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Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use

D.E. Chamberlain *, R.J. Fuller

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

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Abstract

Changes in agricultural land-use may have been responsible for contractions in range that have occurred in a number of bird species over the past three decades. This was considered by examining spatial change in the ranges of 21 farmland bird species at the scale of 10 km squares in relation to spatial change in agricultural land-use variables between the late 1960s and the late 1980s in lowland England and Wales. Seven species showed range declines (local extinction) exceeding 5% over this period and analyses focused on these: Grey Partridge *Perdix perdix*, Lapwing *Vanellus vanellus*, Turtle Dove *Streptopelia turtur*, Yellow Wagtail *Motacilla flava*, Tree Sparrow *Passer montanus*, Corn Bunting *Miliaria calandra* and Reed Bunting *Emberiza schoeniclus*. Individual species loss and change in species richness tended to be related to variables with strong regional trends, reflecting greater losses in western 10 km squares characterized by pastoral agriculture. It is unlikely that many of the variables selected in the regression models are, in themselves, the causal factors behind changes in the ranges of species and changes in species richness. Lapwing was an exception, agricultural variables associated with grassland being consistently selected. Principal Components Analysis (PCA) was applied to the agricultural variables. This identified a major gradient of change in cropping patterns, involving large increases in areas of wheat *Triticum* spp. and oilseed rape *Brassica napus* at the expense of barley *Hordeum* spp., bare fallow and grass. Local extinctions and change in species richness were consistently related to the first PCA axis, showing that local extinctions have occurred most in those squares where there had been relatively little change in crop types. The greater rate of local extinctions in pastoral regions may be associated with a number of factors, including changes in the management of grass and livestock, edge of range effects (where species in less favoured habitats are more likely to become locally extinct) and source-sink effects. These results highlight the need for further research into the effects of agricultural management on birds in pastoral systems. ©2000 Elsevier Science B.V. All rights reserved.

Keywords: Farmland birds; Local extinction; Lowland; Pastoral systems; Principal components analysis; Species richness

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1. Introduction

Birds associated with agricultural land are declining in lowland Britain and elsewhere in western Europe (Tucker and Heath, 1994; Fuller et al., 1995; Siriwardena et al., 1998). In Britain, the evidence comes

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* Corresponding author. Tel.: +44-01842-750050;
fax: +44-0-1842-750030.
E-mail address: dan.chamberlain@bto.org (D.E. Chamberlain).

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from both long-term annual monitoring of local bird abundance (Marchant et al., 1990), and from periodic large-scale atlases that provide information on distributional changes at the level of 10 km squares. There have been two such atlases of breeding birds, firstly between 1968 and 1972 (Sharrock, 1976), and secondly between 1988 and 1991 (Gibbons et al., 1993). Local extinctions (present in the early survey, absent in the later survey) and colonisations (absent in the early survey, present in the later survey) of species between the two surveys can, therefore, be determined. Fuller et al. (1995) reported that 24 out of 28 (86%) species of farmland bird had shown a contraction in range between the two surveys. For species primarily associated with habitats other than farmland, a smaller proportion (51%) had declined in range, and the magnitude of these declines was less than that in farmland.

There is, therefore, an implication that factors specific to farmland are affecting bird distributions in a number of species, and indeed there have been great changes in the management of farmland between the two atlas surveys (O'Connor and Shrubb, 1986; Fuller et al., 1995). This has included changes in the timing of sowing and harvesting operations, simplification of crop rotations, increases in fertilizer application, increases in the use and efficacy of pesticides, changes in the management of grassland and a general change in the diversity of agricultural practices, with individual farms typically being either solely arable or pastoral enterprises, rather than adopting a mixed farming regime. The likely mechanisms by which these changes in management have affected bird populations are diverse and probably vary between species (Fuller et al., 1995), but generally include: effects on food supply via pesticide inputs (Potts, 1986; Campbell et al., 1997), reductions in ley grass (Potts, 1986) or changes in grassland management (Evans et al., 1997); effects on suitable nesting habitat due to changes in sowing regimes (Wilson et al., 1997); effects on winter food through, for example, reduction in over-winter stubbles (Wilson et al., 1996); or, direct effects of farming operations on bird mortality, particularly in association with grassland management (Crick et al., 1994; Green, 1995).

