery may be considerable and it will be important to monitor ecosystem recovery in the future. A future study could link to a dynamic modelling exercise for the UK using a model such as MAGIC which takes into account such

temporal aspects. This may be greatly facilitated by the recent interest shown in dynamic modelling across Europe (for example at the recent Task Force on Integrated Assessment Modelling in Stockholm) which may result in the generation of detailed additional data for the UK.

Achievement of Specific Aims

The overall aim of this project was to undertake an exploratory analysis of extensive bird data sets in relation to acidification variables and ultimately to determine whether this approach is able to identify potential bio-monitors of ecosystem recovery after the implementation of acidification abatement protocols. As part of this, the key aims were as follows:

1. *To distinguish the separate effects of acid deposition and acid sensitivity over a wide geographic scale for terrestrial birds in Britain.*

   This was achieved by analysing two separate variables, Sulphur deposition and exceedance ratio, a measure that combines accumulated exceedance and critical load, thus producing a measure that takes into account both the likely impact of acidification on ecosystems and the underlying susceptibility of those ecosystems. The findings indicate that, in general, species were more sensitive to Sulphur deposition than exceedance ratio.

2. *To assess whether acid deposition is having a detrimental effect on terrestrial birds in Britain and, if so, identify susceptible areas and species.*

   This was assessed both in terms of species distributions and breeding performance. There was evidence of a detrimental effect of acidification (mainly Sulphur deposition) on species distributions in a number of species, but there was less evidence of a detrimental effect on reproductive performance. Change in species distribution is therefore the best candidate for a bio-monitor of effects of acidification. The species most sensitive to changes in Sulphur deposition were Lapwing (in uplands), Little Ringed Plover and Lesser Whitethroat (lowlands). Other species showed some sensitivity to acidification, but the magnitude of these effects in comparison to other significant predictors of distribution (e.g. habitat, climate) was small. There were certain regions that appeared to be more sensitive to changes in acidification, but these tended to be species-specific and it was not possible to identify regions that could be useful for bio-monitoring purposes across a range of species.

3. *To investigate the dynamic aspects of the response of ecosystems to changes in acid deposition, prior to and following the implementation of the UNECE Second Sulphur Protocol.*

   Regression models for distribution and reproductive performance highlight the response of birds to the reduction in Sulphur deposition and critical load exceedance that has occurred between 1968-72 and 1988-91. However, the overall picture for exceedance ratio is unclear as there were a number of conflicting trends within and between species (i.e. both positive and negative effects). Therefore, further work is recommended to obtain a clearer picture of the ecosystem response. The latest deposition data available for use would have been 1995, which does not match a time when the Sulphur protocol has been fully implemented. Thus, assessment of the effect of this protocol and the recent Gothenburg protocol will need to be carried out in the future.

4. *To generate information for modelling the effects of acid deposition on biota that could aid policy development and the public understanding of the impacts of acidification.*

   Information on the models used to predict future effects of acidification on bird distributions are presented so the models can be used in a repeatable way for other data sets, if appropriate. The models that were most sensitive to changes in acidification, and were therefore the best candidates for bio-monitoring, have been identified. It is suggested that further research concentrates on those species that showed evidence of the greatest sensitivity to Sulphur deposition, namely Lapwing, Little Ringed Plover and Lesser Whitethroat.

5. *To provide baseline data for predicting the efficacy and cost-effectiveness of different abatement strategies.*

Predictions derived from the two forecast scenarios of reduction in acidification did not produce substantially different predictions of absolute size of change in species range. Although the WGS31B scenario predictions were 20-40% larger than those for the REFERENCE scenario, the standard deviations of the differences were sufficiently large that currently there is little reason for selecting a given abatement strategy on the basis of the predictive species distribution models constructed under this project. Future work, using other datasets, may allow more precise estimates of the differences between scenarios.

1.0 INTRODUCTION

In December 1999, the UK Government signed up to the UNECE Gothenburg Protocol to Abate Acidification, Eutrophication and Ground-level Ozone under the Convention on Long-Range Transboundary Air Pollution. The Government is also negotiating the EU National Emissions Ceilings Directive (NECD). Ceilings in both this Protocol and NECD apply to NO_x, SO_2, VOC_s and NH_3. While much is known about impacts on aquatic ecosystems in the UK, there is a real need for robust indicators which integrate the effects of acidification on terrestrial ecosystems. They should provide a measure of the impact of abatement strategies and be readily understood by the general public.

Acid deposition can pose a serious threat to wildlife of freshwater rivers and lakes over large geographic areas. Increased acidity can be detrimental in itself, but can also alter the chemical balance within water-bodies to cause increases in toxic chemicals and decreases in essential minerals. A great deal of research has shown severe effects of acidification on aquatic invertebrates (Glooshenko *et al.* 1986, Ormerod *et al.* 1991), fish (Likens & Bormann 1974) and birds (Graveland 1998) in addition to the plant communities of acid-sensitive areas. However, with the exception of evidence for forest die-back in both Europe and North America, our knowledge of the impacts of acidification on terrestrial wildlife lags far behind that for aquatic wildlife.

One of the effects of acid rain is to alter the availability of calcium in the environment. Calcium is particularly important for birds as a major constituent of eggshell (Graveland & Drent 1997). A lack of calcium impairs the breeding performance of certain species by restricting egg formation or by increasing their sensitivity to toxic metals in the environment (Graveland 1998). Such effects have been found in Europe and North America, where they have been related to the scarcity of calcium-rich invertebrates (especially molluscs). These effects have been experimentally reversed by adding calcium to forest soils or by providing breeding birds with supplementary dietary calcium (Graveland *et al.* 1994). While such effects have been shown to occur at relatively local levels by intensive research projects, the possibility that these effects may be evident over a large geographical area and for a large number of bird species has serious conservation implications for birds and the environment that supports them.

The British Trust for Ornithology has organised the collection of important monitoring information on bird populations by volunteer observers for government and other bodies for more than 60 years. In particular, it has two unique, national ornithological databases that can be used to investigate the impacts of acidification: on birds the Nest Record Scheme (NRS) and Breeding Bird Atlas data sets. The NRS holds a million records, dating back to 1939, of the breeding performance of birds throughout Britain. The two Breeding Atlases cover 1968-72 and 1988-91; both provide information on bird distributions at the 10-km square level but the later atlas also maps distribution at the tetrad (2x2-km) level.

These extensive historical national data sets can be analysed with respect to spatially-gridded information on critical loads and acid deposition. This will allow comparisons between acidified and non-acidified areas and the investigation of changes over time. This is particularly timely, considering the recent concern over the long-term decline in eggshell thickness of a number of species of thrush (measured from museum collections) that may be linked to acid deposition (Green 1998). The value of these long-term data sets in investigating aspects of environmental change has been demonstrated in a different field by using NRS data to show the generality of long-term trends towards earlier laying by birds in response to climate change (Crick *et al.* 1997).

If acidification effects are detectable in the national data sets, then birds could provide a very cost-effective bio-monitor of the impacts of acidification abatement strategies through the continued collection of data gathered annually by the extensive network of volunteers of the British Trust for Ornithology. It is likely that the general public would find birds a more readily understood bio-indicator of acidification than information based on air or soil chemistry.

1.1 AIMS AND OBJECTIVES

The aims of this project were to undertake an exploratory analysis of extensive historical national data sets on terrestrial bird populations and critical loads to make comparisons between acidified and non-acidified areas and to investigate changes over time. This approach would help identify whether birds are potential biomonitors of acidification in terrestrial ecosystems. The final selection of study species was based on the availability and suitability of data for each part of the project. Analyses focused on small passerines for which extensive nest record data exist.

The key aims were:

1. To distinguish the separate effects of acid deposition and acid sensitivity over a wide geographic scale for terrestrial birds in Britain.

2. To assess whether acid deposition is having a detrimental effect on terrestrial birds in Britain and, if so, identify susceptible areas and species.

3. To investigate the dynamic aspects of the response of ecosystems to changes in acid deposition, prior to and following the implementation of the UNECE Second Sulphur Protocol.

4. To generate information for modelling the effects of acid deposition on biota that could aid policy development and the public understanding of the impacts of acidification.

5. To provide baseline data for predicting the efficacy and cost-effectiveness of different abatement strategies.

1.2 METHODOLOGY

1.2.1 Overview of acidification data

1.2.1.1 Deposition

The modelled annual deposition of oxidised Sulphur, oxidised Nitrogen and reduced Nitrogen is based on the output of the Hull Acid Rain Model (HARM) (Metcalfe *et al.* 1995). HARM is a receptor orientated Lagrangian statistical model which estimates annual average deposition of S, NO_y-N and NH-N to the UK at a spatial scale of 10-km x 10-km. The model is driven by emissions of SO_2, NO_x and NH_3 across both Europe (EMEP grid area) and the UK represented at the scales of 50-km x 50-km and 10-km x 10-km respectively. The major processes of chemical transformation are represented by a coupled chemical scheme. HARM employs a highly simplified meteorology including a single wind rose, constant drizzle and straight line trajectories. Detailed descriptions are provided in Metcalfe *et al*. (1995) and Metcalfe *et al.* (1998). The performance of HARM has been assessed by comparison with data from the UK's monitoring networks, the best estimates of national deposition provided by the Review Group on Acid Rain (RGAR) and by intercomparison with other models in use in the UK (RGAR, 1997). HARM appears to be able to reproduce the amount and spatial distribution of the deposition of S and oxidised N at least as well as any other model, but it underestimates inputs from the dry deposition of reduced N (NH-N). Modelled reduced N deposition therefore represents a minimum estimate. The model includes orographic enhancement of wet deposition over upland areas (Carruthers and Choularton 1984, CLAG 1997) which considerably increases the acid deposition received by sensitive ecosystems in the U.K. and is clearly particularly relevant to this study.

Modelling past acid deposition is constrained by the availability of spatially disaggregated emissions estimates. In the UK (and across Europe) historical disaggregated emissions data are only available for SO_2. For NO_x and NH_3, national totals become available from 1970 or 1980 and the current spatial distribution of emissions sources has been used. Although nitrogen deposition could not be included singly in the regression analyses owing to the lack of reliable spatially disaggregated emission data, this was not considered to be a serious problem for the analysis since its deposition was considered to have changed only slightly over the years whereas Sulphur deposition has changed dramatically. The anthropogenic emissions used in the scenarios for 1955, 1970 and 1983 are summarised in Table 1.1 and in the approach described below. All model runs used a 1961-1990 rainfall field.

HARM modelled depositions for wet, dry and total S, oxidised and reduced N deposition have been supplied. Due to the availability of the emissions data, backcasts for all three model scenarios (1955, 1970 and 1983) are only available for S (see Figures 1a to d). Modelled deposition of oxidised N (Figure 1e) uses the correct emissions totals for 1970 and 1980 but the spatial distribution is from 1995. Deposition of reduced N (Figure 1f) cannot be regarded as reliable. The deposition budgets are summarised in Table 1.2.

The pattern of S deposition shows clear changes between the 3 time periods. Between 1955 and 1970 total deposition increased reflecting the overall increase in SO_2 emissions. Dry deposition is closely related to areas with concentrations of domestic and industrial sources. Wet deposition, which is highest in the uplands of western and northern Britain, is relatively and absolutely more important in 1970 than in 1955 probably due to greater long range transport from the rest of the EMEP area. By 1983, total S deposition had declined following the downward trend in emissions (see Table 1.2a), although this was more pronounced in dry deposited S than in wet. In the UK, the pattern of dry deposition had changed to cluster around the major coal fired power stations and the Thames estuary. This reflects the switch away from coal as a domestic fuel. The reduction in wet S deposition was not as great as that in dry indicating that long range transport of S continued to be important.

Although it is possible to produce deposition maps in equivalents of H+ ions, in order to represent the combined effect of deposition from both Sulphur and Nitrogen-containing compounds, this approach was not used here. This was because of the lack of reliable detailed emission data for nitrogen containing compounds prior to 1980. Only for 1983 and 1990 are reliable estimates of emissions of nitrogen compounds available, requiring assumptions to be made concerning the situation in 1955 and 1970, as explained above. Thus the maps produced indicate Sulphur and Nitrogen deposition separately. Figures 1a to d show Sulphur deposition in the four years in question and Figure 1e and f show the oxidised and reduced Nitrogen deposition in 1983. Changes in Sulphur deposition have been generally much more pronounced than those of Nitrogen.

HARM has also been used to model acid deposition for 1990 (Figure 1d, g, h) and for possible future scenarios, the REFERENCE scenario and the WGS31B scenario (Table 1.2b). These scenarios are explained below, WGS31B implying the most stringent emissions reductions. Under the WGS31B scenario, UK SO_2 emissions are dominated by emissions from point sources (power stations, oil refineries, industry) which account for 81% of the UK total. Low level sources (18%) and road transport (1%) account for the remainder of the emissions total. UK NO_x emissions are distributed more evenly with point sources, low level sources and road transport accounting for 44%, 30% and 26% of UK NO_x emissions respectively.

In this study, the estimates of Nitrogen deposition were used only in calculating the accumulated exceedances for each of the scenarios (see below) owing to the lack of sufficiently reliable detailed emission data for Nitrogenous compounds. Nitrogen deposition *per se* was not used in the regression analyses. Nitrogen deposition has changed less over the years than Sulphur deposition, so the analysis does include the main factor responsible for changes in accumulated exceedance (i.e. the Sulphur deposition).

Sulphur and Nitrogen deposition for 1992-94 were also provided by David Fowler at Penicuick CEH but was not used in the final analysis, since it was felt that a totally HARM-based approach to deposition would be more consistent. There was also an opportunity to use 1996 data from CEH, but since there were significant methodological differences with the 1992-94 data this data was not used.

1.2.1.2 Critical Load

The critical load (CL) has been defined as the 'deposition below which significant harmful effects on specified sensitive elements of the environment do not occur, according to present knowledge' (Nilsson 1986). CLs were based on a combination of calculations of six different ecosystem types. For acid grassland, calcareous grassland, and heathland, critical loads were calculated using the empirical critical loads of acidity for soils based on weathering rates (Hornung *et al.*1995) whilst for coniferous woodland and deciduous woodland, the simple mass balance method (UNECE 1993, Posch *et al*. 1995) was used. Finally, for freshwaters the FAB (First Order Acidity Balance) model output is used (Hall *et al*. 1988, Curtis *et al*. 1988). The areas covered by these ecosystems are taken from the CEH landcover map. Agricultural and urban areas were not included.

The definition of critical load obviously applies to a single ecosystem, and it is clear that different ecosystems may have different critical loads. A single grid square of size 10x10-km may contain up to six different ecosystem types. Thus, so-called ‘protection isolines’ have been developed (Posch *et al*. 1995), which define combinations of Sulphur and Nitrogen deposition which protect a certain percentage of ecosystems in each grid cell against acidification. These are drawn in the Sulphur-Nitrogen (S-N) plane and join all possible combinations of Sulphur and Nitrogen deposition which equate to a single critical load for acidity. It is possible to approximate each isoline to a three-node form, in which only three values define the critical load: CLMAXS, CLNOPT, and CLMAXN, as shown (Figure 2). This representation was put forward by Posch *et al*. (1995), and taken forward by Bull *et al*. (1994). The highest possible Sulphur deposition on the original multi-node isoline is known as CLMAXS, and the point (CLMAXS, 0) drawn in the Sulphur-Nitrogen (S-N) plane is the first of the nodes in the 3-node form. The highest possible Nitrogen deposition in the multi-node isoline is CLMAXN. The point (0, CLMAXN) defines the second point on the 3-node isoline. It has been common to use the 5% isolines (i.e. those which protect 95% of the ecosystems) as a reference point in the calculations carried out under the auspices of the UN ECE at the Task Force on Integrated Assessment Modelling. Thus 5% three-node isolines were used in this case. As mentioned previously in Sulphur deposition was considered more influential than Nitrogen deposition in determining levels of acid deposition between the 1950’s and the 1980’s. For this reason, the parameter chosen from the 5% isoline to represent critical load was CLMAXS (Figure 3 showing CLMAXS across UK). This was used in the calculation of exceedance ratio (see below).

1.2.1.3 Accumulated Exceedance

The ‘exceedance’ is a measure of the difference between the deposition and the critical load and is therefore a crude indication of environmental damage. In simplistic terms one might assume that this should be the difference between the Sulphur deposition and CLMAXS. However, it would be incorrect to do so since, as can be seen from Figure 1, whether or not a critical load is exceeded depends on the Nitrogen deposition in each grid cell as well as the Sulphur deposition. Therefore, CEH calculated exceedance maps by taking into account both Nitrogen and Sulphur deposition, using the data mentioned above, for the same set of years 1955, 1970, 1983 and 1990. These calculations produced a quantity known as ‘accumulated exceedance’ which could be mapped in every grid cell. Considering Figure 2, if in a particular grid cell the deposition is at the point P shown, there is no unambiguous method of defining the exceedance, firstly because there are many ways of measuring the distance from P to the isoline, and secondly because it is desirable to take into account not only this distance but also the area of ecosystems to which it applies. Figure 4 illustrates this approach, in which ‘accumulated exceedance’ is defined as the product of the magnitude of the exceedance and the area of ecosystems exceeded. The methodology used to calculate accumulated exceedance was originally proposed by Posch (1998). Accumulated exceedance has been shown to be a particularly appropriate method to use for selecting environmental targets for use in international policy (Warren and ApSimon 2000). Figure 5a shows the average accumulated exceedance in each grid cell in the UK for four different scenarios matching the depositions shown Figures 1a to h.

The damage incurred by an ecosystem once its critical load is exceeded will depend on the accumulated exceedance. The relationship between damage and a measure of exceedance is known as a ‘dose-response’ function. Such functions are highly complex and are not known for any ecosystem as a whole although some functions have been calculated for specific indicators of acidification such as water chemistry or changes in the composition of the invertebrate community (Ormerod *et al.* 1990). In Canada some dose-response functions have even been calculated for waterfowl (McNicol *et al.* 1995). However, these are based on empirical observations in particular areas and it may not be appropriate to extrapolate such functions from one species to another or from one catchment to another. In attempting to reduce deposition to critical loads there is an implicit assumption that damage is immediately present once the critical load is exceeded. Further, it might be thought that damage to ecosystems is linearly proportional to some measure of the exceedance. However, a unit of exceedance (for example a gram of Sulphur) is likely to be far more damaging to a sensitive ecosystem than an insensitive one. Therefore, the ratio of the exceedance to the critical load, known as the ‘exceedance ratio’ is likely to be a better indicator of damage to ecosystems than any measure of the exceedance on its own. Figure 5b shows the exceedance ratio for the years 1955, 1970, 1983 and 1990.

1.2.1.4 Use of Acidification Data in the Analysis

Two measures were used in the analysis, each at 10x10-km resolution: Sulphur deposition and ‘exceedance ratio’. The critical load is constant over time, whereas the deposition and the ‘exceedance ratio’ have changed over the years. The critical load gives an indication of the sensitivity of an ecosystem to acid deposition, whilst the deposition indicates the amount of acidifying material deposited from the atmosphere. Deposition takes no account of the critical load of a given 10-km square, which is considered a good measure of the buffering capacity against acidification.

As explained previously the ‘exceedance’ is a measure of the difference between deposition and critical loads, whilst the ‘accumulated exceedance’ is also indicative of the area over which exceedance occurs. After experimentation with different types of exceedance data (for example the area of each ecosystem type exceeded, the accumulated exceedance, and the average accumulated exceedance per 10-km square, the ‘exceedance ratio’ for all ecosystem combined, was selected for use in the final analysis. This quantity is a very crude attempt at estimating the likely damage to ecosystems as a result of acid deposition and is the ratio of accumulated exceedance to critical load (CLMAXS).

1.2.2 Acidification Scenarios for Analysis

Models of the long range transport of air pollutants enable the simulation of both past and future depositions of acidifying pollutants (compounds of Sulphur and Nitrogen) when reasonable estimates of emissions are available. The resulting depositions can then be compared with critical loads to produce ‘accumulated exceedance’ and ‘exceedance ratio’ maps in order to investigate how the environmental damage resulting from acid deposition may have changed through time.

In order to investigate the dynamic nature of any relationships between bird distribution and acidification, maps of Sulphur deposition, accumulated exceedance and exceedance ratio were produced for the following years: 1955, 1970, 1983, and 1990. The years 1970 and 1990 match the years of the two BTO Breeding Bird Atlases (1968-72 and 1988-1991) as explained below and thus are particularly relevant to the studies of changes in bird distribution. Once relationships had been derived between acidification variables and ornithological ones, it was then possible to forecast the effect of future emission scenarios on terrestrial birds in the UK. Thus, Sulphur deposition (Figures 6 a and b), accumulated exceedance (Figure 7a) and exceedance ratio (Figure 7b) maps were also prepared for the following two future emission scenarios for the year 2010: the REFERENCE (REF) scenario and the WGS31B scenario (Table 1.3). The REF scenario is that to which countries are already committed under current legislation (e.g. EC directives or UN ECE protocols) and national current reduction plans. REF is the set of country emissions which takes into account reductions expected to occur by 2010 as a result of both the current reduction plans and current legislation.

International protocols are set up on the basis of the Convention on Long-Range Transboundary Air Pollution (UN ECE 1994, UNECE 1998). The WGS31B scenario formed the basis for the multi-pollutant multi-effect protocol signed by 27 countries in December 1999. The WGS31B scenario was derived by negotiators taking into account information from scientists using a technique called integrated assessment modelling (Alcamo *et al.* 1990, Amann *et al.* 1994, ApSimon *et al.* 1991, ApSimon *et al.* 1994, SEI 1991). This produces cost-effective abatement strategies to reduce acid deposition in Europe towards specified environmental targets based on the critical loads approach. The abatement strategies define the set of emission ceilings which countries must comply with by the year 2010. Such strategies are based upon calculating the additional emission reductions which countries must make beyond the REF scenario.

1.3 OVERVIEW OF ANALYSIS METHODOLOGY FOR BOTH DISTRIBUTIONAL AND REPRODUCTIVE INDICATORS

1.3.1 Summary of calculations carried out to achieve aims

To meet the aims set out in section 1.1, we have:

1. Modelled the frequency of occurrence (proportion of 2x2-km squares occupied per 10-km square) of selected bird species in relation to Sulphur deposition and exceedance ratio for the period 1988-91 combined, using the British Trust for Ornithology's (BTO's) New Breeding Bird Atlas data set. We did not model with respect to Nitrogen deposition since the historical emission inventory is not sufficiently reliable.

2. Modelled the distributional changes of selected bird species in relation to Sulphur deposition and exceedance ratio, using the BTO's two breeding bird atlas data sets (covering 1968-72 and 1988-91).

3. Investigated the dynamics of changes in the breeding performance of selected bird species in relation to Sulphur deposition and exceedance ratio and in relation to extensive historical information provided by the BTO's Nest Record Scheme.

4. Used models developed in 1-3 above to investigate how indicator bird populations might respond to predicted reductions in Sulphur deposition or in exceedance of critical loads after the implementation of different abatement strategies.

5. In addition, we will disseminate the results in the form of scientific papers and in articles in the popular scientific media. In this report, chapters 2 and 3 are in the form of draft manuscripts prepared for submission to peer-reviewed scientific journals. In due course, once these papers are accepted for publication, we aim to publicise the work by preparing articles for the popular scientific press.

1.3.2 Approach

The work program was divided into seven components as follows:

1. Collation of data sets of Official UK Critical Loads (CLs), S & N deposition and Critical Load Exceedance (CLE) data at a scale appropriate to the availability of bird data and also to the reliability and consistency of the available deposition data.
    - Official UK CLs for acidification (i.e. the combinations of Sulphur and Nitrogen deposition which represent the critical loads) were obtained from The Centre for Ecology and Hydrology (CEH) at Monks Wood. Data were provided for six ecosystem types, acid grassland, calcareous grassland, heathland, freshwaters, deciduous woodland and coniferous woodland. In the final analysis only the CLs for all ecosystems combined were used.
    - Forecasts and backcasts of acid deposition (including oxidised Sulphur, oxidised Nitrogen and reduced Nitrogen) were modelled using the Hull Acid Rain Model (HARM) by Dr Sarah Metcalfe at the University of Edinburgh and Dr Duncan Whyatt at the University of Lancaster. Reference was made to the work of RGAR where relevant. The years covered were 1955, 1970, 1983, and 1990 and two forecast scenarios, REFERENCE and WGS31B.
    - CL exceedances were provided by the Centre for Ecology and Hydrology at Monks Wood. These were originally calculated for each of the six single ecosystems (e.g. deciduous woodland), but these were not found to be as useful as the exceedances for all ecosystems

combined (because of the large number of extra variables entered into the regression models and the reduced sample sizes that their use entailed.)

- CLEs were calculated for scenarios specific to the work including forecasts, and expressed in terms of accumulated exceedance.
- Exceedance ratios were calculated from the CLEs and the 5% critical load for Sulphur.

2. Investigation of the geographical distribution of computerised Nest Record Cards to identify gaps in coverage and the computerisation of extra records to fill these gaps. This resulted in the computerisation of all the Ring Ouzel cards, a species considered likely to be most vulnerable to the impacts of acidification, in addition to the computerisation of sets of cards for Song Thrush and Great Tit to increase geographical coverage in the uplands. We also added missing grid references to many earlier cards used in the analysis to allow spatial referencing with the acidification data sets.

3. Investigation of the spatial relationships between frequency of occurrence of at least six species of birds and Sulphur deposition (Nitrogen deposition was not used due to the lack of reliable spatially disaggregated historical emission data, but is thought to have changed only slightly over the years), and deposition and exceedance ratios using breeding bird atlas data from 1988-91.

   - The BTO's New Breeding Bird Atlas data set covers the period 1988-91 and provides information on frequency of occurrence (proportion of 2x2-km squares occupied per 10-km square). Data was extracted for study species and converted into a format ready for analysis.
   - A logistic regression approach was used to investigate the relationships between species distribution Sulphur deposition and exceedance ratios, taking into account the influence of potential confounding variables, such as altitude and land cover type, by reference to CEH Land Characteristics, Land Classification and Land Cover databases, as required.

4. Investigation of changes in the distribution of at least six terrestrial bird species between the two Breeding Bird Atlas periods (1968-72 and 1988-91) in relation to Sulphur deposition and exceedance ratios, using a similar approach to that used in 3, above.

   - The BTO's Breeding Bird Atlas data sets for the periods 1968-72 and 1988-91 both provide data on distribution of all birds at the 10-km square level.
   - A logistic regression approach was used to investigate the relationships between changes in distribution and Sulphur deposition and exceedance ratios taking into account the influence of potential confounding variables, such as altitude and land cover type, by reference to CEH Land Characteristics, Land Classification and Land Cover databases, as required.

5. Investigation of the dynamic relationships between aspects of breeding performance and Sulphur deposition, and exceedance ratios since 1950 for four species.

   - The species chosen were those for which effects were most likely to be found: (a) Dipper *Cinclus cinclus*, because of its status as a key indicator of acidified watercourses; (b) Great Tit *Parus major*, because of the effects of acid-related calcium deficiencies on breeding performance in the Netherlands; (c) Song Thrush *Turdus philomelos* because of long-term trends in eggshell thinning that have been related to acidification and because of its status as a Priority species under the Government's Biodiversity Action Plan; and (d) Ring Ouzel *Turdus torquatus* because it is a thrush species characteristic of upland areas where acidification has had greatest impacts.
   - These analyses used general linear models and logistic regression approaches and included environmental factors to help control confounding factors that may influence the statistical relationships with S deposition and exceedance ratio.

6. Model possible future changes in abundance, distribution and breeding performance of birds using the models developed in 3-5 (above) to predict the impact of potential acidification

abatement strategies in the UK.

- The predictive value of the modelled relationships between bird abundance, distributional change and breeding performance was investigated by predicting the future patterns of bird populations and comparing these with current patterns.
- The models used likely acidification scenarios, based on potential abatement strategies, to assess the potential beneficial impact on bird populations. DETR selected the WGS31B and REFERENCE scenarios for the analysis.

7. Dissemination and reporting

- The results from this work has been written up in the form of manuscripts for submission to scientific journals and bound into this report with additional information as required.
- At least one article will be written for the popular scientific media to describe the main results and to bring the work to the attention of the more general public.
- We envisage that presentations will be made at national and international scientific conferences e.g. British Ecological Society Winter Meeting.

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Table 1.1 Emissions in 1980 (Berge 1997) and at REFERENCE and WGS31B Scenarios kT/yr

Pollutant	SO2	SO2	SO2	NOX	NOX	NOX	NH3	NH3	NH3
Scenario	1980	REF	WGS31B	1980	REF	WGS31B	1980	REF	WGS31B
Country									
Austria	397	40	39	246	103	107	91	67	66
Belgium	828	193	121	442	191	184	89	96	74
Denmark	450	90	55	282	128	127	141	72	69
Finland	584	116	116	295	152	170	35	31	31
France	3338	448	400	1823	858	860	700	777	780
Germany	3164	581	550	2617	1184	1081	572	571	550
Greece	400	546	546	306	344	344	78	74	73
Ireland	222	66	42	73	70	65	126	126	116
Italy	3800	566	500	1480	1130	1000	436	432	419
Luxembourg	24	4	4	23	10	11	7	7	7
Netherlands	490	73	50	583	280	266	234	136	128
Portugal	266	141	170	96	177	260	93	67	108
Spain	3319	774	774	950	847	847	353	353	353
Sweden	508	67	67	448	190	168	61	48	58
UK	4913	980	625	2416	1186	1181	354	297	297
Albania	72	55	55	24	36	36	31	35	35
Belarus	740	494	480	234	316	255	219	163	158
Bosnia-H	480	415	415	80	60	60	31	23	23
Bulgaria	2050	846	856	416	297	266	323	126	108
Croatia	150	70	70	83	90	87	44	37	30
Czech Rep.	2257	366	283	937	296	286	105	108	101
Estonia	239	175	175	93	73	73	29	29	29
Hungary	1633	546	550	273	198	198	170	137	90
Latvia	57	104	107	90	118	84	44	35	44
Lithuania	311	107	145	152	138	110	85	81	84
Norway	140	32	22	192	178	156	21	21	23
Poland	4100	1397	1397	1229	879	879	550	541	468
Moldova	308	117	135	58	66	30	47	48	42
Romania	1055	594	918	523	458	437	340	304	210
Russia	7161	2344	2352	1734	2653	2653	1189	894	894
Slovakia	780	137	110	197	132	130	62	47	39
Slovenia	234	71	27	51	36	45	27	21	20
Switzerland	116	26	26	170	79	79	71	66	63
Macedonia	106	81	81	39	29	29	17	16	16
Ukraine	3849	1488	1457	1145	1433	1222	729	649	592
Yugoslavia	406	269	269	47	152	152	90	82	82
Atlantic	891	641	641	1275	911	911	0	0	0
Baltic	72	72	72	80	80	80	0	0	0
North Sea	475	439	439	710	639	639	0	0	0
Natural Oceanic	724	724	724	0	0	0	0	0	0
Volcanic	2144	2235	2235	0	0	0	0	0	0
TOTAL	59345	15571	15141	23215	16197	15568	8412	6617	6280

Table 1.2a. Emissions used in backcast scenarios

Scenario	Pollutant	Base year	Total in k tonnes
1955	UK SO_2	1955[a]	5114.7
	UK NO_x	1970[s]	2381.4
	UKNH_3	1996	354.4
	UK HCl	1992	271.3
	EMEP SO_2	1960[a]	33213.4
	EMEP NO_x	1980[s]	20801.6
	EMEP NH_3	1980[s]	8097.8
1970	UK SO_2	1970[a]	5786.0
	UK NO_x	1970[s]	2381.4
	UK NH_3	1996	354.4
	UK HCl	1992	271.3
	EMEP SO_2	1970[a]	50066.6
	EMEP NO_x	1980[s]	20801.6
	EMEP NH_3	1980[s]	8097.8
1983	UK SO_2	1983[a]	3864.3
	UK NO_x	1980[s]	2416.4
	UK NH_3	1996	354.4
	UK HCl	1992	271.3
	EMEP SO_2	1980[a]	49174.0
	EMEP NO_x	1980[s]	20801.6
	EMEP NH_3	1980[s]	8097.8
1990	UK SO_2	1995	3754.0
	UK NO_x	1995	2800.0
	UKNH_3	1996	329.3
	UK HCl	1992	375.0
	EMEP SO_2	1995	37946.3
	EMEP NO_x	1995	22556.4
	EMEP NH_3	1995	7608.4

[a] actual emissions inventory [s] scaled emissions inventory

1955. This scenario uses a 1955 UK SO_2 inventory supplied by Simon Egglesdon (NETCen) and 1960 EMEP area emissions supplied by Mylona (1993). For UK NO_x emissions, the earliest published total is for 1970 (AEAT/RAMP/20090001/R/003 ISSUE-1) and the 1995 distribution has been scaled to match this total. Across the rest of the EMEP area, 1995 NO_x emissions have been scaled to 1980 levels (Berge 1997, EMEP-MSC-W). UK ammonia emissions held at 1998 levels, EMEP area 1995 emissions scaled to 1980 levels (Berge 1997, EMEP MSC-W).

1970. This scenario used a 1970 UK SO_2 inventory digitised from a paper by Smith and Jeffrey (1975). 1970 EMEP area SO_x emissions were supplied by Sophia Mylona. NO_x and NH_3 emissions treated as 1955 scenario.

1983. This scenario uses 1983 SO_2 emissions for the UK for point and area sources supplied by NETCen and 1980 EMEP area emissions supplied by Sophia Mylona. UK 1995 NO_x emissions have been scaled to the 1980 total reported in AEAT/RAMP/20090001/R/003 ISSUE-1. EMEP area 1995 NO_x emissions have been scaled to the 1980 total reported in EMEP MSC-W Report 1/97. Ammonia emissions unchanged.

Table 1.2b. Emissions used in 1990 and forecast scenarios

Scenario	Pollutant	Total in k tonnes
REF	UK SO_2	980.0
	UK NO_x	1186.0
	UK NH_3	297.0
	UK HCl	250.0
	EMEP SO_2	18518.2
	EMEP NO_x	16102.6
	EMEP NH_3	6908.5
WGS31B	UK SO_2	605.8
	UK NO_x	1106
	UK NH_3	290.5
	UK HCl	38.0
	EMEP SO_2	18734.3
	EMEP NO_x	15863.9
	EMEP NH_3	6572.1

[a] actual emissions inventory
[s] scaled emissions inventory

WGS31B

The UK emissions are slightly different from the published totals (625 k tonnes SO2, 1181 k tonnes NOx and 297 k tonnes NH3 respectively) since the published totals include emissions from off-shore oil and gas platforms and military sources whereas the mapped totals incorporated in the model runs do not. The HARM implementation was based on SO_2 and NO_x emissions data supplied by Justin Goodwin (NETCEN) and on figures from the DETR for NH_3. EMEP area emissions are country specific based on published lists.

Table 1.3. Deposition budgets for HARM backcasts expressed in k tonnes/yr

	Wet S	Dry S	Total S	Wet NO_y-N	Dry NO_y-N	Total NO_y-N
1955	257.9	228.0	485.9	U	U	U
1970	334.2	278.4	612.6	114.0	63.5	177.5
1983	262.0	204.7	466.7	115.9	62.9	178.8

Not area weighted
U – unreliable

Figure 2 A critical load isoline in 3-node approximation

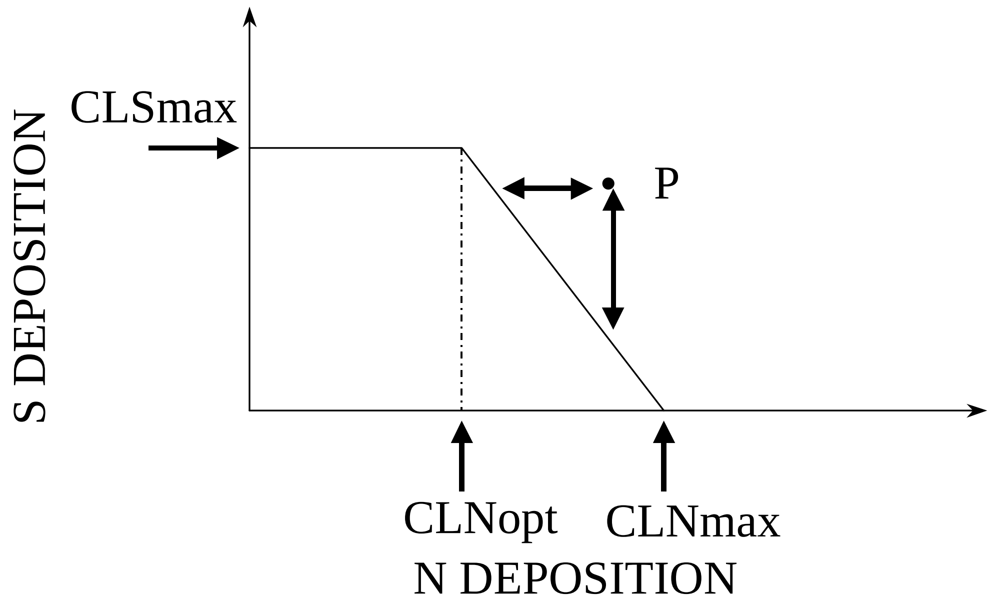

Figure 3

Figure 4 Accumulated exceedance of critical loads in a grid cell

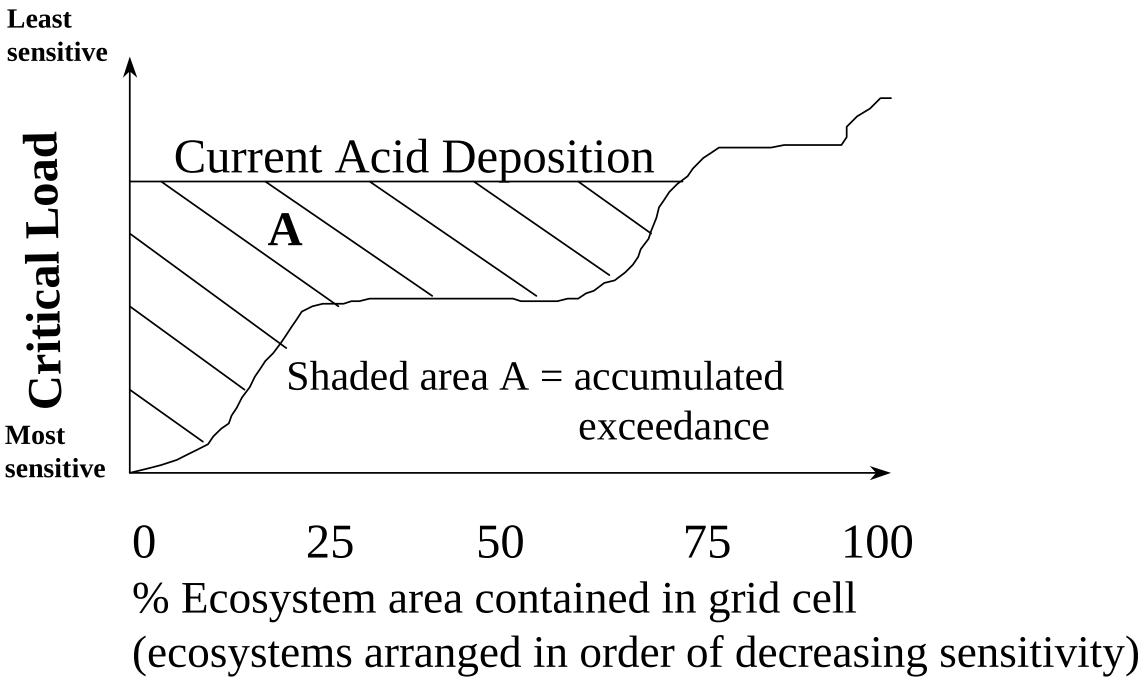

Figure 5a

Figure 5b

Figure 6 a & b

Figure 6 c & d

Figure 6 e & f

Figure 7a

Figure 7b

APPENDIX

A.1 Reporting

Three progress updates were produced as required under the contract and are reproduced below:

A1.1 Progress Update 1 - 27 April 1999

We held a project consortium meeting at Monks Wood on 21 January, chaired by Humphrey Crick and involving Juliet Vickery and Dan Chamberlain from BTO; Rachel Warren from IC; Jane Hall, Dan Morton & Tim Warr from ITE; Sarah Metcalfe from University of Edinburgh; and Steve Ormerod from University of Cardiff. We agreed that it was important to carry out the investigations within a hypothesis testing framework - in particular: do acidification effects account for more of the variance in the bird data than other confounding processes or factors?

At the meeting we discussed the pros and cons of the various data sets that are available and decided which should be used and the spatial scale at which the data will be analysed. Critical loads will be calculated for 6 standard habitats (i.e.: acid and calcareous grassland, heathland, deciduous and coniferous woodland, and freshwater). Exceedance data will include: a) the total area of each ecosystem exceeded; b) the total area of each ecosystem in each 10-km sq; and c) for each ecosystem type, the accumulated exceedance (i.e. Area x Exceedance) integrated over a grid square. Historical data for acid precipitation and exceedances will be calculated for 1955, 1970, 1983 and 1992; 1970 and 1992 being relevant to the bird atlas data sets.