There have been a few studies that have explicitly analysed the effects of land-use change on change in farmland bird distributions (Gates et al., 1994; Gibbons and Gates, 1994; Gates and Donald, 1999; Chamberlain et al., 1999). Chamberlain et al. (1999) found that local extinction rates differed between broad geographical regions defined according to arable : grass ratio. Losses in seven species, Grey Partridge *Perdix perdix*, Lapwing *Vanellus vanellus*, Turtle Dove *Streptopelia turtur*, Yellow Wagtail *Motacilla flava*, Tree Sparrow *Passer montanus*, Corn Bunting *Miliaria calandra* and Reed Bunting *Emberiza schoeniclus*, were significantly lower in 10 km squares from predominantly arable regions compared to pastoral or mixed farming regions. Decrease in species richness was also significantly lower in arable dominated regions.

Gates et al. (1994) modelled the effects of a large number of land-use variables (including agricultural data) on the abundance of selected farmland bird species using data from the later (1989–1991) atlas survey. The derived models consisted of large numbers of variables and whilst they were often good predictors of abundance, many model variables were difficult to interpret in terms of likely ecological effects on birds. The predictive models developed for the later atlas also failed to explain adequately the change in the distribution of species when applied to data from the early atlas survey. This example illustrates that interpretation of such modelling approaches must be carried out with some caution, particularly when there is evidently a high degree of inter-correlation and many variables are effectively interchangeable with many other (possibly unmeasured) variables (Donald and Fuller, 1998). Gibbons and Gates (1994) avoided this problem by considering specific hypotheses concerning likely factors affecting the change in range of Corn Buntings, but there was no evidence to suggest that changes in the area of barley, particularly that sown in the spring, was associated with Corn Bunting declines. Gates and Donald (1999) reduced a large number of land-use variables to axes of environmental variation using Principal Components Analysis (PCA) and related these to changes in the distribution of selected farmland bird species. They found that 10 km squares where a species had been lost were more similar in terms of land-use to 10 km squares where the species had never been recorded, implying that population declines have occurred in the least favoured habitats.

There is as yet little evidence that declines in range of any farmland species are strongly related to *specific* changes in agricultural practice, although as illustrated above, no studies have addressed this question directly, with the exception of Gibbons and Gates (1994) who considered only one farmland species and few land-use variables. In this paper, the effects of changes in a large number of spatially referenced land-use variables are considered in relation to the probability of loss of selected farmland species from 10 km squares between the two atlas surveys and in relation to changes in species richness in order to identify factors that may have been responsible for contractions in species' geographical range. Land-use is described firstly in terms of individual agricultural and other habitat variables and secondly using PCA to describe general gradients of spatial change in lowland agriculture.

2. Methods

2.1. Land-use data

The main source of spatial land-use data was the MAFF Agricultural June Census, which details the area of land under a wide range of agricultural use. Data at the 10 km square level were used from 1969 and 1988, each of which falls within a period covered by the Breeding Bird Atlas (Gibbons et al., 1993). Variables were selected on the quality of the data and consistency between the two censuses. There were, for example, certain variables such as temporary grassland that changed definition between the two censuses, so permanent and temporary grass were combined in one category of improved grass. The available data were biased towards arable farmland, there being comparatively little detailed data on grass-dominated agriculture in marginal uplands. For this reason, the analyses were restricted to lowland farmland in England and Wales, only considering 10 km squares with an initial (i.e. 1969) minimum area of 5000 ha of lowland agricultural land, so 10 km squares with a large amount of urban, coastal or upland habitat were omitted. All variables of agricultural change used in the analyses, the total extent (either in terms of area or number of animals) and the total change in area/numbers in lowland England and Wales are given in Table 1. MAFF June Census data were used to define predominantly arable and non-arable regions in England and Wales defined at the county level, where counties defined as predominantly arable were those where arable farmland occupied over 10 times the area of grassland in 1988. The geographical location of the regions is shown in Fig. 1. Non-arable counties were divided into two regions

Table 1

The total extent of 15 agricultural variables in 1969 and 1988 and the change between these years over 1089 lowland farmland 10 km squares in England and Wales[a]