The following species were suggested for the analysis of relative abundance and distributional change data: Ring Ouzel, Treecreeper, Wood Warbler, Dipper, Redshank, and Whinchat. For the analysis of breeding performance, we suggested Song Thrush, Dipper, Great Tit, and Ring Ouzel. Although we have included a number of migrants that might be affected by factors on their wintering grounds, we still consider them to be useful because effects mediated through shortage of calcium will affect them just as much as residents. (Small birds can only store a relatively small quantity of calcium in their body and have to forage for it actively just prior to egg-laying)

Following the meeting, progress has been made with the preparation of the acidification data sets. Duncan Whyatt at the University of Lancaster and Sarah Metcalfe at the University of Edinburgh have prepared backcasts of deposition maps as a 10x10-km resolution showing Sulphur deposition for the years 1955, 1970, and 1983 using the HARM model. The deposition is calculated by combining the contribution from UK sources with that from non-UK sources. For SO2, emissions for the UK taken from emission inventories provided by NETCEN and Smith and Jeffrey (1975). For non-UK sources, historical SO2 emissions were supplied by Sophia Mylona (EMEP).

For oxidised and reduced Nitrogen, deposition calculations for 1955, 1970 and 1983 have also been carried out. In the absence of reliable published emission data for oxidised Nitrogen in 1955, and for reduced Nitrogen in both 1955 and 1970, the earliest available emission data were used, scaling where appropriate by the 1955 distribution. For 1983 some scaling was also necessary. The overall UK deposition budgets for the wet and dry components of the deposition have also been provided.

The maximum of Sulphur deposition occurred in the year 1970, when dry deposition was associated with concentrations of industrial/domestic sources. Wet deposition, which is highest in the uplands of W and N Britain, is relatively and absolutely more important in 1970 than in 1955. In 1983, S deposition had declined, the change being more pronounced in the dry component. Dry deposition in 1983 clusters around major coal fired power stations and the Thames estuary.

Jane Hall and Daniel Morton at ITE Monks Wood have supplied a series of 5-percentile[1] critical load data-sets for the UK at 10x10-km resolution on the national grid. These contain values for ecosystem area in the grid cell, maximum critical load of Sulphur, maximum critical load for Nitrogen, and minimum critical load for Nitrogen. The first data-set refers to the combination of all ecosystems simultaneously, whereas the rest refer to the six standard ecosystems already mentioned.

ITE have also provided the critical load exceedance backcasts for 1955, 1970 and 1983, using the deposition backcasts provided by Sarah Metcalfe and Duncan Whyatt, and the critical loads for all ecosystems combined. These exceedance data have been made available on a 10x10-km resolution. Maps have been produced for each of the three years detailing:

(1) percentage of ecosystem areas where acidity critical loads are exceeded;
(2) area (km^2) of ecosystems for which acidity critical loads are exceeded;
(3) average exceedance ([2]accumulated exceedance/area exceeded) for acidity critical loads.

The complete Ring Ouzel Nest Records data set has been coded and prepared for computerisation, covering some 1,100 records. We have also prepared 500 Great Tit Nest Records to increase sample sizes from upland areas. These are currently with the data processing company and will be computer checked and made ready for analysis using existing programs at BTO HQ. We plan to computerise further upland and other Nest Record Cards for Song Thrush and Great Tit to increase sample sizes required for spatial analysis with acidification data.

Data on relative abundance and distributional change have been extracted and collated into a format ready for analysis. Preliminary analysis of the bird distribution data has been made using multiple regression modelling. In addition to critical load and critical load exceedance (in relation to Sulphur), we have included various landscape variables from ITE Landcover and Land Characteristics databanks and sheep densities from MAFF June Census data. For each species, we have restricted analysis to grid squares which contained the species in either breeding atlas (1970 and 1990) and have further restricted square selection, depending on the species, to those squares that are most appropriate (thus for Wood Warbler and Treecreeper, squares must contain at least 5% deciduous woodland; for Dipper, Whinchat and Ring Ouzel, squares must be upland or marginal upland).

The initial models show that a number of habitat variables enter the models as significant predictors of the bird distributions. We have analysed relative abundance and distributional change with respect to critical loads for all ecosystems combined and found that high critical loads are associated with a low probability of occurrence for Redshank and Treecreeper but a high probability of occurrence for Dipper. (Since the analysis is restricted to upland areas, this result does not mean that in the UK Dippers are found in areas where soils are not sensitive, but means that this is the case *within* the more sensitive upland areas, Dippers being more abundant in the least sensitive of upland areas). The probability of loss from a 10-km square was higher where critical loads were high for Redshank. It is reassuring to see that critical load enters into a number of the models for different species. However, these models need refining because they tend to be statistically over-dispersed and the relationships between independent variables need to be assessed before we can become more confident in them.

One final point, which may be of interest, is that we have had a meeting with Jorn Scharlemann who is a doctoral student that has just started a three-year study of eggshell thinning in relation to acidification, using museum collections. The study as funded by RSPB and the British Museum and could provide valuable complementary historical information that might help in the interpretation of any changes that we find. We have agreed to keep in contact and to try to use similar acidification data sets to ease comparison of our results.

[1] Associated with each 10 * 10-km square on the UK grid are a number of ecosystem records, each comprising 4 fields: area, maximum critical load for Sulphur, maximum critical load for Nitrogen, and minimum critical load for Nitrogen. The first step in determining a 5-percentile critical load involves sorting these records into ascending order on one of the critical load fields. A cumulative area distribution is generated against the sorted records, and the 5-percentile critical load is the critical load at 5% of the cumulative area distribution. If the 5-percentile critical load is not exceeded at least 95% of ecosystem will be protected.

[2] Accumulated exceedance is a cumulative measure of the product of (ecosystem area exceeded * magnitude of exceedance).

A1.2 Progress Update 2 - 2 August 1999

We held a second project consortium meeting at Monks Wood on 20 July, again chaired by me and involving Dan Chamberlain from BTO; Rachel Warren from IC; Jane Hall and Dan Morton from ITE; and Steve Ormerod from University of Cardiff. Sarah Metcalfe kindly sent some comments on the agenda by e-mail. The main aim of the meeting was to discuss various issues surrounding the use of the acidification data sets and to review the modelling approach undertaken by Dan Chamberlain in the analysis of the bird atlas data.

With regard to the acidification data sets, we decided that it would not be advisable to use the 1996 deposition data because of the differences in methodologies used in their calculation compared with the other data sets. The 1992-1994 data set is useful for comparison with the 1988-91 bird atlas data set because it represents the average of three years (thereby eliminating outliers due to unusual conditions in any one year). When analysing temporal changes, we decided that the 1990 data set should be used as the reference data set, especially as it was the basis of the backcasts undertaken using HARM. Jane Hall has undertaken to provide the 1990 deposition data for analysis.

When considering fore- and back-casts using HARM, the question arose about whether we should be using the latest version, introduced since the calculation of the backcasts by Edinburgh/Lancaster. It was decided that we should use the same (older) version of HARM for both the back- and fore-casts because resources limited our ability to re-run the back-casts.

Dan Chamberlain presented example results from the analyses undertaken to date. The analyses used data on bird 'abundance' per 10-km square in 1988-91; changes in distribution between 1968-72 and 1988-91; ITE land cover, ITE landscape type, climatological data, sheep abundances, all as potentially confounding variables; and CLE/CL ratios for 1970 and 1992-94. The methods involved the use of logistic regression, in which we selected the best fitting (uncorrelated) habitat variables before seeing whether CL variables added significantly to the final models for each species. (These analyses will need to be re-run using data for 1990 rather than 1992-94 because of the lack of comparability between 1970 and 1992-94 acidification data sets, but the results provided some valid generalities that are discussed below.)

First, the distribution of a range of species is affected strongly by some of the habitat variables included in the analyses. Second, some species are also significantly affected by acidification data even after the habitat effects are taken into account. The fact that we can detect effects on the loss of distribution of some species suggests that there are some strong effects because large population density declines within squares will be masked so long as a small number of birds remain. Currently we cannot refute the hypothesis that deposition affects bird distribution, but the analysis needs refinement and the use of 1990 data, not 1992-94 data.

Further work that should be undertaken, before moving on to the analysis of breeding performance data, includes:

a) The investigation of deposition *per se*, which might have effects independent of CLs (e.g. perhaps through direct effects on invertebrate food supplies).
b) Statistical interaction terms should be included judiciously within the modelling process.

c) Investigations should be undertaken to compare models that use the single combined CLE against those in which all appropriate single ecosystem CLEs are entered as potential predictors.

d) In addition to analysing species gains and losses, an approach that combines gain/stasis/loss in one analysis should be attempted.

e) An approach based on species richness might provide a better general indicator than approaches based on single species. Species richness could be calculated with reference to groupings based on, for example, habitat preferences (e.g. woodland species), foraging positions (ground vs foliage feeders); body size; migrants vs residents.

Finally we discussed potential forecast scenarios. It was suggested that the Reference Scenario for 2010 and a contrasting scenario (for example MFR) should be used to provide a reasonable range of future conditions.

A1.3 Progress Update 3 – 1 November 1999

We recently held a meeting at Imperial College to discuss the results from further analyses of the bird distributional data and the first results from the analyses of reproductive performance.

It has become clear that the large number of acidification variables we have been using in our modelling confuses the analyses and their interpretation. The majority of the ecosystem-specific exceedances are highly correlated with each other and with "total ecosystem exceedance" (i.e. exceedance for all ecosystems combined). Thus we have decided that future modelling will only use data for "total ecosystem" exceedance and critical loads. This has the advantage that total ecosystem values are available for every 10-km square, unlike ecosystem-specific values, so sample sizes will be maximised. (N.B. The notes below refer to analyses using single ecosystem variables, but these will be re-run using total ecosystem information to produce a final set of results.)

The distributions of 4 upland bird species were strongly correlated with a range of single ecosystem acidification variables. When habitat and climate variables were included, the correlations tended to disappear, but there were significant interaction terms between habitat and acidification variables that need to be explored to fully understand how bird distributions are related to acidification. Stonechat appeared to provide the clearest example, in which there was still a residual effect of exceedance after interaction and habitat terms were taken into account. There were more examples of detrimental effects of acidification among lowland species, which may be because these species may be less adapted to base-poor conditions compared with upland species.

The probability of local extinction between early (1968-72) and late (1988-91) breeding bird atlases in association with increased acidification tended to be confounded by habitat variables, but is unlikely to be detected because acidification has tended to decline over this period. However, colonisation probability does appear to increase with declining acidification among several lowland species (for example Little Ringed Plover, Wood Warbler and Yellow Wagtail).

Analyses of species richness show promise, with species richness of various functional groups (such as insectivores, upland birds etc.) being lower where acidification levels were higher. However, again, these results need refining because of complications due to significant interaction terms with habitat variables.

Preliminary analyses of data on breeding performance were discussed at the meeting in October. The approach is similar to that used in the analysis of bird distributions, but data was considered from a greater span of years, divided into four periods (1953-57, 1968-72, 1981-85 and 1990-94). Initial analyses of the effects of critical load exceedance on reproductive performance in Dipper, Song Thrush and Great Tit found few clear detrimental effects of acidification. There were two exceptions: Song Thrush brood size decreased with increasing exceedance and Great Tit clutch failure rates increased with increasing exceedance. Certain variables showed more complex relationships with acidification, e.g. laying date in both Dipper and Great Tit showed a quadratic relationship with exceedance. A number of other variables had significant effects on reproductive performance including latitude and period. When these were combined with acidification variables, only clutch failure rate in Great Tit showed an effect of exceedance. However, relationships were often complex involving significant interaction terms, thus indicating that the effects of acidification may vary according to period and latitude. These interaction terms will be explored in further analyses, as will the effect of variables describing the nesting habitat.

We will soon be in a position to derive the final models from the distribution and breeding performance data sets. These will be used to predict the consequences of the forecast reduction in acidification. It was decided that we will use the accumulated exceedance forecasts per 10-km square for 2010 using MFR and reference scenarios. In the meantime we will proceed with the preparation of a manuscript on the effects of acidification on bird distributions, which will be sent to you for comment when completed.

(After consultation with DETR, we decided to replace the MFR scenario with the WGS31b scenario, because the latter used more realistic assumptions about likely reductions in Sulphur and Nitrogen emissions).

2.0 SPATIAL ASSOCIATIONS BETWEEN ACIDIFICATION AND SPECIES DISTRIBUTION IN THE UK

Abstract

The hypothesis that anthropogenic acidification has had a detrimental effect on bird species distributions in Britain was tested by analysing three ornithological data sets in relation to Sulphur deposition and a measure of critical load exceedance (exceedance ratio): (a) frequency of species occurrence in 1988-91 (indicator of abundance in 10-km squares) (b) species extinction in 10-km squares between 1968-72 and 1988-91 (change in presence/absence in 10-km squares) and (c) species gain in 10-km squares between 1968-72 and 1988-91. The analyses were based on the known distributions of all breeding bird species in Britain and Ireland which have been measured by two Breeding Bird Atlases in 1968-72 and 1988-91. The main aim was to identify potential bio-monitors of acidification abatement strategies in terrestrial ecosystems. Of nine invertebrate-feeding species selected for analysis, all showed some support for the above hypothesis. For some species, frequency of occurrence in 1988-91 was less likely in 10-km squares with greater Sulphur deposition (Redshank, Dipper) or greater exceedance value (Stonechat, Lesser Whitethroat). For others, species extinction between 1968-72 and 1988-91 was less likely (Lapwing, Redshank, Dipper, Redstart, Ring Ouzel), or species colonisation over the same period was more likely (Little Ringed Plover, Lesser Whitethroat) in 10-km squares showing decreases in Sulphur deposition. These associations were significant even when habitat variables that were also significant predictors of species distributions were included in the models. The number of significant models showing an apparently detrimental effect of Sulphur deposition was 13, compared with 5 apparently beneficial effects and 8 non-significant or inconclusive relationships. The corresponding numbers for exceedance ratio were 4, 9 and 13 suggesting that Sulphur deposition, *per se,* and not exceedance ratio appears to be more consistently detrimental with respect to bird species distribution. There was no evidence that species richness in 1988-91 was lower in acidified areas, but richness of resident insectivorous, migrant insectivorous and resident omnivorous passerines increased significantly in 10-km squares that had experienced the greatest decreases in acidification. Forecast reductions in deposition (the most consistent predictor) over the next decade were used to predict changes in species range by 2010 using the WGS31B scenario. Lapwing, Little Ringed Plover and Lesser Whitethroat showed the greatest predicted changes with deposition, with increases in range of 13%, 13% and 9% respectively compared to 1990. Species richness was predicted to change by only an average of 1 species per 10-km square under the same scenario. Although the REFERENCE scenario, which predicts minimal reductions in acidification based on current reduction plans, produced results that were 20-40% smaller than the WGS31B scenario, the standard deviations were relatively large and absolute sizes of the differences were relatively small. It is suggested that the associations found here are more likely to represent genuine effects of acidification in species whose diet consists of foliage rather than soil invertebrates, thus Lesser Whitethroat is likely to be most sensitive bio-monitor of acidification. However, work at a finer scale of resolution is needed to investigate these associations further.

2.1 INTRODUCTION

The domestic and industrial combustion of fossil fuels, traffic emissions and even intensive animal husbandry all contribute to the rate of soil and water acidification through the formation of sulphate, nitrate and ammonium compounds (Graveland 1998). Soil acidification leads to a decrease in pH, leaching of base cations (especially calcium) from the topsoil and an increase in the concentration of toxic metals such as aluminium. Anthropogenic acidification was first recognised as an environmental problem due to its effects on commercial fish stocks (Likens & Bohrman 1974), but since then potential impacts have been investigated in a wide range of organisms (Alstad *et al*. 1982, Schindler 1988, Ormerod *et al*. 1991, Graveland 1998).

For birds, one of the most serious potential consequences of acidification is the lowered availability of calcium which is needed for eggshell formation and skeletal growth. Graveland *et al.* (1994) investigated the effects of calcium availability on reproductive success of Great Tits from a population that had shown an increase in the rate of eggshell defects. They found that snail shells were the main source of calcium in base-poor soils and that snail abundance declined due to a decrease in calcium caused by acidification. Graveland and Drent (1997) provided evidence that calcium limitation of breeding success is widespread in avian populations from calcium-poor areas.

The effects of acidification on invertebrate food supply has been most thoroughly investigated in aquatic ecosystems. Acidification of surface waters has been shown to affect the abundance of a number of invertebrate species that are important foods of the Dipper *Cinclus cinclus* (Buckton *et al*. in press) and consequently the reproductive success of the Dipper is poorer in acidified streams (Ormerod *et al*. 1991, Vickery 1991). Similar effects have been found for a number of other species e.g. Tree Swallow *Tachycineta bicolor* (Blancher & McNicol 1988), Black Duck *Anas rubripes* (Rattner *et al*. 1988) and Ring-Necked Duck *Aythya collaris* (McAuley & Longcore 1988). However, certain invertebrate groups seem less affected by acidification and consequently no significant effects have been detected in their main predators e.g. Grey Wagtails *Motacilla cinerea* and Diptera (Ormerod & Tyler 1991), Common Sandpipers *Actitis hypoleucos* and earthworms (Vickery 1991). There is less evidence for effects of acidification on invertebrate abundance in forests and it seems that effects on foraging are due to changes in forest structure (e.g. canopy thinning) rather than direct effects on prey abundance (Graveland 1998).

A number of studies have found evidence of an effect of acidification on bird abundance. In some cases, declines in abundance have been linked with a decrease in reproductive success e.g. Dipper (Ormerod, Tyler & Lewis 1985) or recruitment rate e.g. Crested Tit *Parus cristatus* and Coal Tit *P. ater* (Möckel 1992), most probably due to changes in prey availability. Möckel (1992) also found that spruce seed abundance was lower in acidified stands showing that plant as well as animal food availability could be affected by acidification, although Hölzinger & Kroymann (1984) reported an increase in spruce seed production with acidification. Changes in habitat structure may also have important consequences for bird populations. Extreme acidification can cause extensive forest die-back and subsequent shifts in the bird community from forest species to species of open woodland (Stastny & Bejack 1985, Oelke 1989). Other species may have benefited from effects of acidification due to an increase in dead timber and associated invertebrate prey e.g. Three-Toed Woodpecker *Picoides tridactylus* (Hölzinger & Kroymann 1984), White-Headed Nuthatch *Sitta carolinenesis* (DesGranges 1987).

Awareness of the effects of acidification has led to international legislation designed to decrease the rates at which acidifying compounds are released into the atmosphere. As a result, there has been a decrease in acid deposition in Europe and North America in recent years (Stoddard *et al*. 1999). In Great Britain, levels of Sulphur deposition probably peaked in the early 1970s (Chapter 1, Fig 1a-f), although there are still areas subject to high levels of acidification. With the exception of Dipper (Ormerod, Lewis & Tyler 1985, Logie *et al.* 1996), there has been little investigation into possible effects of acidification on the distribution of bird species in Great Britain, but evidence from European and North American studies indicate that a number of species are likely to be vulnerable to acid deposition, particularly in regions of base-poor soil that have little buffering capacity (Graveland 1998). The aim of this study is to determine whether species distribution and the change in distribution over time may have been affected by acidification. The majority of studies carried out on the effects of acidification on bird populations have shown a negative effect, with only a few exceptions showing the opposite trend. In this study, all analyses are constructed around a hypothesis of a detrimental effect of acidification. Positive associations, where they are detected, have not been considered in final predictive models because the aim of the study is to identify those species that are most sensitive to acid deposition and therefore would be the most appropriate to act as indicators for the recovery of ecosystems from acid deposition in terrestrial ecosystems.

2.2 METHODS

2.2.1 Acidification Data

Details of these data are given in Section 1.2. Acidification data, in terms of both Sulphur deposition and exceedance ratio, from 1970 and 1990 were used in the analysis, each of which falls within one of the periods when bird data were collected (see below). Change in acidification between these periods was also considered in certain analyses. A summary of acidification variables used is given in Table 2.1.

Forecast scenarios for 2010 were used to predict future effects of acidification on birds. This used estimates from the WGS31B scenario (the most extreme predicted changes of the models available) and the REFERENCE scenario.

2.2.2 Habitat Data

The majority of habitat data were taken from Institute of Terrestrial Ecology (ITE) data sets. Squares were classified into four broad landscape types (arable, pastoral, marginal upland and upland) at the level of the 10-km square (Bunce *et al*. 1996). These were used to select subsets of squares of the most appropriate landscapes for analyses for a given species. For each 1-km square, the percentage cover of each of 25 land cover types, taken from the ITE remotely sensed land cover map (Fuller & Parsell 1990), was available. These data were combined at the level of the 10-km square. Median altitude and daily average rainfall and temperature over the whole year per 10-km square were taken from the ITE Land Characteristics data base (Ball *et al*. 1983). Sheep numbers per 10-km square were taken from MAFF June census data derived by the Edinburgh University Data Library from parish summaries. A summary of the habitat variables considered is given in Table 2.2. Note that weather data is also included, but for the sake of brevity, all variables in Table 2.2 will subsequently be referred to as habitat variables. All of the ITE data were taken from a single time period (early 1980s in the case of Land Characteristics, late 1980s in the case of Land Cover data). No measure of change in all of these variables in all squares was available.

2.2.3 Bird Data

The distribution of all breeding bird species in Britain and Ireland has been estimated by visiting every 10-km square of the national grid in two Breeding Bird Atlas surveys, firstly between 1968 and 1972 (Sharrock 1976), and secondly between 1988 and 1991 (Gibbons *et al.* 1993). The change in species' geographical range can therefore be determined by considering the number of 10-km squares where a given species was either lost (present in the early survey, absent in the later survey), retained (present in both surveys) or gained (absent in the early survey, present in the later survey). The methods differed slightly between the two surveys. In the early survey, the amount of a 10-km square surveyed and the time spent surveying was more-or-less left to the judgement of survey workers (Sharrock 1976). In the later survey, coverage was standardised by specifying a minimum number of eight tetrads (2H2-km squares) per 10-km square that had to be visited, with a set survey time of 2 hours per tetrad (Gibbons *et al*. 1993). Additionally, supplementary records of birds recorded outside of the set timed counts were available. There were variations in the number of tetrads visited per 10-km square (e.g. in some 10-km squares all tetrads were visited, whilst in others only the minimum number). The tetrad-based survey approach meant that frequency of occurrence (an approximate measure of species abundance) could be indexed per 10-km square for the later Atlas, when previously only presence/absence data were collected. So, for analysis of species change between the two atlas periods, data are expressed as loss or retention of a species at the 10-km square level; for species distribution in the later atlas period, data are expressed as the number of tetrads occupied out of the total number of tetrads visited per 10-km square.

Nine species were selected for analysis. All species were invertebrate feeders that had shown a change in range (either increase or decrease) of at least 10% between periods. Otherwise, they represented species with a broad range of ecological requirements. The species considered were Lapwing *Vanellus vanellus*, Little Ringed Plover *Charadrius dubius*, Redshank *Tringa totanus*, Dipper, Lesser Whitethroat *Sylvia curruca*, Wood Warbler *Phylloscopus sibilatrix*, Redstart *Phoenicurus phoenicurus*, Stonechat *Saxicola torquarta* and Ring Ouzel *Turdus torquatus*. A number of other species may have potentially been affected by acidification, but these were not considered if the change in range was too small (e.g. Blackbird *Turdus merula*, SongThrush *T. philomelos*) or if major habitat changes were deemed more likely to have been responsible for changes in range (e.g. Yellow Wagtail *Motacilla flava*). The selection of 10-km squares was restricted to the main landscape types, upland (including marginal upland) or lowland (arable and pastural landscapes) with which the species were most closely associated. Squares where the species had never been recorded in either atlas survey were omitted. Thus the models described species distributions within a known potential range and did not involve regions that were wholly unsuitable. If these regions had been included, the habitat variables selected in the models were more likely to have been those that dictated these very broad patterns. More detailed and ecologically relevant predictions of bird distributions may then have been obscured.

In addition to modelling change in distribution of individual species, change in species richness in relation to acidification was also considered. This was expressed as the percentage change between periods (number of species in late period - number of species in early period divided by the number in the early period). Four groups of similar species were identified based on migratory status, predominant diet in the breeding season and breeding habitat. The groups were resident invertebrate-feeding passerines, migrant invertebrate-feeding passerines, omnivorous or granivorous passerines and upland birds including non-passerines (Appendix 2.1). Note that the first three groups were mutually exclusive and were considered only for lowland landscapes (preliminary analysis indicated a highly significant difference in species richness between upland and lowland landscapes for these groups). The number of species of each group present per 10-km square was determined for early and late periods.

2.2.4 Statistical Analysis

Three different measures of bird distribution were analysed: frequency of occurrence (1988-91 only); changes in species distribution between 1968-72 and 1988-91; and species richness (both for species richness in 1988-91 and change in species richness between 1968-72 and 1988-91). The same modelling approach was taken for each of these measures, which was to identify separately the single acidification variable and the habitat variables that were most closely associated with bird distribution. A large number of habitat variables were considered in these models (Table 2.2) and many of these were correlated. The presence of highly correlated independent variables in a statistical model is undesirable, so steps were taken initially to select models with a reduced number of variables that showed a minimum degree of collinearity. For each species (or species group), bird distribution was modelled in relation to all habitat variables, with the exception of very uncommon habitats (those that occupied less than 1% of the total area of eligible squares). Stepwise selection procedures were used to identify the habitat variables that explained bird distributions in order of significance. The significant variables selected from this procedure were then put into a correlation matrix in the order in which they were selected, with the variable explaining the greatest amount of deviance in the model appearing first. All variables that were significantly correlated ($P < 0.0017$) with this first variable were omitted from the model. This significance level is the Bonferroni correction including all possible habitat variables (i.e. 0.05 / 30).

Analysis with respect to acidification variables was carried out separately for exceedance ratio and Sulphur deposition. In cases where there was more than one acidification variable (analysis of change in species distributions and change in species richness), each acidification variable was analysed in a univariate model. The variable that was the best predictor of bird distributions was identified from these analyses. The reduced set of significant habitat variables and the single best acidification variable were then combined in a final model in order to see if effects of acidification were still significant when habitat distributions were included. In all models, Type 3 statistics were produced which test the partial significance of model variables.

The probability that a species would be present in a 10-km square in 1988-91 was modelled using frequency of occurrence data in relation to habitat variables and acidification variables with logistic regression. This used an events/trials model syntax where the numerator was the number of tetrads per 10-km square in which a species was present and the denominator was the number of tetrads visited. The frequency of occurrence of each species was analysed in relation to habitat variables with a stepwise selection procedure using the LOGISTIC procedure in SAS (SAS Institute 1996), with a model entry level of $P = 0.0017$. The same logistic regression model was used for univariate analyses of exceedance ratio and Sulphur deposition separately. Exceedance ratio was log-transformed prior to analysis to normalise the data (Sulphur deposition was distributed approximately normally). The next step was to combine the best fitting acidification variable with the reduced set of habitat variables in order to see whether there were effects of acidification in addition to effects of habitat

The analysis of change in species distribution was carried out using a similar variable procedure, using logistic regression with a stepwise selection procedure to identify the significant habitat predictors. Exceedance ratio and Sulphur deposition were described by three acidification variables each. Univariate logistic regression was used to identify the single acidification variable that explained the most deviance. The bird data was expressed as a binomial response (1 = loss/gain, 0 = retained) per 10-km square, losses and gains being modelled separately. The acidification variables for both early and late periods and also the change in exceedance ratio between these periods were added to the reduced habitat variables in the final models.

Species richness in the late period and change in species richness between periods were determined and these values were modelled in relation to habitat and acidification variables using linear regression with the REG procedure in SAS (SAS Institute, 1996), species richness variables being approximately normally distributed. As before, significant habitat variables were identified using a stepwise selection procedure and the best fitting acidification variable was identified with separate univariate regressions (for analysis of change only). These were combined in a final model as described for the analysis of frequency of occurrence (see above).

Finally, model parameter estimates were used to predict effects of future changes in acidification on species distributions by putting forecast deposition and exceedance ratio values for 2010 into the models where significant effects were detected. Change in the predicted probability per 10-km square used in a given could then be determined and geographic patterns of sensitivity to acidification could be examined. For each model only the acidification variable was altered, thus the models assume no change in habitat cover between 1990 and 2010.

2.3 RESULTS

2.3.1 Species Distribution

The effects of exceedance ratio, Sulphur deposition and habitat cover on the probability of occurrence per 10-km square in the late period is shown in Table 2.3. Stonechat showed a significantly higher probability of occurrence in 10-km squares with a lower exceedance ratio in the univariate models and a weaker significant effect when habitat variables were included (Table 2.3a). Dipper and Ring Ouzel showed positive associations between exceedance ratio and probability of occurrence but effects were not significant with the addition of habitat variables for Ring Ouzel. The significance of exceedance ratio increased with addition of habitat variables for Lapwing, but in this species and Dipper there were significant interactions between exceedance ratio and habitat indicating that effects of exceedance may vary according to habitat (see below). Sulphur deposition had a significant negative effect for Dipper and Stonechat i.e. 10-km squares with higher Sulphur deposition have a lower probability of species occurrence. In Dipper, this relationship also held when significant habitat predictors were included in the model. It should be noted that in this species, the effects of exceedance ratio and Sulphur deposition were opposite. This is because 10-km squares with the highest Sulphur deposition also tended to have the highest critical load within this species' distribution.

There were two lowland species that showed a significant negative effect of exceedance ratio in the univariate models, Redshank and Lesser Whitethroat (Table 2.3b). These effects of exceedance ratio were not affected by the addition of significant habitat predictors, although there were significant interactions between habitat variables and exceedance ratio in Redshank, indicating that effects of exceedance ratio may differ at different levels of habitat extent. Two species, Redshank and Redstart, showed a significant negative effect of Sulphur deposition, and this effect was still significant when habitat variables were added to the model.

Models with significant interaction terms were explored further by attempting to reduce the variation in the significant habitat term by dividing the data into two using the mean of the habitat variable and running the same model. For example, for Redshank there was a significant interaction between Sulphur deposition (DEP90) and cover of deciduous woodland (DWOD). The data set was divided into two, taking only values greater than mean DWOD in one data set and only values less than or equal to the mean DWOD in the other. In both models, the interaction term was no longer significant and was dropped. The effects of DEP90 were significant in 10-km squares with lower than average woodland cover, but there was no significant effect in 10-km squares of high woodland cover. Similarly, Lapwing showed a significant negative effect of Sulphur deposition in 10-km squares with high cover of coniferous woodland. In the other cases, interaction terms were still significant, or no significant effect of acidification was detected after the data had been divided.

The effects of acidification on the number of species per 10-km square in the late period, divided into groups of differing ecological requirements, are shown in Table 2.4. Generally, species richness increased with increasing acidification, the exception being upland species where richness decreased with increasing Sulphur deposition. This effect was no longer significant when habitat variables were included. A feature of these models was that high-level interaction terms were usually significant. Given the complex nature of these relationships and the fact that there was little evidence of a detrimental effect of acidification on species diversity, these interactions will not be considered further.

2.3.2 Change in Distribution

The individual effects of six acidification variables on the probability of local extinction for generally declining species is shown in Table 2.5. A striking feature of these results is that very few species show any significant positive relationship between exceedance ratio and probability of loss, apart from Lapwing and Redshank, but all species apart from Wood Warbler show a significant positive relationship with at least one of the three deposition variables. Relationships between the three exceedance ratio variables were in the same direction and tended to be negative i.e. local extinction was more likely in 10-km squares with low exceedance ratio and decrease in exceedance ratio. However, both positive and negative relationships existed between probability of loss and the three deposition variables. Dipper and Ring Ouzel were less likely to have become locally extinct in 10-km squares that had high Sulphur deposition in either period. However, they (and Redstart) were significantly less likely to have become extinct in 10-km squares where Sulphur deposition had decreased between periods. (The apparently contradictory results for change in exceedance ratio for Dipper and Ring Ouzel may be due to the non-linear relationship between Sulphur deposition and exceedance radio and the geographical distribution of changes in Sulphur deposition compared with the underlying critical loads.) Two out of three species were significantly more likely to have colonised 10-km squares that had low Sulphur deposition in both periods, Little Ringed Plover and Lesser Whitethroat (Table 2.6). Also, Lesser Whitethroat was more likely to have colonised 10-km squares that had decreased in exceedance ratio.

The probability of species loss was considered in relation to significant habitat predictors along with the most highly significant exceedance and deposition variables from Tables 2.5 and 2.6. The models describing species loss are shown in Table 2.7. Addition of habitat variables increased slightly the significance of the acidification variables for upland species. Generally, probability of species loss increased with decreasing exceedance ratio (Dipper, Redstart, Ring Ouzel and Wood Warbler). Lapwing extinction increased in 10-km squares with a high 1970 exceedance ratio and with a high Sulphur deposition in the late period and Dipper and Ring Ouzel extinction probability decreased in 10-km squares that had decreased in Sulphur deposition between periods. Redshank and Redstart both showed an increased extinction probability in 10-km squares with higher Sulphur deposition in the later period. The effects of acidification on species colonisation are shown in Table 2.8. In Lesser Whitethroat, the effect of change in exceedance ratio was no longer significant when rainfall was added to the model. For Little Ringed Plover, addition of habitat variables actually increased the significant effect of exceedance ratio. However, the relationship was not straight forward, but contained a significant interaction term indicating that effects of acidification vary at different levels of habitat. The deposition model was more straightforward in this species, local colonisation increasing in 10-km squares with a low early Sulphur deposition.

Interactions were explored in the same way as in the previous analysis of species distribution, by dividing data into two based on the mean of the significant habitat variable in the interaction. There were only three species analysed. Little Ringed Plover showed no significant effect of exceedance ratio after the data had been divided. Redstart showed two significant interaction terms, with deciduous woodland and altitude. There were still significant interaction terms when divided according to deciduous woodland area and also in low altitude 10-km squares. However, at high altitude squares there were no longer significant interaction terms in the model and there was a negative effect of exceedance ratio on the probability of Redstart loss. The probability of local colonisation by Lesser Whitethroat showed a significant negative effect of Sulphur deposition in 10-km squares of high rainfall.

2.3.3 Change in Species Richness

Univariate effects of acidification variables on change in species richness between the 1968-72 and 1988-91 atlases are shown in Table 2.9. Increases in species richness of all but upland species occurred where exceedance ratio had decreased. Low 1990 exceedance ratio was also associated with increases in invertebrate feeders, but low 1970 and 1990 exceedance ratio was associated with decreases in omnivorous species. Species richness of omnivorous species, migrant and resident invertebrate feeders increased in 10-km squares where Sulphur deposition was low in both periods (although migrant invertebrate feeders also showed a significant decrease in 10-km squares that had decreased in exceedance ratio). There were no significant effects of acidification on upland species.

The acidification variable with the most significant effect on change in species richness in univariate models was combined with significant habitat predictors in a single model. Addition of habitat variables reduced the partial significance of exceedance ratio in invertebrate-feeding residents and of both measures of Sulphur deposition in omnivorous species, but increased the significance of Sulphur deposition in invertebrate-feeding residents (Table 2.10). However, the models for all but upland species had significant interaction terms. In common with previous analyses, these interactions were explored further by reducing the variation in the significant habitat variable by dividing the data set at the mean value of the habitat variable. For omnivorous species, there was a positive association between species change and exceedance ratio in 10-km squares of lower than average sheep numbers and a negative association in 10-km squares with lower than average sheep numbers. However, significant interactions between sheep numbers and exceedance ratio persisted in both of these models. For invertebrate feeding residents, there was a significant negative effect of exceedance ratio in both 10-km squares with a lower and higher than average temperature and of Sulphur deposition on change in species richness (i.e. loss in richness associated with high acidification) in 10-km squares with lower than average temperature. Interaction terms were no longer significant in these models. Squares with higher than average temperature showed no significant effect of Sulphur deposition. For invertebrate feeding migrants, there was still a significant interaction term in a model considering only 10-km squares with below average temperature. In 10-km squares with above average temperature, there was no significant interaction term, but the effect of exceedance ratio was positive.

2.3.4 Predicting the Effects of Acidification

Exceedance ratio was a much less consistent predictor of probability of occurrence or of species range change than Sulphur deposition. Stonechat and Lesser Whitethroat (lowlands) had a lower probability of occurrence and Lapwing (uplands) showed an increase in the probability of local extinction in 10-km squares with a high exceedance ratio (Tables 2.3 and 2.7). However the probability of species loss increased with decreasing exceedance ratio in several cases (Dipper, Redstart, Ring Ouzel and Wood Warbler: Table 2.7); and Table 2.3a shows that for Dipper the effects of exceedance ratio and Sulphur deposition were opposite. The grid squares relevant to this species with the highest exceedance ratio were not those with the highest Sulphur deposition since the latter also tended to be the less sensitive areas where critical loads were high in magnitude. Figures 1d and 5b in Chapter 1 show clearly that the areas of upland UK where exceedance ratio is high do not correspond to those where Sulphur deposition is high. For these reasons, exceedance ratio was not considered to be as useful as Sulphur deposition and was not investigated further as a potential predictor of species distribution or species richness.

The future effects of a reduction in acidification between 1990 and 2010 were considered by using the deposition models generated above. The species modelled were those that showed a significant detrimental effect of Sulphur deposition on distribution or range change when considered in conjunction with habitat. The species were Lapwing, Redshank and Dipper (distribution); Lapwing, Redshank, Dipper, Ring Ouzel and Redstart (local extinction); and Little Ringed Plover and Lesser Whitethroat (local expansion). Some of these species only showed significant effects on certain subsets of data as revealed by significant interaction terms in Tables 2.3-2.8. For most species, 1990 values of deposition were replaced by the forecast values for 2010 in the models. However, two species, Dipper and Ring Ouzel, showed that change in deposition between 1970 and 1990 was the best predictor of local extinction, so modelling the effects of future change in acidification used the change between 1990 and the forecast value for 2010 in the model. Local colonisation of Little Ringed Plover and Lesser Whitethroat in 1990 were best predicted by 1970 values of deposition. So, the model for 2010 used the 1990 data to predict distribution in these species (i.e. it was assumed that deposition 20 years previously determined the species' status).

The mean predicted probabilities of occurrence, local extinction and local colonisation of species showing a significant detrimental effect of deposition variables using the predicted WGS31B scenario from 2010 are shown in Table 2.11. Also shown are the corresponding mean probabilities from the 1990 models and the mean change in probability between the 1990 and 2010 models. The species forecast to show the greatest increases in distribution were Lapwing and Little Ringed Plover, both with predicted increase of approximately 13% by 2010. Lesser Whitethroat showed a predicted increase in the probability of local colonisation of 9% by 2010. Other species showed only very small increases in distribution (<3%) and so are unlikely to be particularly affected by decreases in acidification. Change in the probability of local extinction was also not affected greatly by decreases in acidification in these models. Redstart showed a decrease in the probability of local extinction of 12% by 2010, but other species showed less than a 10% decrease in probability.

The predicted change in the probability of presence per 10-km square for the three applicable species in Table 2.11 are shown in Fig. 2.1, where the probabilities have been ranked and placed into five groups of equal sample size. The squares in the highest rank indicate those regions where forecast reductions in deposition are likely to have the greatest effect on bird distributions and therefore those regions where the species is most sensitive to acidification. Predictions were made only for those squares from which the model was derived (as with any regression model, it would be erroneous to extrapolate the model beyond the range of data considered), but in most cases, general geographical regions that are likely to be most sensitive can be identified. In Lapwing, the regions identified as the most sensitive to acidification were in southern Scotland and Wales, although there were rather few squares involved in this analysis due to restrictions on habitat cover, only squares with higher than average coniferous woodland being considered (Table 2.11). Dipper showed three main regions of greatest sensitivity, west Wales, southern Scotland and, most strikingly, the Pennines and Cumbria. Note, however, that the actual magnitude of predicted increases in the probability of occurrence were low, indicating a generally weak effect of acidification. There were no particular regions where Redshank was most sensitive to acidification.

A similar procedure was carried out for changes in predicted probabilities of species colonisation (Fig. 2.2). For Little Ringed Plover, predicted increases in the probability of colonisation were most striking in Greater London and the north Midlands in a region bordering the uplands of the Pennines. The sensitivity of Lesser Whitethroat to deposition was also high in the region surrounding the southern Pennines as well as in an area surrounding the Severn Estuary. Predicted probabilities of species local extinction were considered in a similar way. Change in predicted values were ranked from highest to lowest probability of extinction, so squares where forecast reduction in acidification was likely to have had the most beneficial effect for a given species were identified in a similar way to Figs 2.1 and 2.2. The Lapwing model showed regions of greatest sensitivity to be in west Wales, western Scotland and Cumbria (Fig. 2.3). This region was not identified as being particularly sensitive in the analysis of probability of occurrence, although few of the same squares from this region were used to derived this model (Fig. 2.1). Sensitivity to reduced deposition was predicted to be greatest in the Midlands and central-southern England in Redshank and in the Midlands and east Yorkshire in Redstart. There was less of a regional pattern in Dipper and Ring Ouzel, although there were small pockets of squares particularly sensitive to acidity in south Wales and the North York Moors respectively.

The same modelling procedure was carried out on change in species richness for three groups that showed some evidence of an effect of Sulphur deposition: resident omnivores (all data), resident insectivores and migrant insectivores (both for 1-km squares with below average temperatures). Predicted change in species richness is shown in Table 2.12. Resident species had shown virtually no change in mean species richness between 1970 and 1990. The predicted effects on species richness of decreased deposition were negligible in omnivores, but decreased deposition predicted an average 8% increase in the species richness of resident invertebrate feeders. Mean species richness in 1990 was 11.1∀8.3 species per 10-km square, so this increase would, on average, result in a gain of approximately one species. Migrant passerines had shown an average increase of 7% between 1970 and 1990, and this pattern of increase was predicted to continue. Decreases in acid deposition were predicted to increase species richness by an average of 16% by 2010, which, with a 1990 mean species richness of 8.5∀6.9 per 10-km square, also equates to a gain of approximately one species per 10-km square. Note however, that in this latter species group, change in species richness was best predicted by the conditions in the earlier period from which the change in richness was determined, so these models use data from 1990 rather than forecast deposition variables for 2010. (Model parameter estimates are given in Appendix 2.2).