Definition	1969	1988	Change 1969–1988	Units
Wheat *Triticum* L.	734580	1650929	916349	ha
Barley *Hordeum* L.	1855765	1282982	−572783	ha
Oilseed rape *Brassica napus* L.	4884	279030	274146	ha
Orchards and small fruit	70545	41373	−29172	ha
Potatoes *Solanum tuberosum* L.	166494	122343	−44154	ha
Sugar beet *Beta vulgaris* L.	168982	186249	17267	ha
Other root vegetables	69734	52654	−17080	ha
Other vegetables	185830	360371	174541	ha
Bare fallow	144170	40575	−103595	ha
Improved grassland	4399642	3823395	−576347	ha
Rough grazing	442022	321042	−120980	ha
Total tilled land	4233567	4134180	−99387	ha
Total agricultural land	8633209	8278518	−354691	ha
Cattle	7226916	6714914	−512002	No. of animals
Sheep	11656837	18836451	7179614	No. of animals

[a] These data are adapted from the Parish Summaries of the MAFF Agricultural June Census and were provided by the University of Edinburgh Data Library.

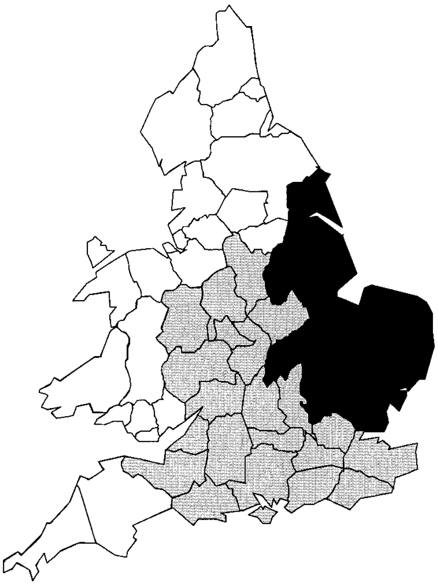

Fig. 1. The distribution of arable counties (black), mixed counties (shaded) and pastoral counties in England and Wales.

that represented counties of predominantly mixed and pastoral farmland, respectively. For the sake of brevity, these three regions are referred to as 'arable', 'mixed' and 'pastoral'. As agricultural statistics were used from only 2 years, 1969 and 1988, but atlas data were collected over a number of years (1968–1972 and 1988–1991), the analyses assume that the agricultural census data is representative of land-use within the respective atlas periods. This was justified as the main periods of agricultural change occurred from the mid-1970s to the early 1980s, the majority of variables showing little change in area before or after this period (Chamberlain et al., 1999). Shannon diversity indices (Krebs, 1980) for crop types were determined for each 10 km square using the variables defined in Table 1.

MAFF Census data only include agricultural land, but it is likely that other habitats in close proximity may affect birds on farmland, particularly when the area of farmland is small. For this reason, the proportion of woodland and urban land per 10 km square, derived from ITE land cover data (Fuller and Parsell, 1990) and the median altitude per 10 km square derived from the ITE Land Characteristics data base (Ball et al., 1983) were considered in the analyses. These values, unlike crop variables, were absolute measures rather than measures of change, having been determined for only a single time period.

2.2. *Bird data*

The geographical range of each bird species was taken from two atlas surveys of the UK and Ireland coordinated by the BTO during 1968–1972 (Sharrock, 1976) and 1988–1991 (Gibbons et al., 1993). 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 standardized by specifying a minimum number of eight tetrads (2×2 km squares) per 10 km square that had to be visited, with a set survey time of 2 h per tetrad (Gibbons et al., 1993). 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). This may be taken into consideration when analysing changes in species distribution by using a weighting procedure (see below). Additionally, the change in species richness (i.e. number of species present) per 10 km square was analysed in relation to farming practice, concentrating mainly on a group of 21 target species, selected on the basis of the quality of the available data and whether the bird was considered characteristic of lowland farmland in England and Wales. The species selected were Kestrel *Falco tinnunculus*, Grey Partridge, Lapwing, Stock Dove *Columba oenas*, Turtle Dove, Skylark *Alauda arvensis*, Yellow Wagtail, Starling *Sturnus vulgaris*, Rook *Corvus frugilegus*, Whitethroat *Sylvia communis*, Blackbird *Turdus merula*, Song Thrush *T. philomelos*, Tree Sparrow, Chaffinch *Fringilla coelebs*, Bullfinch *Pyrrhula pyrrhula*, Greenfinch *Carduelis chloris*, Goldfinch *C. carduelis*, Linnet *C. cannabina*, Corn Bunting, Reed Bunting and Yellowhammer *Emberiza citrinella*. Certain farmland species, although of great conservation concern, were too rare for any valid analysis (e.g. Stone Curlew *Burhinus oedicnemus* and Cirl Bunting *Emberiza cirlus*). Other common farmland species are typically poorly censused and so were not considered (e.g. Pheasant *Phasianus colchicus*, Woodpigeon *Columba palumbus* and House Sparrow *Passer domesticus*).