The percentage change in the number of species predicted under the forecast reductions in acidification for each 10-km square used in each relevant model (Table 2.12) are shown in Fig. 2.4. There was a clear region where the richness of omnivorous species was most likely to be affected by reduction in acidification, covering most of the Midlands and central northern England (note that this model is for lowland squares only), with relatively minor impacts in East Anglia, southern England, Scotland or Wales. The model showed that north-east England, north Wales and the Pennines were likely to be the most sensitive to acidification. Finally, invertebrate feeding migrants (in areas of lower than average temperature) showed very similar predicted changes to those of invertebrate feeding residents, indicating that north-east England and the Pennines were predicted to be particularly sensitive to reductions in acidification.
The above predictions of future acidification levels were derived from the WGS31B scenario which predicts the largest reduction in acidification out of a number of possible scenarios of future acidification. Although substituting the REFERENCE scenario, which predicts minimal reductions in acidification based on current reduction plans, produced results that were 20-40% smaller than the WGS31B scenario, the standard deviations were relatively large and the absolute sizes of the differences in predicted changes in species range or species richness were relatively small (Appendix 2.3).

2.4 DISCUSSION

Several species tested showed a detrimental effect of acidification on either distribution or change in distribution that was significant in addition to the effects of habitat extent. Stonechat and Lesser Whitethroat (lowlands) had a lower probability of occurrence and Lapwing (uplands) showed an increase in the probability of local extinction in 10-km squares with a high exceedance ratio. More species showed significant associations with Sulphur deposition. Dipper (uplands), Redshank and Redstart (lowlands) had a lower probability of occurrence and Lapwing, Dipper, Ring Ouzel (uplands), Redshank and Redstart (lowlands) showed an increase in the probability of local extinction in 10-km squares with a high Sulphur deposition. Also, Lesser Whitethroat and Little Ringed Plover showed increased probability of local expansion in less acidified 10-km squares. Relationships between acidification and species richness in 1988-91 were inconclusive, most models showing significant interaction terms. Decreases between the 1970s and 1990s in species richness of migrant and resident invertebrate feeders and of resident omnivores occurred where either Sulphur deposition or exceedance ratios were high.

There were a number of species whose sensitivity to forecast changes in acidification were associated with particular regions, indicating there were certain regions where impacts of reduced acidification on a given species were likely to be greatest. Particular examples include Redshank in the Midlands, Dipper in the Pennines, Cumbria and west Wales, Stonechat in western Scotland, Redstart in the Midlands and East Yorkshire and omnivorous species in central and northern England. Of the species that showed the greatest sensitivity (and hence greatest predicted overall changes in range), Lapwing increases were largest in southern Scotland and Wales, Little Ringed Plover increases were largest in Greater London and the southern edge of the Pennines and Lesser Whitethroat increases were largest in the same area near the Pennines and an area surrounding the Severn Estuary. However, there were no areas that were consistently the most sensitive across species. Even within species, there were sometimes conflicting results according to the model used (e.g. Lapwing). Given the specific nature of the models for each species or species group and the lack of consistent spatial trends, it is difficult to identify regions where there is high sensitivity to changes in acidification across a range of species. Any consideration of areas particularly sensitive to acidification within a monitoring framework would have to be undertaken on a species-by-species basis.

These results provide evidence that acidification may be having impacts on a wider range of species than has hitherto been suspected. The majority of studies have concentrated on birds associated with wetland habitats, but our study suggests that the detrimental effects found by Graveland and co-workers (Graveland *et al.* 1994) on woodland Paridae might be more widespread among other species associated with terrestrial habitats. The earlier atlas data sets take no account of the relative abundance of a species in each grid square, but just record presence or absence; whilst the later atlas provides only a crude indicator of abundance, which has been termed frequency of occurrence. An environmental factor such as acidification can reduce populations substantially without causing extinction within a square. Thus the detection of relationships between acidification and presence/absence in grid squares suggests that substantial further impacts may be found if data were available on relative abundance. It is likely that data from the BTO/JNCC/RSPB Breeding Birds Survey (BBS), which began in 1994 and covers 2000 1-km squares in the UK, would provide an excellent data set for investigating these relationships further. The Waterways Breeding Birds Survey would also be a useful source of data for examining relationships between acidification and the distribution of riverine bird species at a finer scale of resolution.

What might be the mechanisms by which these terrestrial birds could have been affected by acidification and how likely are they? There are a number of apparently positive relationships between bird distributions and acidification that need to be considered. Some species were more likely to occur where exceedance ratio or Sulphur deposition is higher. This may arise because these species are primarily associated with upland habitats (e.g. Dipper, Ring Ouzel) or geographical areas (Little Ringed Plover) where acidification is naturally higher and the restrictions on landscape types (e.g. selection of upland or lowland squares) were too crude to control adequately for such large scale distributional patterns. High species richness, rather against expectations, was associated with acidification. Again, this may be associated with large scale patterns in species distributions. For example, within lowland landscapes, squares that are on the margin of the uplands (i.e. in the north and west) are more likely to have high acidification, but also may have a high diversity of habitats and hence have a greater range of species. However, it is important to note that species richness has increased between the two atlas periods in areas with lower acidification.
Generally, this paper has concentrated on results that supported the initial hypothesis outlined in the Introduction, that acidification has had a detrimental effect on birds, based on previous work (e.g. Graveland 1988). In order to see how far this was supported across the species analysed, the number of significant results showing detrimental effects on species distribution and the number showing apparently beneficial effects on species distributions, were determined from all analyses involving habitat and acidification variables (Tables 2.3, 2.4, 2.7, 2.8 and 2.10, but also including cases where there was evidence from data sets that had been reduced to deal with significant interaction terms). For exceedance ratio, 4 models showed a detrimental effect, 9 showed a beneficial effect and there was no significant effect, or effects were inconclusive due significant interaction terms in the model, in 13 models. For Sulphur deposition, the respective figures were 13, 5 and 8. Therefore, there is little general evidence that exceedance ratio affects species in the expected direction. Sulphur deposition however, showed consistent detrimental effects on species distributions and was therefore used in predicting likely impacts of future reductions in acidification (see below).

In terms of diet, all individual species considered were invertebrate feeders, so acidification could be detrimental to their food supply, although not all invertebrates are affected by acidification. For example, no effect of stream acidification on abundance of Diptera sampled in the riparian zone has been found (Ormerod & Tyler 1991) and there is circumstantial evidence to suggest that this is the case with other prey items, for example those important to Common Sandpipers such as earthworms (Vickery 1991).

Species that feed mostly on these prey items (Lapwing and Redshank on earthworms) may be expected to be less affected. Dipper is the only species considered where previous evidence of an effect of acidification has been shown (Ormerod *et al.* 1985, 1991). However, this species only showed significant detrimental associations with deposition and there was no significant effect when controlling for the natural acidification in a 10-km square by using the exceedance ratio. Logie *et al.* (1996) did detect effects of critical load exceedance on Dipper density, although the exceedance was expressed in a different way to our exceedance ratio. The exceedance ratio is merely a step in the direction of expressing ecosystem damage in a realistic way. In a complex ecosystem the dose response function may be much more complex and so simple relationships between exceedance and effects will not necessarily be found. More importantly, it is possible that presence or absence in a 10-km square was at too crude a scale to detect many effects.

Species affected by acid deposition may be more likely to be those that feed on terrestrial or canopy invertebrates that could be affected by acid deposition (either through direct mortality or due to canopy thinning) independently of the local buffering capacity (or critical load) of the soil, such as Lesser Whitethroat, Stonechat and Redstart. Lesser Whitethroat has increased since the early atlas, particularly in the north and west of Britain. The reasons for this increase are unclear, but there is no evidence that changes in its wintering grounds are responsible, unlike the closely related Whitethroat *Sylvia communis* (Gibbons *et al*. 1993) Thus colonisation of areas that have decreased in acid deposition between the two periods remains a possible contributory factor. The Stonechat, conversely, has decreased in range but this change in distribution showed no association with deposition. Rather, the distribution in the late atlas was associated with exceedance ratio which could potentially be related to prey abundance or calcium availability. Acidification can cause changes to forest canopy structure and there is evidence that prey abundance may be affected (Hughes *et al*. 1982, Gunnarsson 1988, Heliövaara *et al*. 1989). Redstart was the only woodland species considered that showed some evidence of an effect of acidification which may have been caused by changes in prey abundance. Furthermore, this relationship depended on the type of woodland, the probability of extinction increasing in 10-km squares with low areas of deciduous woodland which is more likely to have a higher critical load than coniferous forests.

Of the species considered, a number are suspected to have been affected by habitat change caused by factors other than acidification. This is particularly true of Little Ringed Plover whose expansion is likely to have been facilitated by man-made habitats such as gravel pits (Gibbons *et al*. 1993). To some extent these effects should have been statistically controlled by the addition of habitat variables. However, most of the variables were measures from a single time period rather than measures of change. For certain variables, there is likely to have been little change over time, but others (particularly those associated with agriculture or commercial forestry) are likely to have changed substantially. It is likely that there is significant correlation between current habitat extent and habitat change, so including habitat variables may still control for some variation caused by habitat change, but correlations may have been stronger if measures of habitat change were available for the majority of data.

The species selected for analysis were all invertebrate feeders and were expected to have been relatively sensitive to acidification. As a control, we also analysed the association between species distribution and acidification in species that are very unlikely to be affected by acidification, at least in terms of diet, as they commonly feed on vertebrates and therefore would have a calcium rich diet. These species were Hen Harrier, Kestrel and Raven. In terms of species distribution, neither Kestrel nor Raven showed evidence of any detrimental effect of acidification. However, Hen Harriers were more likely to be present in upland 10-km squares that had low exceedance ratio and low acid deposition. Change in species distribution showed no association with acidification variables in any species. Hen Harrier distribution is apparently limited by human persecution in the uplands (Etheridge *et al*. 1997) and it is very unlikely that acidification has any affect on the birds' choice of habitat. The relationship between distribution and acidification, even after taking into account habitat variation, shows that caution must be exercised in interpreting associations between acidification and bird species distribution or range change. It may be useful in the future to investigate the mechanisms behind any relationships between bird distribution and acidification by targeted intensive field studies.

2.4.1 Effects of Future Reductions in Acidification

The predicted effects of decreases in acidification on individual species range showed that generally, predicted range changes were small (<10%). The most notable exceptions were Lapwing, Little Ringed Plover and Lesser Whitethroat, whose ranges would increase by 13%, 13% and 9% respectively with the modelled decrease in deposition between 1990 and that predicted in 2010 if the WGS31B scenario is achieved. It should be noted, however, that the predictions for Lapwing apply only to regions containing large coniferous woodland area. Species richness also tended to show small predicted change, only migrant passerines showing a substantial percentage increase of 16%, although as the species pool was small for this group, this represents an average gain of only one species. There were some species that showed relatively large predicted decreases in the probability of local extinction under the WGS31B scenario, notably Redstart (12%) and Redshank (6%). However, interpretation of changes in the probability of local extinction is difficult and it is not possible to relate these estimates to actual changes in range, although these results do indicate that distribution in these species may be sensitive to deposition. Predictions based on the REFERENCE scenario, which predicts a lower reduction in acidification, resulted in smaller predictions of change in species distributions. The largest absolute difference in predicted change was only 5% for Lapwing distribution (compare Table 2.11 and Table A2.3.1) and the majority of others were less than 1%. The standard deviations of the changes were relatively large and the differences would not be statistically significant. Similarly there was very little difference in predicted changes in species richness between the two scenarios.

These models make a number of assumptions. Firstly, they assume that other habitat variables in the models will remain constant. The validity of this assumption is of course unlikely to be true in the majority of variables measured here, including weather variables that are likely to be affected by climatic change in the next few decades. However, these models provide a baseline of the likely effects of changes in acidification and also allow incorporation of predicted habitat change if required (Appendix 2.2). Secondly, the predictions assume a causal effect of acidification on bird distribution and species richness. One of the most highly affected species is Lapwing, for which effects have been demonstrated in afforested upland areas where acidification has been greatest. The presence of coniferous woodland greatly exacerbates the acidification of upland catchments accelerating the leaching of base cations, including Calcium. This effect is unlikely to be reflected in the critical load data for upland areas, since the degree of afforestation and effects of the trees are not taken into account in the calculations However, Lapwing is known to have been affected by a number of land-use changes such as conversion of rough grassland to pasture or silage (Wilson *et al*. in press) and increases in sheep stocking densities (Fuller & Gough 1999). Also the Lapwing’s diet (soil invertebrates) may be more buffered against the effects of acidification than foliage invertebrates. The diet of the Little Ringed Plover (insects and freshwater invertebrates) is perhaps more likely to have been affected by direct acidification, but it is likely that habitat change is a major factor in the expansion of this species (see above). However, the species with the third greatest predicted range expansion, the Lesser Whitethroat, feeds on foliage and aerial insects and so direct effects of deposition may be more likely. Similarly, the species group that showed the greatest predicted change, migrant insectivores, was also the group most likely to be affected by deposition, because species in this group tend to be dependent on flying and foliage dwelling invertebrates, where as resident invertebrate feeders take a wider range of prey.

Where the analysis draws on exceedance data, changes in Nitrogen deposition are taken into account. Although it is not possible to calculate exceedance without doing so, it has to be borne in mind that the HARM-modelled oxidised Nitrogen deposition in 1970 is based on a 1995 spatial distribution of emission sources whilst the deposition of reduced Nitrogen is not considered reliable. In addition, since the commencement of this project the HARM model has been altered to include an improved representation of dry deposition of reduced Nitrogen. Reduced Nitrogen deposition was significantly underestimated using the version of HARM available for use in this study. Due to the uncertainties in Nitrogen deposition, the analysis of acid deposition was based upon Sulphur deposition only. There have also been much greater changes in Sulphur deposition than in Nitrogen deposition over the time in question. However, future studies of changes in acid deposition should be based upon both Sulphur and Nitrogen deposition using the newly available, updated version of HARM. This will be feasible due to the fact that since 1990 Nitrogen emissions and therefore deposition are clearly documented in the UK and also in the rest of Europe. It is therefore possible that some of the changes in accumulated exceedance (and thus exceedance ratio) used in the analysis for this study are subject to significant margins of error owing to the unavoidable lack of historical data for emissions of oxidised and reduced Nitrogen. However, the overall picture is so dominated by changes in Sulphur deposition that general conclusions of this study are unlikely to be affected.

In general, acid deposition has greatly decreased between 1970 and 1990 and it might have been expected that large improvements in ecosystems would already have occurred, leading to matching increases in bird distribution. A number of issues need to be considered. These are: the relevance of the critical load approach to Calcium availability in the soil, and hence to the proposed mechanism of the effects of terrestrial birds; the nature of the dynamic response of ecosystems to acid deposition; and the recently discovered non-linear dependence of acid deposition in the UK upon recent emission reductions. The last two of these factors are likely to introduce a time-lag between deposition and/or exceedance levels and ecosystem recovery. It is interesting that for Lesser Whitethroat, Little Ringed Plover and for species richness of migrant passerines that the model identified the deposition 20 years previously as the predictive variable. The three factors mentioned will now be addressed in more detail.

There arises the whole question as to whether critical load exceedances are really likely to be representative of ecosystem effects, particularly in animals and birds high up in the food chain. Since the proposed mechanism for effects on birds is via decreasing Calcium availability (and possibly Aluminium toxicity) the question arises as to whether critical loads are linearly or otherwise related to Ca:Al ratios in the soil. For the empirical critical loads, which were used for acid grassland, calcareous grassland and heathland, the basis is the mineralogy of the dominant soil type in each 1-km square. However, Ca concentrations are not directly used in this approach, although there is likely to be a very broad relationship between Ca and critical loads. For the simple mass balance acidity critical loads, used for coniferous and deciduous woodland, these *are* based on the Ca:Al ratio in soil solution; although not the concentrations in the solid soil. However, many other factors are involved in determining the critical load, so again there is a broad relationship between the critical loads and the Ca:Al ratio. Other base cations such as Mg and K are also strongly influential in the critical load calculations. A substantial amount of research has been carried out into the relevance of critical loads to Ca:Al ratios in ecosystems. Thus, future work could diversify further to include local or regional scale studies of Ca availability in the soil in relation to the abundance and distribution of birds.

Referring to the specific methodology used in this study, the single ecosystem approach was not used because sample sizes were much reduced compared to the combined measure. Hence, critical loads for all ecosystems combined in a 10-km square have been used, unavoidably taking the study a step further away from addressing the Ca:Al ratio on a bird's territory. Although, the use of the accumulated exceedance approach ensures all ecosystems in a 10-km grid cell where deposition exceeds critical loads are included in the calculations, the use of exceedance ratio again took the study a step further away from the Ca:Al ratios, since the complex nature of the critical load isolines meant that in order to calculate the ratio the 5% CLMAXS value was used for each grid cell, which is not representative of all ecosystems in the grid cell and takes no account of sensitivity to Nitrogen deposition. In the future a more sophisticated 'accumulated ratio' could be devised in collaboration with critical load scientists in order to close the gap between the use of the critical load data and the ecosystem response. It would be advisable to maintain the use of a ratio approach since this does reflect the fact that damage to an ecosystem by a unit of deposition is more likely in a sensitive area than in an insensitive one. This is completely unaccounted for in the critical load approach that assumes that there is a certain amount of acid deposition that ecosystems can sustain without incurring any damage, and that once this level is exceeded damage does occur. This may be an oversimplification and use of dose-response functions might improve the analysis considerably.

Considering now the dynamic nature of ecosystem response to deposition, if we examine the geographical distribution of Sulphur deposition and accumulated exceedance in different years (Figures 1a to d, Figures 5a to d in Chapter 1), it is possible to comment on the length of time for which particular parts of Britain have been exposed to acid deposition in excess of critical loads. However, unavoidably, the modelling approach used in this study only correlates changes in exceedances between 1970 and 1990 with effects on bird populations/distribution, rather than incorporating more detailed temporal aspects. Such dynamic aspects that affect the onset of damage following the first excess deposition at a site and the rate of recovery of various ecosystems on removal of excess deposition, may be important. In order to address these aspects properly detailed dynamic models such as SMART (Simulation Model for Acidification's Regional Trends) (Cosby *et al*. 1985a, b), MAGIC (Modelling Acidified Groundwater in Catchments) (De Vries *et al*. 1989) and SAFE/PROFILE (Jonnsson *et al*. 1993) would be needed. It is entirely possible that, whilst an ecosystem may appear to have recovered in deposition terms, in ecosystem terms recovery has not yet begun. Indeed, it has been shown empirically that there are time lags involved between reductions in acid deposition and reversals in surface water acidification, particularly in Scandinavia where recovery was not seen until 1990's instead of in the 1980's when emission reductions began (Stoddard *et al.* 1999). This time scale of a decade or so is very similar to that identified by some of the predictive models. Clearly areas which have suffered less from acid deposition might be expected to recover first. The strong trends for Lesser Whitethroat, a lowland species, might thus indicate that lowland areas of the UK are already on the road to recovery, whilst upland areas are still 'turning the corner'.

Empirical studies show that in the UK deposition of Sulphur is not responding linearly to the reduction in UK SO_2 emissions (Fowler and Smith in prep.). For example, between 1986 and 1997, UK and non-UK S emissions declined by approximately 55%. Although, as a whole, S deposition declined by 50% during this period, 61% of the decline was in dry deposition and only 42% in wet deposition. However, declines in non-marine sulphate precipitation were only detectable close to major sources, whilst at remote sites the decline was barely detectable. Furthermore, most of the decline in S deposition has occurred at or near the major source regions of the UK, whilst the reductions in S deposition in the high rainfall West coast areas of the UK are much smaller than the reductions in S emissions. This means that the exceedances of critical loads in upland and western Britain are declining much more slowly than predicted. The reasons for this are currently under debate, but may include climate variations, in-cloud oxidation of Sulphur Dioxide on stratus cloud or enhanced long-range transport of Sulphur in the form of ammonium sulphate (Kayin, 1993; ApSimon, Barker and Kayin 1994). The derivation of the acidification data used in this study was based on the HARM model which assumes a linear relationship between emissions and deposition. This non-linearity implies that ecosystem recovery (perhaps in terms of bird distributions) is likely to be delayed further, especially in the upland areas of the UK.

There is also the question of scale. The higher the resolution, the higher the potential to correctly match (in spatial terms) ornithological and acidification data. At high resolution, the effects of local terrain are much more prominent. Deposition can vary by a factor of up to four between the base and summit of individual hills (RGAR 1997). Thus if it was desired to increase the resolution of the model, it would be necessary to include very detailed topography and other local effects in order to avoid large percentage errors in deposition, and to ensure that finer resolution would result in an improvement in the results. Such fine scale spatial variation indicates that the assumption of a uniform deposition across a 10x10-km square is rather crude. If birds are not distributed uniformly across a grid cell, they might be inhabiting areas which are receiving considerably higher (or lower) deposition than the average values produced by the HARM model. It may be much easier to relate critical load exceedances to ecosystem effects when modelling individual catchments rather than using a regional model which may simply be too crude to resolve local detail.

Thus, non-linearities between emissions and deposition, together with the time taken for ecosystems to recover from acid deposition, may imply that it is currently too early to observe substantial recovery of ecosystems in terms of bird populations. Similarly, the onset of ecosystem damage may have occurred a considerable time after the very high acid deposition levels of 1970. Thus, the years between the two atlas periods may be exactly the ones when ecosystem 'bottomed out' in terms of damage due to acid deposition. Recovery may be imminent in the twenty-first century. Since both acid deposition and bird population density can vary on scales much finer than the 10x10-km grid used in the analysis, it is likely that the scale of the calculations was too crude to discern correlations between the two data sets except where very large changes have occurred. Thus, different results might be obtained if acid deposition and exceedances were calculated at finer resolution and if ornithological data could include factors relating to population density rather than presence/absence of breeding birds in a large 10x10-km grid cell. However, the fact that significant relationships between acidification and bird distribution was found for a number of species despite the limitations in the data outlined above, suggests that bird distributions have the potential to be useful bio-indicators of acidification abatement strategies in the near future.

2.4.2 Suggestions for future work

The slow response time of ecosystems to reductions in acid deposition may have delayed recovery due to reductions in acid deposition as a result of emission control protocols. Thus future studies of this type might be expected to show larger trends than the existing study, particularly as deposition in upland areas has not fallen as fast as expected in response to emission reductions. In addition, better data is becoming available on both acid deposition and bird abundance that should improve the power to detect the effects of acidification abatement strategies. Improvements to the methodology could be achieved by the following:

1. Make use of the BBS and Waterways Breeding Bird Survey Data to provide more detailed ornithological information on relative abundance.

2. Use the MAGIC, SAFE (or other appropriate) dynamic model to try to link the dynamic response of soils to reducing acid deposition to effects on terrestrial birds.

3. Use a more sophisticated exceedance ratio approach taking into account critical loads of all ecosystems.

4. Link the work to the close monitoring of how deposition is actually falling in the UK subsequent to emission reductions, instead of relying on model predictions.

Additional studies could be carried out as follows:

1. Attempt to close the gap between Ca availability in the soil and critical loads by carrying out local or regional studies linking Ca availability with bird densities/distributions and continuing studies of eggshell thickness.

2. Study relationships between exceedance and bird densities/distributions on a scale sufficiently small that local spatial differences in deposition, which are important in upland areas, can be taken into account.

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Table 2.1 A summary of acidification variables used in the analysis. Variable codes are used in subsequent tables.

Variable	Code	Definition
Exceedance ratio (late period)	EXR	Critical load exceedance divided by critical load per 10-km square (1990)
Exceedance ratio (early period)	EXE	As above for 1970
Change in exceedance ratio	EXCH	EXR-EXE
Deposition (late period)	DEP90	Sulphur deposition rates per 10-km square (1990)
Deposition (early period)	DEP70	As above for 1970
Change in deposition	DEPCH	DEP90-DEP70

Table 2.2 Habitat data used in the analyses. All data at 10-km square level. Abbreviated codes are used in subsequent Tables.

Variable	Code	Units	Source
Sea, estuary	SEA	km^2	ITE Land Cover Map
Inland waters	LAKE	km^2	ITE Land Cover Map
Beach, flats	COAS	km^2	ITE Land Cover Map
Saltmarsh, seaweed	SALT	km^2	ITE Land Cover Map
Lowland grass heaths	LOWG	km^2	ITE Land Cover Map
Pasture, amenity turf	PAST	km^2	ITE Land Cover Map
Meadows, verges	MEAD	km^2	ITE Land Cover Map
Marsh, rough grassland	MARS	km^2	ITE Land Cover Map
Montane/hill grass	HILL	km^2	ITE Land Cover Map
Mixed heather/grass moorland	MORM	km^2	ITE Land Cover Map
Heather moorland	MORH	km^2	ITE Land Cover Map
Bracken	BRAC	km^2	ITE Land Cover Map
Lowland heather	LOWH	km^2	ITE Land Cover Map
Scrub, orchard	SCRU	km^2	ITE Land Cover Map
Deciduous wood	DWOD	km^2	ITE Land Cover Map
Coniferous wood	CWOD	km^2	ITE Land Cover Map
Upland bog	UBOG	km^2	ITE Land Cover Map
Arable land	ARAB	km^2	ITE Land Cover Map
Ruderal weeds	RUDE	km^2	ITE Land Cover Map
Suburban, farms	SUBU	km^2	ITE Land Cover Map
Urban, industrial	URBA	km^2	ITE Land Cover Map
Bare ground	BARE	km^2	ITE Land Cover Map
Felled forest	FELL	km^2	ITE Land Cover Map
Lowland bog	LBOG	km^2	ITE Land Cover Map
Lowland mixed grass/heather	LOWM	km^2	ITE Land Cover Map
Median altitude	ALT	Meters	ITE Land Characteristics
Mean daily rainfall	RAIN	Mm	ITE Land Characteristics
Mean daily temperature	TEMP	C	ITE Land Characteristics
Sheep density (1988)	SHEEP	sheep/km^2 of grazing land[1]	MAFF June Census
Change in sheep density (1969-1988)	SHDF	sheep/km^2 of grazing land[1]	MAFF June Census

[1]Grazing land comprises LOWG, PAST, MEAD, MARS, HILL, MORM, MORH, LOWH, LOWM.

Table 2.3 The effects of exceedance ratio, Sulphur deposition and habitat (see Tables 2.1 and 2.2) on the probability of species occurrence per 10-km square. The final model is the model and significant interaction terms for the effects of exceedance ratio. Interaction terms were dropped when not significant. Signs indicate the effect on the probability of occurrence determined from logistic regression. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001.

(a) Upland species

Species	Acidification		Habitat variables	Final exceedance ratio model		Final deposition model	
	Exceedance ratio	Deposition		Variables	Dispersion (n)	Variables	Dispersion (n)
Lapwing	ns	ns	RAIN--- BRAC--- CWOD---	EXR++ RAIN ns BRAC--- CWOD ns EXRHRAIN* EXRHCWOD*	3.67 (601)	DEP90 ns RAIN--- BRAC--- CWOD+ DEP90HCWOD***	3.63 (601)
Dipper	+	--	HILL+++ TEMP---	EXR ++ HILL ++ TEMP- EXRHHILLHTEMP*	2.12 (626)	DEP90-- HILL+++ TEMP-	2.12 (626)
Stonechat	---	---	CWOD--- SHEEP---	EXR- SHEEP --- CWOD---	1.48 (356)	DEP90 ns SHEEP--- CWOD---	1.49 (356)
Ring Ouzel	+++	ns	ALT+++ BRAC+++	EXR ns ALT+++ BRAC+++	2.05 (546)	DEP90+++ ALT+++ BRAC+++	2.05 (546)

Table 2.3 cont.

(b) Lowland species

Species	Acidification		Habitat variables	Final exceedance ratio model		Final deposition model	
	Exceedance ratio	Deposition		Variables	Dispersal (n)	Variables	Dispersal (n)
Little Ringed Plover	ns	++	SUBU++ LAKE++	EXR ns SUBU++ LAKE++	1.43 (472)	DEP90+ SUBU++ LAKE+	1.42 (476)
Redshank	---	---	DWOD--- ARAB---	EXR-- DWOD--- ARAB--- EXRHDWOD*** EXRHARAB*** EXRHDWOD HARAB**	2.61 (1462)	DEP90--- DWOD--- ARAB--- DEP90HDWOD***	2.68 (1462)
Lesser Whitethroat	---	ns	RAIN---	EXR--- RAIN---	2.96 (1325)	DEP90+ RAIN ns DEP90HRAIN*	3.00 (1325)
Wood Warbler	+++	ns	RAIN+++ DWOD+++	EXR+++ RAIN+++ DWOD+++	2.36 (508)	DEP90 ns RAIN ns DWOD+++ DEP90HRAIN*** DEP90HDWOD**	2.42 (480)
Redstart	+++	--	RAIN+++ SHDF+++	EXR+++ RAIN+++ SHDF+++	2.27 (1294)	DEP90--- RAIN ns SHDF ns DEP90HRAIN*** DEP90HSHDF*	2.34 (1294)

Table 2.4 The effects of exceedance ratio, Sulphur deposition and habitat (see Tables 2.1 and 2.2) on species richness per 10-km square. The final model is the model and significant interaction terms for the effects of exceedance ratio. Interaction terms were dropped when not significant. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001. Species groups are given in Appendix 2.1. Note that the first three groups are passerines only in lowland landscapes.

Species group	Acidification		Habitat variables	Final exceedance ratio model		Final deposition model	
	Exceedance ratio	Deposition		Variables	Model statistics	Variables	Model statistics
Omnivorous species	+++	+++	MORM--- BRAC+++	EXR+++ MORM--- BRAC+++ EXRHMORM** EXRHBRAC** EXRHMORM HBRAC***	$F_{6,2126}$=202*** r^2=0.36 n=2127	DEP90+++ MORM--- BRAC+++ DEP90HMORM*** DEP90HMORM HBRAC*	$F_{5,2121}$=183*** r^2=0.30 n=2127
Invertebrate feeding migrants	+++	+++	MORM--- BRAC+++	EXR+++ MORM--- BRAC+ EXRHMORM* EXRHBRAC* EXRHMORM HLOWM***	$F_{6,2120}$=147*** r^2=0.29 n=2127	DEP90+++ MORM--- BRAC ns DEP90HMORM*** DEP90HBRAC*	$F_{5,2121}$=127*** r^2=0.23 n=2127
Invertebrate feeding residents	+++	+++	DWOD+++ ARAB+++	EXR+++ DWOD+++ ARAB++ EXRHARAB*** EXRHDWOD** EXRHDWOD HARAB**	$F_{6,2120}$=190*** r^2=0.35 n=2127	DEP90+++ DWOD+++ ARAB+++ DEP90HDWOD*** DEP90HARAB*** DEP90HDWOD HARAB***	$F_{6,2120}$=199*** r^2=0.36 n=2127
Upland species	ns	---	MORM+++	EXR++ HILL++ EXRHMORM**	$F_{3,626}$=58*** r^2=0.22 n=630	DEP90 ns MORM+++	$F_{2,627}$=82*** r^2=0.21 n=642

Table 2.5 Univariate relationships between probability of species loss and acidification variables. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001.

Species	Landscape	Exceedance ratio (late)	Exceedance ratio (early)	Change in exceedance	Deposition (late)	Deposition (early)	Change in deposition
Lapwing	Upland	+	++	ns	++	ns	ns
Dipper		--	ns	---	---	---	+++
Ring Ouzel		---	---	-	--	--	++
Redshank	Lowland	+	ns	ns	+++	+++	ns
Wood Warbler		---	-	---	ns	ns	ns
Redstart		---	---	ns	++	ns	+++

Table 2.6 Univariate relationships between probability of species gain and acidification variables. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001.

Species	Landscape	Exceedance ratio (late)	Exceedance ratio (early)	Change in exceedance	Deposition (late)	Deposition (early)	Change in deposition
Stonechat	Upland	ns	ns	+	ns	ns	ns
Little Ringed Plover	Lowland	ns	ns	ns	---	---	ns
Lesser Whitethroat		ns	+	--	---	---	ns

Table 2.7 Effects of habitat cover, exceedance and Sulphur deposition on the probability of local extinction of selected species from 10-km squares between 1968-72 and 1988-91. Exceedance and Sulphur deposition variables appearing in the final model are those that showed the most significant partial effects. Interaction terms were dropped from the model when not significant. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001. Variable codes are given in Tables 2.1 and 2.2.

Species	Landscape	Habitat variables	Final model for exceedance variables		Final model for deposition variables	
			Variables	Dispersion	Variables	Dispersion
Lapwing	Upland	RAIN+++	EXE++ RAIN+++	0.62 (611)	DEP90+ RAIN+++	0.63 (611)
Dipper		LOWM+++	EXCH--- LOWM+++	0.45 (621)	DEPCH++ LOWM+++	0.45 (621)
Ring Ouzel		ALT---	EXE- ALT---	1.03 (529)	DEPCH+++ ALT---	1.02 (529)
Redshank	Lowland	COAS---	EXE ns COAS---	1.05 (1279)	DEP90+++ COAS---	1.05 (1020)
Wood Warbler		ALT-- MEAD++	EXE--- ALT--- MEAD+	0.89 (442)	DEP70 ns ALT--- MEAD+	0.96 (429)
Redstart		ALT--- DWOD---	EXE--- ALT--- DWOD+ EXEHDWOD* EXEHALT**	1.19 (1133)	DEP90++ ALT--- DWOD---	1.21 (1100)

Table 2.8 Effects of habitat cover, exceedance and Sulphur deposition on the probability of local colonisation of selected species in 10-km squares between 1968-72 and 1988-91. Exceedance and Sulphur deposition variables appearing in the final model are those that showed the most significant partial effects. Interaction terms were dropped from the model when not significant. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001. Variable codes are given in Tables 2.1 and 2.2.

Species	Landscape	Habitat variables	Final model for exceedance variables		Final model for deposition variables	
			Variables	Dispersion	Variables	Dispersion
Stonechat	Upland	RAIN---	EXCH+ RAIN--	1.27 (272)	DEP90 ns RAIN---	1.30 (272)
Little Ringed Plover	Lowland	SUBU---	EXR+ SUBU ns EXRHSUBU**	1.29 (391)	DEP70- SUBU--	1.30 (381)
Lesser Whitethroat		RAIN+++	EXCH ns RAIN+++	0.88 (1235)	DEP70--- RAIN ns DEP70HRAIN *	0.87 (1201)

Table 2.9 Univariate relationships between change in species richness and acidification variables. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001.

Species	Exceedance ratio (late)	Exceedance ratio (early)	Change in exceedance	Deposition (late)	Deposition (early)	Change in deposition
Omnivorous species	+	+++	---	---	-	ns
Invertebrate feeding migrants	---	--	---	---	---	+++
Invertebrate feeding residents	-	ns	---	-	--	ns
Upland species	ns	ns	ns	ns	ns	ns

Table 2.10 The effects of exceedance ratio, Sulphur deposition and habitat (see Tables 2.1 and 2.2) on change in species richness (late-early) per 10-km square. The final model is the model and significant interaction terms for the effects of exceedance ratio. Interaction terms were dropped when not significant. -/+ P<0.05, --/++ P<0.01, ---/+++ P<0.001. Species groups are given in Appendix 2.1. Note that the first three groups are passerines only in lowland landscapes.

Species group	Habitat variables	Final model for exceedance variables		Final model for deposition variables	
		Variables	Model statistics	Variables	Model statistics
Omnivorous species	SHEEP+++	EXE++ SHEEP+++ EXEHSHEE*	$F_{3,2159}$=14.33*** r^2=0.02 n=2163	DEP90-- SHEEP+++	$F_{2,2074}$=21.28*** r^2=0.020 n=2077
Invertebrate feeding migrants	TEMP---	EXR--- TEMP--- EXRHTEMP***	$F_{3,2170}$=32.61*** r^2=0.043 n=2174	DEP70--- TEMP--- DEP70HTEMP***	$F_{3,2084}$=42.04*** r^2=0.057 n=2088
Invertebrate feeding residents	TEMP---	EXCH ns TEMP--- EXCHHTEMP*	$F_{3,2175}$=8.91*** r^2=0.01 n=2179	DEP90--- TEMP--- DEP90HTEMP***	$F_{3,2089}$=16.74*** r^2=0.024 n=2093
Upland species	CWOD---	EXR ns CWOD---	$F_{2,639}$=8.73*** r^2=0.03 n=642	DEP90 ns CWOD---	$F_{2,639}$=8.68*** r^2=0.026 n=642

Table 2.11 Mean predicted percentage change in probability of presence, loss and gain in 10-km squares between 1990 and 2010 under a scenario of predicted reductions in acid Sulphur deposition (WGS31B scenario). 2010 estimates were derived from models only where there was evidence of a significant detrimental effect of Sulphur deposition on species distributions in Tables 2.3, 2.7 and 2.8. Data sets were divided according to habitat type where significant interactions were previously indicated in these tables. Parameter estimates are given in Appendix 2.2.

Species	Data	Acidification variable	Dependent variable	n	2010 estimate	1990 estimate	Mean difference
Lapwing	High CWOD	DEP90	Probability of presence	194	29.88∀10.90	17.11∀9.98	12.77∀4.24
Redshank	Low DWOD	DEP90		982	15.05∀7.08	12.21∀6.83	2.84∀1.25
Dipper	All	DEP90		627	16.12∀2.80	13.20∀2.66	2.93∀1.11
Lapwing	All	DEP90	Probability of loss	611	8.46∀9.64	12.11∀12.30	-3.65∀3.33
Redshank	All	DEP90		1279	17.32∀5.94	23.69∀9.66	-6.37∀4.97
Dipper	All	CHDEP		621	5.84∀4.45	6.44∀5.05	-0.60∀1.38
Ring Ouzel	All	CHDEP		529	25.74∀16.64	27.41∀17.63	-1.66∀4.41
Redstart	All	DEP90		1133	27.52∀13.24	39.10∀16.88	-11.58∀5.66
Little Ringed Plover	All	DEP70	Probability of gain	391	63.02∀14.83	50.13∀15.56	12.89∀7.04
Lesser Whitethroat	High RAIN	DEP70		451	51.00∀15.17	41.91∀15.98	9.09∀3.91

Table 2.12 Mean predicted percentage change in species richness in 10-km squares between 1990 and 2010 under a scenario of predicted reductions in acid deposition (WGS31B scenario). 2010 estimates were derived from models only where there was evidence of a significant detrimental effect of deposition on species richness in Tables 2.4 and 2.10. Data sets were divided according to habitat type where significant interactions were previously indicated in these tables. Parameter estimates are given in Appendix 2.2.

Species	Data	Acidification variable	n	1990-2010 estimate	1970-1990 estimate
Omnivorous passerines	All data	DEP90	2180	1.56∀2.50	-0.98∀2.84
Invertebrate feeding residents	low TEMP	DEP90	899	8.45∀1.88	0.92∀0.42
Invertebrate feeding migrants	low TEMP	DEP70	896	16.08∀6.13	7.25∀9.78

Appendix 2.1 Species groups used in the analysis of species richness.

This is based on predominant adult diet in the breeding season. Very rare species are not included.

Omnivorous passerines	Invertebrate-feeding migrant passerines
Bullfinch *Pyrrhula pyrrhula*	Blackcap *Sylvia atricapilla*
Chaffinch *Fringilla coelebs*	Chiffchaff *Phylloscopus collybita*
Carrion Crow *Corvus corone*	Garden Warbler *Sylvia borin*
Corn Bunting *Miliaria calandra*	Grasshopper Warbler *Locustella naevia*
Crossbill *Loxia curvirostra*	House Martin *Delichon urbica*
Goldfinch *Carduelis carduelis*	Lesser Whitethroat *Sylvia curruca*
Greenfinch *C. chloris*	Nightingale *Luscinia megarhynchos*
Hawfinch *Coccothraustes coccothraustes*	Pied Flycatcher *Ficedula hypoleuca*
House Sparrow *Passer domesticus*	Redstart *Phoenicurus phoenicurus*
Jackdaw *Corvus monedula*	Reed Warbler *Acrocephalus scirpaceus*
Jay *Garrulus glandarius*	Sand Martin *Riparia riparia*
Linnet *Cardulis cannabina*	Sedge Warbler *Acrocephalus schoenobaenus*
Magpie *Pica pica*	Spotted Flycatcher *Muscicapa striata*
Raven *Corvus corax*	Swallow *Hirundo rustica*
Redpoll *Carduelis flammea*	Tree Pipit *Anthus trivialis*
Reed Bunting *Emberiza schoeniclus*	Wheatear *Oenanthe oenanthe*
Rook *Corvus frugilegus*	Whinchat *Saxicola rubetra*
Siskin *Carduelis spinus*	Whitethroat *Sylvia communis*
Skylark *Alauda arvensis*	Willow Warbler *Phylloscopus trochilus*
Tree Sparrow *Passer montanus*	Wood Warbler *P. sibilatrix*
Twite *Carduelis flavirostris*	Yellow Wagtail *Motacilla flava*
Yellowhammer *Emberiza citrinella*	

Invertebrate feeding resident passerines	Upland species
Blackbird *Turdus merula*	Black Grouse *Tetrao tetrix*
Blue Tit *Parus caeruleus*	Black-throated Diver *Gavia artica*
Coal Tit *P. ater*	Buzzard *Buteo buteo*
Dipper *Cinclus cinclus*	Curlew *Numenius arquarta*
Dunnock *Prunella modularis*	Dipper *Cinclus cinclus*
Great Tit *Parus major*	Dotterel *Charadrius morinellus*
Grey Wagtail *Motacilla cinerea*	Golden Eagle *Aquila chrysaetos*
Long-tailed Tit *Aegithalos caudatus*	Golden Plover *Pluvialis apricaria*
Mistle Thrush *Turdus viscivorus*	Goosander *Mergus merganser*
Meadow Pipit *Anthus pratensis*	Hen Harrier *Circus cyaneus*
Marsh Tit *Parus palustris*	Meadow Pipit *Anthus pratensis*
Nuthatch *Sitta europea*	Merlin *Falco columbarius*
Pied Wagtail *Motacilla alba*	Peregrine *F. peregrinus*
Robin *Erithacus rubecula*	Ptarmigan *Lagopus mutus*
Rock Pipit *Anthus spinoletta*	Raven *Corvus corax*
Song Thrush *Turdus philomelos*	Red Grouse *Lagopus lagopus*
Starling *Sturnus vulgaris*	Red-Breasted Merganser *Mergus serrator*
Stonechat *Saxicola torquata*	Red-Throated Diver *Gavia stellata*
Treecreeper *Certhia familiaris*	Ring Ouzel *Turdus torquatus*
Willow Tit *Parus montanus*	Short-Eared Owl *Asio flammeus*
Woodlark *Lullula arborea*	Stonechat *Saxicola torquata*
Wren *Troglodytes troglodytes*	Twite *Carduelis flavirostris*
	Wheatear *Oenanthe oenanthe*

Appendix 2.2 Parameter estimates for predictive models used in Tables 11 and 12.