2.3. Analyses

The change in area of agricultural variables from MAFF data were determined between the two atlas periods for each 10 km square. A total of 1089 10 km squares were included in the analysis out of a total possible 1719 10 km squares across England and Wales. Land-use change was also described by carrying out PCA to reduce the large number of variables to simpler gradients of land-use change (Afifi and Clark, 1996). The difference in agricultural land-use between 1988 and 1969 was analysed using PCA to ordinate all farmland 10 km squares in the sample, the goal being to identify gradients made up of 10 km squares with varying levels of land-use change using all 15 variables in Table 1. Axes were derived using the correlation matrix of variables, thus allowing consideration of variables measured on different scales (James and McCulloch, 1990). Only the first three axes, labelled PRIN1 to PRIN3, were considered. Axes were derived firstly for the whole sample of 10 km squares and secondly for each region (Fig. 1) separately.

The number of 10 km squares occupied in both atlas surveys was determined for all the species. Many of the 21 target species, whilst showing evidence of population declines, have not shown evidence of a contraction in range (Gibbons et al., 1993). Therefore, only those species with a range contraction of over 5% were considered for this analysis. There were seven such species: Grey Partridge, Lapwing, Turtle Dove, Yellow Wagtail, Tree Sparrow, Corn Bunting and Reed Bunting. The number of 10 km squares where a bird species was lost and the number of 10 km squares where a bird species was retained between the two atlas surveys was determined. For the species selected for analysis, the proportion of 10 km squares that gained a species was usually too small to warrant separate analysis (c. 1% of the total sample of 10 km squares) and these records were not included in the analysis of local extinction. Those 10 km squares where a species was not recorded in either survey were not considered in the analysis. The loss or retention of a species was modelled in relation to change in land-use variables (Table 1) using logistic regression procedures, selecting the single variable that maximised the deviance over a given sample of 10 km squares (the whole data set, and then data sets broken down by region). More complex modelling approaches were carried out, selecting a large number of variables and maximizing model fit, but we were aware of a high level of collinearity in the data (Chamberlain et al., 1999) that made interpretation of these multi-variable models difficult (see Donald and Fuller, 1998, for a discussion of the difficulties of interpreting such analyses, with particular reference to Gates et al., 1994). However, the goal of the analysis was to identify the factors that best fitted population change, rather than to build predictive models from the data. Therefore, it was decided to adopt the simplest approach of single variable selection.

The dependent variable in the models was the probability that a species would not be recorded in the second atlas survey where it had been recorded in the first (i.e. it had become locally extinct). Data were thus reduced to a binomial response where $1 =$ loss of a species from a 10 km square and $0 =$ stayed the same. The independent variables were measures of change in various agricultural land-use types per 10 km square between 1988 and 1969 (Table 1), and the change in total agricultural area and in diversity index of land-use between 1988 and 1969. Area and diversity of land-use in the early survey and non-agricultural habitats (woodland, suburban/urban land and altitude) were not considered initially, but were included in a repeat analysis of local extinction. Change in the number of species recorded (species richness) was determined in absolute terms (number recorded in early survey-number in late survey) and relative terms [(number recorded in new survey/number recorded in old survey)-1] per 10 km square, gains in species being included in this calculation. Change in species richness per 10 km square of all species recorded, and of the 21 target species, was also analysed in relation to land-use change using linear regression, selecting the single variable that resulted in the largest r^2 value. The variation in observer effort per 10 km square was taken into consideration by weighting both logistic and linear regression analyses according to the number of tetrads visited per 10 km square in the later survey, so tetrads with fewer visits effectively have test statisitics adjusted downwards and detection of a significant effect is less likely (SAS Institute, 1996). The variation in effort between 10 km squares was not known for the earlier survey, but this is less important