Table A2.2.1. Model parameter estimates for the effects of acidification and habitat variables on species distribution in 188-91 and change in species distribution between 1968-72 and 1988-91. See Table 2.11 for other details.

Species	Data	Dependent variable	Model
Lapwing	high CWOD	probability of presence	1.321 - 1.438DEP90 - 0.001RAIN - 2.351CWOD
Redshank	low DWOD		-0.990 - 0.531DEP90 - 33.729DWOD - 1.486ARAB
Dipper	All		-1.086-0.379DEP90 + 1.292HILL - 0.098TEMP
Lapwing	All	probability of loss	-5.061 + 0.684DEP90 + 0.002RAIN
Redshank	All		-1.432 + 0.636DEP90 - 42.412COAS
Dipper	All		-2.363 + 1.370CHDEP + 16.418LOWM
Ring Ouzel	All		2.812 + 1.419CHDEP - 0.009ALT
Redstart	All		0.260 + 0.897DEP90 - 0.009ALT – 8.502DWOD
Little Ringed Plover	All	probability of gain	2.306 – 1.011DEP70 – 4.733SUBU
Lesser Whitethroat	high RAIN		-2.358 - 0.798DEP70 + 0.003RAIN

Table A2.2.2 Model parameter estimates for the effects of acidification and habitat variables in change in species richness between 1968-72 and 1988-91. See Table 2.12 for other details.

Species	Data	Model
Omnivorous passerines	All data	0.196 - 0.042DEP90 + 0.015SHEEP
Invertebrate feeding residents	low TEMP	-0.095 - 0.171DEP90 + 0.027TEMP
Invertebrate feeding migrants	low TEMP	-0.090 - 0.239DEP70 + 0.052TEMP

Appendix 2.3 Predicted changes in species distributions and species richness using the REF scenario.

Table A2.3.1 Mean predicted percentage change in probability of presence, loss and gain in 10-km squares between 1990 and 2010 under a scenario of predicted reductions in acid deposition (REFERENCE scenario). Details as Table 2.11.

Species	Data	Acidification variable	Dependent variable	n	2010 estimate	1990 estimate	Mean difference
Lapwing	high CWOD	DEP90	probability of presence	194	24.82∀10.96	17.11∀9.98	7.71∀2.65
Redshank	low DWOD	DEP90		982	14.27∀7.09	12.21∀6.83	2.06∀1.07
Dipper	All	DEP90		627	15.10∀2.79	13.20∀2.66	1.90∀0.67
Lapwing	All	DEP90	Probability of loss	611	9.48∀10.14	12.11∀12.30	-2.63∀2.47
Redshank	All	DEP90		1279	19.02∀6.72	23.69∀9.66	-4.67∀4.50
Dipper	All	CHDEP		621	7.39∀4.88	6.44∀5.05	0.95∀1.67
Ring Ouzel	All	CHDEP		529	31.14∀17.92	27.41∀17.63	3.73∀5.66
Redstart	All	DEP90		1133	31.08∀14.12	39.10∀16.88	-8.02∀4.77
Little Ringed Plover	All	DEP70	Probability of gain	391	63.02∀14.83	50.13∀15.56	12.89∀7.04
Lesser Whitethroat	high RAIN	DEP70		451	50.99∀15.17	41.91∀15.98	9.09∀3.91

Table A2.3.2 Mean predicted percentage change in species richness in 10-km squares between 1990 and 2010 under a scenario of predicted reductions in acid deposition (REFERENCE scenario). Details as Table 2.12.

Species	Data	Acidification variable	n	1990-2010 estimate	1970-1990 estimate
Omnivorous passerines	All data	DEP90	2180	0.68∀0.51	-0.98∀2.84
Invertebrate feeding residents	low TEMP	DEP90	899	6.62∀2.32	0.92∀0.42
Invertebrate feeding migrants	low TEMP	DEP70	896	16.08∀6.13	7.25∀9.78

3.0 THE EFFECTS OF ACIDIFICATION ON REPRODUCTIVE PERFORMANCE IN BIRDS

Abstract

Anthropogenic acidification may affect the reproductive performance of birds primarily by reducing the availability of calcium, an essential nutrient for egg formation and nestling growth. The effects of acidification, as measured by critical load exceedance and acid deposition, were analysed with respect to reproductive performance in four invertebrate-feeding passerines, Dipper *Cinclus cinclus,* Song Thrush *Turdus philomelos*, Ring Ouzel *T. torquartus* and Great Tit *Parus major*. The main aim was to identify potential bio-monitors of acidification abatement strategies in terrestrial ecosystems. Regression models were constructed using acidification variables and other habitat and geographic variables that were significantly associated with measures of reproductive performance. There was a negative quadratic (i.e. troughed) association between Song Thrush clutch survival and exceedance, but brood survival significantly increased with an increase in exceedance. There were no significant effects of exceedance in Dipper and Ring Ouzel. Clutch survival rates of Dipper decreased with increasing Sulphur deposition as did Ring Ouzel brood survival rates, but brood survival rates in Dipper showed a troughed quadratic relationship with Sulphur deposition. Measures of reproductive performance tended to improve with increasing exceedance and Sulphur deposition in Great Tit. Model parameters from all of these models were used to predict effects of reductions in acidification forecast for 2010 under the WGS31B scenario. Predicted decreases in breeding performance with declining deposition or exceedance outnumbered increases in breeding performance by 7 versus 3. Brood survival rates in Dipper and Ring Ouzel were predicted to increase by 23% and 13% respectively and Song Thrush clutch survival was predicted to increase by 7% under a scenario of reduced acid deposition by the end of the decade. These parameters in these species are likely to be the most sensitive to acidification and therefore are likely to be the components of reproductive success that have the greatest potential for use as bio-monitors. However, predicted effects of reductions in deposition for other models, and reductions in exceedance generally, were of low magnitude. Predictions based on the REFERENCE scenario, which predicts minimal reductions in acidification based on current reduction plans, produced estimates of change of lower magnitude than those from the WGS31B scenario, but the standard deviation of the differences between the scenarios were relatively large.

3.1 INTRODUCTION

Reproduction in a number of bird species is limited by calcium availability, particularly in base-poor environments (Graveland & Drent 1997). Anthropogenic acidification can further reduce the availability of calcium and can cause effects on reproductive performance in areas where the soil is already relatively acidic. For example, Graveland *et al.* (1994) found that the proportion of Great Tit *Parus major* nests showing signs of calcium stress, characterised by thin-shelled eggs that were less likely to hatch, had increased over the course of a decade in an area subject to high acid deposition. Clutch desertion rates had also increased. Snail shells had been the main source of dietary calcium for nesting females, but increasing acidification had reduced the abundance of snails. Acidification also affects other calcium-rich invertebrates such as millipedes and crustaceans as well as the calcium content of plant material (Graveland 1998). Similar effects of acidification have been found on eggshell thickness in Eastern Kingbirds *Tyrannus tyrannus* (Glooshenko *et al.* 1986), hatching success in Tree Swallows *Tachycineta bicolor* (St. Louis & Barlow 1993) and eggshell thickness, hatching success and lay date in Dippers *Cinclus cinclus*, the latter factor resulting in reduced clutch size (Ormerod *et al.* 1988, 1991). There is also some evidence that the incidence of females building nests but then failing to produce a clutch is associated with eggshell defects (Graveland & Drent 1997) and acidification (Carlsson *et al.* 1991, Graveland 1998). However, at least one study found no evidence that calcium availability constrained the ability of Blue Tits *Parus caeruleus* to form eggs in a highly acidified area (Ramsay & Houston 1999). A further consequence of a reduction in calcium availability is impaired skeletal growth of nestlings. Bone malformations have been observed in a number of passerine species from calcium-poor areas, particularly Paridae, but also Meadow Pipits *Anthus pratensis* and Chiffchaffs *Phylloscopus collybita*, but there is no evidence in these species that these malformations have increased over time or are the result of anthropogenic acidification (Graveland 1998). The only reasonable evidence that such effects may have been caused by acidification come from a relatively small-scale study of Black Tern *Chlidonias niger* in The Netherlands, where the small population of 10 pairs failed to raise any chicks, all due to bone malformations (Beintema *et al.* 1997). Calcium deficiency was shown to be the cause, as a supplementary feeding experiment resulted in normal development of nestlings. The results of this study also provide compelling circumstantial evidence that acidification has been a major factor in the decline of this species in The Netherlands as calcium-rich food sources, particularly small fish, have declined in abundance in the tern's preferred breeding habitat (Leuven & Oyen 1987).

In addition to prey quality, the actual abundance of prey may be adversely affected. For example, the abundance of a number of stream-dwelling invertebrate groups is lower on acidified streams which may have affected reproductive performance in Dipper, although it is difficult to separate the effects of decreases in prey abundance and decreases in high quality calcium-rich prey (Ormerod *et al*. 1991). The abundance of certain invertebrate groups has also been found to be lower in acidified forests (DesGranges *et al*. 1987, Gunnarsson 1988), although acidification can actually increase the abundance of phytophagous and xylophagous insects (Graveland 1998). Changes to the structure of forest canopy may also affect the foraging and brooding behaviour of adults, although there is little evidence for any associated effect on reproductive success in forest species (Darveau *et al*. 1993, Mahony *et al*. 1997).

The aims of this study are to determine whether measures of reproductive performance of individual nesting attempts are associated with acidification and whether trends in reproductive performance over time may be explained by acidification. We focus on four invertebrate-feeding species that are likely to have been affected by acidification according to previous work, Dipper, Song Thrush, Ring Ouzel and Great Tit. There is convincing evidence that reproductive success in the Dipper is affected by acidification and that this has had a detrimental effect in some parts of this species' range that are subject to high levels of acid deposition (Ormerod *et al*. 1991). Studies of Song Thrush eggshells have shown that they have become increasingly thinner over the past century and acidification is a possible cause (Green 1998). Such an effect would be expected to be accompanied by lower clutch sizes and lower hatching success, as observed in a number of other species subject to calcium stress (Graveland 1998). The Ring Ouzel is closely related to the Song Thrush and it occupies upland habitat that is typically subject to the highest rates of acidification in the UK, and so may also be affected. Finally, there have been a number of studies on the Great Tit showing the effects of calcium stress caused by acidification, as outlined above. In this paper we test the hypothesis that acidification has had a significant effect on reproductive performance per individual nesting attempt, the ultimate goal being to identify species that may be used as indicators for the effects of acidification on avian reproductive performance in terrestrial ecosystems.

3.2 DATA SOURCES

Two measures of acidification were used, the exceedance ratio (critical load exceedance divided by the critical load) and Sulphur deposition. The definition of these variables is given in detail in Section 1.2. An estimate of the exceedance ratio per 10-km square in Great Britain (England, Wales and Scotland) was available for four years, 1955, 1970, 1983 and 1990. An estimate of Sulphur deposition rates per 10-km square was available for only two years, 1970 and 1990. Both measures of acidification peaked in 1970 (Fig. 3.1).

The Nest Record Scheme (NRS) was set up in 1939 and now monitors the annual breeding performance of a wide range of species. (For a complete review of the NRS, see Crick & Baillie, 1996). Data collection is carried out by volunteer ornithologists who complete Nest Record Cards (NRCs) for each nest found. Information recorded on the NRC includes details of nest site, habitat, the contents of the nest at each visit, and evidence of success or failure. The number of breeding attempts per pair per season cannot be estimated from NRS data.

The effects of acidification on six different measures of breeding performance for Dipper, Song Thrush, Ring Ouzel and Great Tit were considered: date of the first egg laid in a clutch (referred to as lay date), clutch size, brood size, partial brood survival (ratio of maximum brood size to clutch size and so measures losses both due to hatching failure and brood reduction), clutch and brood failure rates. For the analysis, NRCs were selected from four five-year periods: 1953-57, 1968-72, 1981-85 and 1988-92. These were selected to coincide with the years having estimated exceedance data (including two years either side). Calculations of average lay date only included cases where estimation by back-calculation was within ∀5 days. Clutch sizes were not accepted if egg laying could have continued after the last visit during the egg stage. Brood size was taken as the maximum recorded. As partial brood survival is likely to be affected by clutch size (larger initial broods more likely to experience lower hatching rate and brood reduction), analysis involving this variable was restricted to the commonest clutch sizes. These were clutches of 4 and 5 for Dipper (constituting 88% of the whole sample), clutches of 3 and 4 for Song Thrush (75%), clutches of 4 for Ring Ouzel (81%) and clutches of between 7 and 9 for Great Tit (60%). A minimum of two nest visits was required to calculate each variable, apart from brood size. As these criteria were different for different variables, sample sizes differ. The six different measures are referred to collectively as reproductive performance throughout this paper.

The merging of acidification and NRS data was done by 10-km grid reference. Systematic recording of grid references has been carried out on the majority of cards since the 1980s, but before then, this was left up to the observer and so sample sizes are sometimes small for earlier periods.

3.3 METHODS

For each NRC variable, simple univariate analyses were carried out to identify linear and quadratic trends. The independent variables in these analyses were exceedance ratio or Sulphur deposition, latitude, longitude, altitude, lay date (many species show seasonal trends in reproductive performance) and period as a class variable. Exceedance ratio was log-transformed prior to analysis. Habitat is recorded on NRCs, but this practice has not been routine or consistent over much of the period in question. Inclusion of NRCs with adequate habitat data would result in small samples and would not enable analysis of trends over time as very little habitat data was collected in the earlier periods in question. However, latitude, longitude and altitude are included in the models. Whilst these variables are at a relatively course scale, it is likely that they will be correlated with a large number of habitat variables and so can describe general habitat gradients.

Lay date, clutch size and brood size were analysed with a general linear model approach using PROC GLM in SAS (SAS Institute 1998). These variables were distributed approximately normally. Probability of partial brood survival was modelled with logistic regression using an events/trials model syntax, taking clutch size as the denominator and brood size as the numerator. Failure rate was analysed using binomial regression, modelling the probability that a nest would fail using an events/trials modelling approach. Each nest was either successful (0) or failed (1), but the period that a nest was monitored varied between individual NRCs. This was taken into account by taking the denominator as the number of days that the nest was known to have survived for nests which were still active at the last visit (or where fledging date was known). For nests where a failure had occurred some time between the last two visits, the denominator was taken as the number of days between first and penultimate visits plus the mid-point between penultimate and last visits. The effects of acidification on trends in reproductive performance over time were considered by analysing interactions between period and acidification.

For any variable where there was evidence of significant ($P<0.05$) univariate effects, NRC variables were analysed with multivariate models, including interaction terms. High order interactions are difficult to interpret and, where class variables are involved, sometimes result in poor model fits or failure of the model to converge (for logistic regression) due non-orthogonality. For this reason, these models were initially run without interaction terms. Interaction terms involving acidification variables were only added for those variables that showed evidence of a significant effect and were retained only if significant. All non-significant variables were omitted from final models. Significant interaction terms were investigated further by reducing the variation in the significant non-acidification variable involved in the interaction term. For significant interaction with period, this simply entailed re-running the models separately by each period. For continuous variables, the models were re-run on data where extreme values had been omitted by only including values within ∀1 SD.

The final models derived from the above procedure were used to predict the effects of future reductions in acidification on reproductive performance where there were significant effects of either exceedance ratio or Sulphur deposition. This used forecast values for exceedance and deposition for 2010 derived from the WGS31B scenario and the less stringent REFERENCE scenario matching current reduction plans (both scenarios are described in detail in a companion paper) in conjunction with parameter estimates derived from the above multivariate models. Other variables in these models were assumed to remain constant. For these predicted changes, daily survival rates were converted to survival rates over the whole nesting period by raising the survival rate (1-failure rate) to the power of N, where N = the average number of days for a given clutch or brood period (from Cramp 1988).

3.4 RESULTS

The effects of exceedance ratio on the six measures of reproductive performance are shown in Table 3.1. There was a significant increase in lay date with exceedance ratio in Dipper, but there was no significant effect in any other measure of reproductive performance in this species. There was a significant negative quadratic (i.e. troughed) relationship with exceedance ratio and lay date, a significant decrease in the probability of brood failure with an increase in exceedance ratio and significant positive quadratic (i.e. peaked) relationships between clutch failure and exceedance ratio in Song Thrush. For Ring Ouzel, only clutch failure rate showed a significant univartiate relationship, decreasing with increasing exceedance ratio. In the Great Tit, clutch size and partial brood survival decreased and brood size and clutch failure rates increased with increasing exceedance ratio. Lay date showed a negative quadratic relationship and brood failure a positive quadratic relationship with exceedance ratio (Table 3.1).

This analysis was repeated for Sulphur deposition (Table 3.2). Dipper lay date increased and clutch size decreased with increases in Sulphur deposition. Clutch and brood failure rates showed positive quadratic associations with Sulphur deposition. Song Thrush brood size decreased with increasing Sulphur deposition. Ring Ouzel clutch size and clutch failure rate increased with increasing Sulphur deposition and brood failure rates showed a peaked relationship with Sulphur deposition. Great Tit clutch and brood size increased with increasing Sulphur deposition, but brood failure rate showed a negative quadratic association. A summary of the significance of exceedance ratio and the continuous variables lay date, latitude, longitude and altitude on reproductive performance derived from univariate models is shown in Table 3.3. There were a large number of significant effects, showing that several factors can affect reproductive performance and that these variables will need to be controlled before analysing the effects of acidification.

The effects of exceedance ratio, period and the interaction between the two were analysed with respect to reproductive performance (Table 3.4). Quadratic terms were also included if significant in Table 3.1. In most cases, effects detected in univariate models (Table 3.1) were still significant along with period. Exceptions were lay date and clutch failure in Song Thrush and partial brood survival and clutch size in Great Tit. The effects of these variables may therefore have been confounded by general temporal trends. This was evident for a number of variables that showed significant interactions between exceedance ratio and period: clutch size in Dipper, lay date in Song Thrush, clutch size in Ring Ouzel and clutch failure rate in Great Tit. Several measures of reproductive performance had changed significantly over the four time periods. There were few cases where the period of the worst average reproductive performance coincided with the period of greatest acidification, 1968-1972 (Fig. 3.1). The exceptions to this were partial brood survival and clutch failure in Dipper, partial brood survival in Song Thrush and clutch failure rates in Great Tit.

Table 3.5 shows the same analysis for Sulphur deposition data. Again there were relatively few effects of acidification. Effects of Sulphur deposition were broadly similar to those detected in univariate models. The exceptions to this were lay date in Dipper, lay date, clutch size and brood size in Great Tit, all of which showed significant interactions with period. Furthermore, there was a significant decrease in lay date (i.e. laying became earlier) with increasing acidification in Ring Ouzel and increase in clutch failure rate for Song Thrush, results not previously apparent (Table 3.5).

Significant interactions between period and acidification variables detected in Tables 3.4 and 3.5 were explored further by analysing the relationship between reproductive performance and acidification within each period. A summary of results is shown in Table 3.6. There was a negative effect of exceedance ratio on Dipper clutch size in 1953-57, an increase in Song Thrush lay date with increasing exceedance ratio in 1981-85, and an increase in Great Tit clutch size (1988-92) and a decrease in lay date (1968-72) with increasing Sulphur deposition. Also, opposite significant effects were detected in different periods for the effects of exceedance ratio on Great Tit clutch failure and Sulphur deposition on Great Tit brood size. There was no tendency for significant effects to be detected in any particular time period.

Multivariate models (Table 3.7) were constructed for those variables where there was evidence of an effect of exceedance ratio for a given species in Tables 3.1 and 3.4. Exceedance ratio was entered into the models along with any other variable that had a significant effect in Tables 3.3 and 3.4 and non-significant variables were deleted. For Dipper and Ring Ouzel, there was no significant effect of exceedance ratio on reproductive performance when including other significant variables, so effects of acidification variables on reproductive performance had weaker effects than other predictors. Song Thrush clutch failure rates showed a significant positive quadratic relationship with exceedance ratio (failure rates also tended to decrease with an increase in latitude and showed lower rates in the middle of the breeding season). Brood failure rates showed a significant decrease with increasing exceedance ratio and also declined with increasing lay date. Great Tit clutch and brood size increased significantly (but weakly for the latter) with exceedance ratio. Brood failure rate showed a significant quadratic relationship with exceedance ratio, failure rate peaking at intermediate exceedance levels, but clutch failure rates decreased. There was no significant effect of period in any of these models once other significant predictors had been added.

Multivariate models were also constructed for those variables where there was evidence of an effect of Sulphur deposition for a given species in Tables 3.2 and 3.5 (Table 3.8). Brood failure in Dipper, Ring Ouzel and Great Tit all showed non-linear associations. Clutch failure of Dipper and clutch size of Great Tit increased with increasing Sulphur deposition. The model describing lay date in Dipper was the same as found in Table 3.5, for which the analysis of separate periods had shown no significant effect of Sulphur deposition (Table 3.6). There was no significant effect of Sulphur deposition on Song Thrush reproductive performance in these multivariate models.

The effects of a reduction in acidification on reproductive performance were considered in the above models where there was a significant effect of exceedance ratio or Sulphur deposition detected. Forecast changes in reproductive performance are presented in Table 3.9. In cases where period was significant in the model, data only from the most recent period were used and effects of period between 1988-92 which could not be accounted for in changes in acidification, were assumed to be negligible. However, this altered the effect of the acidification in one model, that for clutch failure in Dipper, where there was a significant positive effect of Sulphur deposition when including period (Table 3.7), but a non-significant effect when using only the 1988-92 data. This model was therefore not considered in Table 3.9. The largest predicted changes were for brood survival in Dipper and Ring Ouzel, an average increase of 23% and 13% being predicted respectively (Table 3.9). Average increases of around 7% in clutch survival were predicted for Song Thrush. All other predictions were for decreases in reproductive performance with decreases in acidification, although these were of relatively low magnitude. These models used predicted acidification values from the scenario with the most extreme forecast reductions, WGS31B. An alternative scenario (the REFERENCE scenario - see companion paper) resulted in estimates of change of generally lower magnitude, but these were not substantially different to those presented in Table 3.9 (Appendix 3), especially when considered relative to the size of the associated standard deviations.

3.5 DISCUSSION

There were a number of cases where there were significant associations between exceedance ratio and measures of reproductive performance. In the univariate analyses, Dipper lay date increased, Great Tit clutch size and partial brood survival decreased and Great Tit brood failure showed a peaked relationship with exceedance ratio. However, relationships were often non-linear (nest failure rates peaked for Great Tit and Song Thrush and lay dates were earliest for Great Tits at intermediate exceedance ratio) or indicated improving reproductive performance with increases in acidification (brood size increased in Great Tit, brood failure rate decreased in Song Thrush and clutch failure decreased in Ring Ouzel). Addition of other significant predictors of reproductive performance did not provide any more evidence of a detrimental effect of exceedance ratio. Indeed, the effects of acidification on lay date in Dipper, and clutch size, partial brood survival and brood failure rates in Great Tit were no longer apparent or even reversed, indicating that these results probably arose due to confounding effects of other variables (Table 3.3). Similarly, there was little evidence of general detrimental effects of Sulphur deposition on reproductive performance. Dipper (clutch failure rate) showed a linear relationship with Sulphur deposition which indicated a detrimental effect of acidification, but this effect was only significant when period was also included in the model. Quadratic associations were evident in Dipper and Ring Ouzel (brood failure rate for both species).

In those models where acidification variables were significant in addition to other predictors, the effects were generally weak as shown by the predicted effects on reproductive performance using forecast acidification for 2010 under the WGS31B scenario. There were few cases where decreases in acidification had detrimental effects on reproductive performance (i.e. decreases in predicted survival or clutch size). Predicted increases in performance were less common than decreases (3 versus 7 in Table 3.9). However, predicted increases tended to be of greater magnitude, notably effects of a reduction in deposition on brood survival rates in Dipper and Ring Ouzel which were predicted to increase by over 23% and 13% respectively by 2010. While the absolute levels of predicted brood survival may be unrealistically high for these species (99%), the predicted increase can be considered a reasonable estimate that reductions in acidification will be beneficial.

The majority of significant effects were on variables describing survival rates of broods or clutches (7 out of 10 models in Table 3.9). Generally, about 50% of these measures are likely to describe predation rates rather than failure due to abandonment or starvation (Crick *et al*. 1994). They do not measure brood reduction, only failure of whole broods, although partial brood survival combines a measure of brood reduction and hatching failure. Most published examples of effects of acidification on reproductive performance in birds involve effects on clutch size, hatching rate and brood reduction due to calcium limitation. There are few examples of effects on failure rates of whole clutches or broods. However, Graveland *et al*. (1994) found that Great Tits were more likely to abandon clutches when calcium availability was low. Effects of acidification on prey abundance have been detected (e.g. Ormerod 1991), but the only example of this resulting in the starvation of whole broods comes from a non-passerine, the Black Tern (Beintema *et al.* 1997). However, it is possible that broods that are fed less or fed lower quality (i.e. calcium-poor) prey may beg more loudly and so be more apparent to predators.

We were surprised not to detect more evidence of effects of acidification on reproductive performance in terms of variables likely to be directly affected by calcium limitation (clutch and brood size and partial brood survival) in these species, particularly as they were chosen as likely indicators of acidification based on previous work (e.g. Dipper, Ormerod *et al.* 1991; Song Thrush, Green 1998; Great Tit, Graveland *et al.* 1994). Dipper in particular has shown a lot of evidence for effects of stream acidity on reproductive performance, yet there was only evidence for an effect of deposition on clutch and brood survival in this species. There are a number of reasons why we may not have found greater evidence of significant effects. Firstly, this may be to do with the scale of the study. Previous evidence for effects of acidification on reproductive success, with the exception of Green (1998), has been from intensive small-scale studies that are able to measure acidification and other habitat variables at a much finer scale than possible in this study. Indeed, streams in relatively close proximity (e.g. within a 10-km square) can have quite differing acidification levels (Logie *et al.* 1996) and therefore show different effects on Dipper reproductive performance. Estimating acidification levels at a 10-km square level may therefore be too crude to detect any effects relevant to the nests recorded in that square. Secondly, we were only able to control for broad-scale landscape variables so effects could be confounded by other habitat variables that we were unable to measure, particularly when such variables are highly correlated with exceedance. There are localised studies that show no significant effect of acidification or reduced calcium availability on reproductive performance (Ramsey & Houston 1999), contradicting other studies on similar species from different areas (Graveland *et al*. 1994). In these cases, site-specific differences in habitat may be responsible. Thirdly, we were only able to measure reproductive performance per individual nesting attempt. It is conceivable that calcium stress caused by acidification may affect the number of nesting attempts in a breeding season, rather than the size of an individual clutch (although this wouldn't affect the Great Tit which is single brooded in the UK). Also, there may be affects on adult or juvenile survival, the former possibly because adults may have to work harder to raise an under-nourished brood and the latter because fledglings may be in poorer condition when they become independent and so have lower survival prospects. Such factors would affect the lifetime reproductive success of individual birds but would be impossible to detect without intensive studies of identifiable individual breeders.

Calcium availability is affected not just by deposition but also by the chemistry of the soil and the exceedance ratio variable has been derived to take this latter factor into account. There were similar numbers of significant effects of deposition rates and exceedance ratios in the final analysis (5 each in Table 3.9), but deposition tended to have effects of greater magnitude (i.e. predicted changes were larger for this variable). It could be argued that for species feeding on terrestrial or aquatic invertebrates, deposition is unlikely to have a direct effect on reproductive success as these species will be buffered against acidification in a region of high critical load. However, species that feed most on foliage-dwelling invertebrates are more likely to be affected by direct deposition. If we accept this premise (a highly conservative definition), then the result most likely to reveal a genuine biological effect is that of Song Thrush clutch Survival and therefore this would be the best candidate for a bio-monitor of the effects of acidification on birds' reproductive performance. However, given that the low magnitude of predicted change in this species and the large number of predicted improvements in reproductive performance in other models (Table 9), it is doubtful whether any species would be a good bio-monitor at this scale. More research is needed into the effects of direct deposition on a range of invertebrate prey species before firmer conclusions can be drawn.

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Table 3.1 Regression analysis of the effects of exceedance ratio on reproductive performance in four species. Lay date, clutch size and brood size were analysed with normal regression; failure probabilities were analysed with binomial logistic regression. Data from four periods (1953-57, 1968-72, 1981-83 and 1988-92) were pooled. Signs indicate direction of effect, n = significant quadratic effect (peaked relationship), u = significant quadratic effect (troughed relationship), NS = not significant. Numbers of symbols (+, -, n, u) indicate significance as follows: * P<0.05, **P<0.01, ***P<0.001.

	Dipper	Song Thrush	Ring Ouzel	Great Tit
Lay date	+	uu	NS	uuu
Clutch size	NS	NS	NS	-
Brood size	NS	NS	NS	++
Partial brood survival	NS	NS	NS	-
Clutch failure probability	NS	n	-	+
Brood failure probability	NS	-	NS	n

Table 3.2 Regression analysis of the effects of Sulphur deposition on reproductive performance in four species. Details are as Table 3.1 except data are pooled from only two periods (1968-72 and 1988-92).

	Dipper	Song Thrush	Ring Ouzel	Great Tit
Lay date	++	NS	NS	NS
Clutch size	-	NS	+	+++
Brood size	NS	-	NS	++
Partial brood survival	NS	NS	NS	NS
Clutch failure probability	nn	NS	++	NS
Brood failure probability	nnn	NS	n	uu

Table 3.3 Summary of univariate effects. Details as Table 3.1, except * indicates a significant difference between period categories.

	Dipper	Song Thrush	Ring Ouzel	Great Tit
Lay date	Clutch size^{nnn} Brood size^{nnn} Brood failure^{u}	Clutch size^{nnn} Brood size^{nnn} Brood failure--- Clutch failure^{uuu}	Clutch size^{nn} Brood size^{n} Clutch failure^{nnn}	Clutch size^{n} Brood size^{nn} Partial survival+ Clutch failure^{uu}
Latitude	Clutch size^{uuu} Brood size-- Lay date^{nn} Partial survival^{u} Clutch failure^{nnn} Brood failure---	Brood size++ Lay date^{n} Partial survival+ Clutch failure-	Lay date+ Clutch failure--	Clutch size^{nnn} Brood size^{nnn} Lay date+++ Clutch failure++
Longitude	Clutch size--	Lay date- Brood size++	Lay date++ Partial survival^{u} Clutch failure-	Clutch size+ Brood size^{nnn} Lay date^{u} Clutch failure+
Altitude	Clutch size^{nnn} Brood size^{nn} Lay date+	Brood size^{nn} Lay date+++	Clutch failure^{n} Brood failure^{n}	Clutch size^{n} Brood size^{nn} Lay date+++ Clutch failure-
Period	Clutch size*** Lay date* Partial survival* Clutch failure*** Brood failure*	Brood size** Lay date*** Partial survival*** Clutch failure***		Clutch size** Lay date*** Partial survival* Clutch failure**

Table 3.4 The effects of exceedance ratio (EXT) and period (PER) per 10-km square on reproductive performance of four species, Dipper, Song Thrush, Ring Ouzel and Great Tit. Four periods were considered (1953-57, 1968-72, 1981-83 and 1988-92). Only variables with significant partial effects (Type III) are shown. Interactions were dropped and the model re-run if not significant. Quadratic terms with a positive sign indicate a peaked relationship and with a negative sign, a troughed relationship.

(a) Dipper

NRS variable	Model effects
Lay date	EXT+ PER*
Clutch size	PER* EXTHPER***
Partial brood survival	PER*
Clutch failure	PER***
Brood failure	PER**

(b) Song Thrush

NRS variable	Model effects
Lay date	EXTHPER***
Brood size	PER*
Partial brood survival	PER*
Clutch failure	PER***
Brood failure	EXT--

(c) Ring Ouzel

NRS variable	Model effects
Clutch size	EXT+ PER* EXTHPER*
Clutch failure	EXT-

(d) Great Tit

NRS variable	Model effects
Lay date	EXT--- EXT^2+++ PER***
Clutch size	EXT+ PER**
Brood size	EXT+++
Partial brood survival	PER*
Clutch failure	PER*** EXTHPER***
Brood failure	EXT^2-

Table 3.5 The effects of Sulphur deposition (DEPS) and period (PER) per 10-km square on reproductive performance of four species, Dipper, Song Thrush, Ring Ouzel and Great Tit. Two periods were considered (1968-72 and 1988-92). Only variables with significant partial effects (Type III) are shown. Interactions were dropped and the model re-run if not significant.

(a) Dipper

NRS variable	Model effects
Lay date	PER** PERHDEPS*
Clutch size	DEPS- PER*
Clutch failure	DEPS++ PER**
Brood failure	DEPS+++ DEPS^2---

(b) Song Thrush

NRS variable	Model effects
Brood size	DEPS-
Partial survival	PER*
Clutch failure	DEPS+ PER***

(c) Ring Ouzel

NRS variable	Model effects
Lay date	DEPS- PER*
Clutch size	DEPS+
Clutch failure	DEPS--
Brood failure	DEPS+ DEPS^2-

(d) Great Tit

NRS variable	Model effects
Lay date	DEPS--- PER*** DEPSHPER***
Clutch size	PER* DEPSHPER*
Brood size	PER* DEPSHPER**
Clutch failure	PER***
Brood failure	DEPS- DEPS^2++

Table 3.6 The effects of acidification on measures of reproductive performance analysed in four separate periods. Analyses only involve variables where a significant interaction with period was shown in Tables 3.4 and 3.5. Four periods were analysed for exceedance ratio (EXR), two for Sulphur deposition (DEPS). Signs indicate direction of effect, n = significant quadratic effect (peaked relationship), u = significant quadratic effect (troughed relationship), NS = not significant. * P<0.05, **P<0.01, ***P<0.001.

Species	Acidification variable	NRS variable	Univariate effect			
			1953-57	1968-72	1981-85	1988-92
Dipper	EXR	clutch size	--	NS	NS	NS
	DEPS	lay date		NS		NS
Song Thrush	EXR	lay date	NS	NS	+++	NS
Ring Ouzel	EXR	clutch size	NS	NS	NS	NS
Great Tit	EXR	clutch failure	NS	NS	+++	--
	DEPS	lay date		--		NS
	DEPS	clutch size		NS		+++
	DEPS	brood size		-		+++

Table 3.7 Final models describing the effects of exceedance ratio and other significant variables on reproductive performance. Only models where there is a significant effect of exceedance ratio or a significant interaction including an exceedance term are shown. Signs indicate direction of effect for continuous variables. NS not significant, * P<0.05, **P<0.01, ***P<0.001.

(a) Song Thrush

NRS variable	Error distribution	Model fit	Partial significance
Clutch failure	Binomial	D_{2834}=2649	EXT+++ EXT^2--- LATITUDE- $LAYDATE^2$---
Brood failure	Binomial	D_{1842}=1988	EXT- LAYDATE---

(b) Great Tit

NRS variable	Error distribution	Model fit	Partial significance
Clutch size	Normal	$F_{3,994}$=13.40*** r^2=0.038	EXT++ LATITUDE+++ $LATITUDE^2$---
Brood size	Normal	$F_{6,1466}$=14.51*** r^2=0.056	EXT+ LAYDATE++ $LAYDATE^2$--- LATITUDE+++ $LATITUDE^2$--- $LONGITUDE^2$-
Clutch failure	Binomial	D_{907}=389	EXT-- LATITUDE - LAYDATE-- $LAYDATE^2$ ++
Brood failure	Binomial	D_{2234}=1234	EXT^2---

Table 3.8 Final models describing the effects of Sulphur deposition and other significant variables on reproductive performance. Only models where there is a significant effect Sulphur deposition or a significant interaction including a Sulphur deposition term are shown. Signs indicate direction of effect for continuous variables. NS not significant, * P<0.05, **P<0.01, ***P<0.001.

(a) Dipper

NRS variable	Error distribution	Model fit	Partial significance
Lay date	Normal	$F_{3,470}$=5.67*** r^2=0.035	PER** DEPSHPER*
Clutch failure	Binomial	D_{868}=391	DEPS++ PER**
Brood failure	Binomial	D_{183}=131	DEPS++ $DEPS^2$-- $LAYDATE^2$++

(b) Ring Ouzel

NRS variable	Error distribution	Model fit	Partial significance
Brood failure	Binomial	D_{91}=42	DEPS++ $DEPS^2$-- ALT+

(c) Great Tit

NRS variable	Error distribution	Model fit	Partial significance
Clutch size	Normal	$F_{8,728}$=11.62*** r^2=0.046	DEPS++ LATITUDE+++ $LATITUDE^2$---
Brood failure	Binomial	D_{1602}=883	DEPS- $DEPS^2$++

Table 3.9 Predicted changes in measures of reproductive performance under a scenario of reduced acidification by 2010 (WGS31B scenario). Estimates are average values (∀SD) derived from models in Table 3.7 and 3.8.

Species	Acidification variable	Dependent variable	n	2010 estimate	1990 estimate	Mean difference
Dipper	DEPS	Brood survival (%)	1374	99.41∀0.56	75.96∀17.97	23.44∀17.60
Song Thrush	EXR	Clutch survival (%)	6334	82.37∀5.12	75.18∀6.08	7.19∀5.81
	EXR	Brood survival (%)	6336	69.03∀6.61	74.16∀5.93	-5.13∀2.56
Ring Ouzel	DEPS	Brood survival (%)	285	99.97∀0.01	86.52∀11.44	13.45∀11.41
Great Tit	EXR	Clutch size	2939	7.66∀0.39	7.94∀0.37	-0.28∀0.13
	EXR	Brood size	2939	4.74∀0.53	5.30∀0.52	-0.57∀0.24
	EXR	Clutch survival (%)	3314	92.50∀3.42	93.37∀3.27	-0.87∀0.46
	EXR	Brood survival (%)	1607	84.79∀1.72	88.44∀1.71	-3.75∀2.12
	DEPS	Clutch size	2413	7.69∀0.34	7.96∀0.40	-0.27∀0.12
	DEPS	Brood survival (%)	2755	83.48∀0.54	87.74∀4.46	-4.27∀4.60

Appendix 3

Predicted changes in measures of reproductive performance under a scenario of reduced acidification by 2010 (REFERENCE scenario). Estimates are average values (∀SD) derived from models in Table 3.7 and 3.8.

Species	Acidification variable	Dependent variable	n	2010 estimate	1990 estimate	Mean difference
Dipper	DEPS	Brood survival (%)	1374	92.50∀7.00	75.96∀17.97	16.53∀14.61
Song Thrush	EXR	Clutch survival (%)	6334	81.14∀5.59	75.18∀6.08	5.97∀5.84
	EXR	Brood survival (%)	6336	69.63∀6.68	74.16∀5.93	-4.52∀2.58
Ring Ouzel	DEPS	Brood survival (%)	285	99.13∀1.48	86.52∀11.44	12.61∀10.89
Great Tit	EXR	Clutch size	3418	7.70∀0.41	7.94∀0.37	-0.24∀0.14
	EXR	Brood size	2939	4.89∀0.54	5.30∀0.52	-0.50∀0.26
	EXR	Clutch survival (%)	2633	92.62∀3.41	93.37∀3.27	-0.75∀0.47
	EXR	Brood survival (%)	1607	85.15∀2.19	88.44∀1.71	-3.50∀2.35
	DEPS	Clutch size	2413	7.77∀0.35	7.96∀0.40	-0.19∀0.12
	DEPS	Brood survival (%)	2755	85.83∀0.82	87.74∀4.46	-1.91∀4.42

Fig. 3.1 Mean (∀SD) acidification rates per 10-km square in Great Britain. (a) Exceedance ratio in four years, N = 2884 10-km squares; (b) Sulphur deposition rate in two years, N = 2720 10-km squares. Error bars represent 95% confidence limits.