Table 2
PCA on the change in area of various agricultural land-use types per 10 km square between 1969 and 1988, considering squares with a minimum farmland area of 5000 ha ($n = 1089$)[a]

Agricultural variable	PRIN1	PRIN2	PRIN3
Barley	0.34	0.23	−0.12
Improved grassland	0.32	−0.03	0.48
Bare fallow	0.30	0.12	−0.11
Sheep	0.27	−0.03	0.15
Cattle	0.24	0.15	0.35
Potatoes	0.16	0.33	−0.37
Root crops	0.02	−0.08	0.18
Sugar beet	0.01	0.46	−0.18
Orchards and small fruit	0.02	0.07	−0.10
Total agricultural land	0.00	0.55	0.52
Rough grazing	−0.24	0.30	−0.08
Vegetables	−0.28	0.05	0.21
Total tilled land	−0.33	0.42	−0.06
Oilseed rape	−0.38	−0.09	0.13
Wheat	−0.39	−0.01	0.20
Eigenvalue	5.20	1.69	1.43
Variance explained	34.7	11.3	9.5

[a] The coefficients of the variables from each of the first three axes (PRIN1-3), in order of the first axis, and the percentage of variation explained by each axis, are presented.

given that we are dealing mainly with 10 km squares where a species was present in the early survey (i.e. gains are not included apart from determination of species richness). The weighting procedure was carried out in order to take into account the possibility that birds were present in the late survey but were not recorded.

One problem interpreting regression models involving land-use data is that there was a high degree of collinearity. The effects of variables such as change in wheat and oilseed rape area were very similar and, therefore, essentially interchangeable. PCA reduced a large number of variables to fewer uncorrelated axes of environmental variation and so avoided the problem of collinearity. PCA scores, which give a value to each square according to its position on the PCA axis (Afifi and Clark, 1996), were derived from the first three PCA axes and were used as independent variables in a logistic regression model in place of individual agricultural change variables used in Table 1. The approach using PCA scores was identical in all other respects to the previous logistic regression analysis.

3. Results

3.1. Spatial changes in farming practice

The amount of variation between 10 km squares explained by the first three PCA axes and the correlation coefficients of individual variables between axes and variables (Afifi and Clark, 1996) are shown in Table 2. The first axis (PRIN1) explained 34.7% of variation in the data and identified a major pattern of change in cropping. A clear geographical pattern was evident, with most of the scores of greatest negative magnitude occurring from Lincolnshire southwards to the northern Home Counties and eastward to Essex and Suffolk (Fig. 2). The spatial change of the five agricultural variables at either end of PRIN1 (i.e. variables with the highest and lowest coefficients) is shown in Fig. 3. The 10 km squares that have experienced large

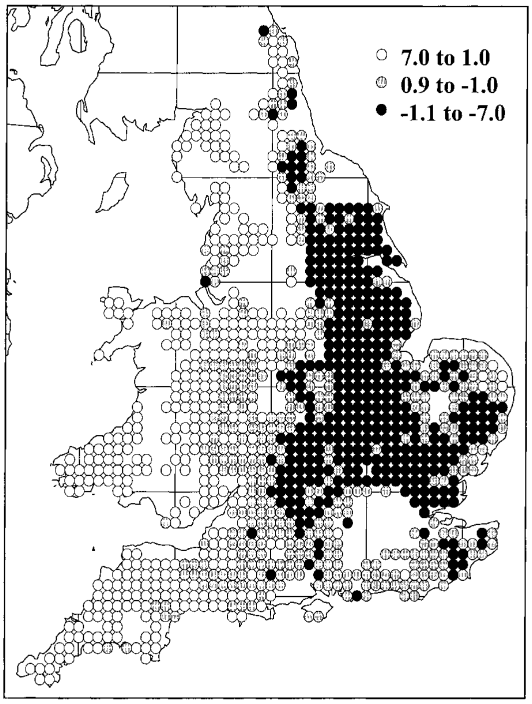

Fig. 2. Scores (arbitrary units) for 10 km squares in lowland England and Wales for the first principal component, PRIN1, showing a gradient from squares that have increased in wheat and oilseed rape and decreased in barley and grass (black circles) to squares that have increased in grass and barley. Circles represent PCA scores ranked into three groups of equal sample size.

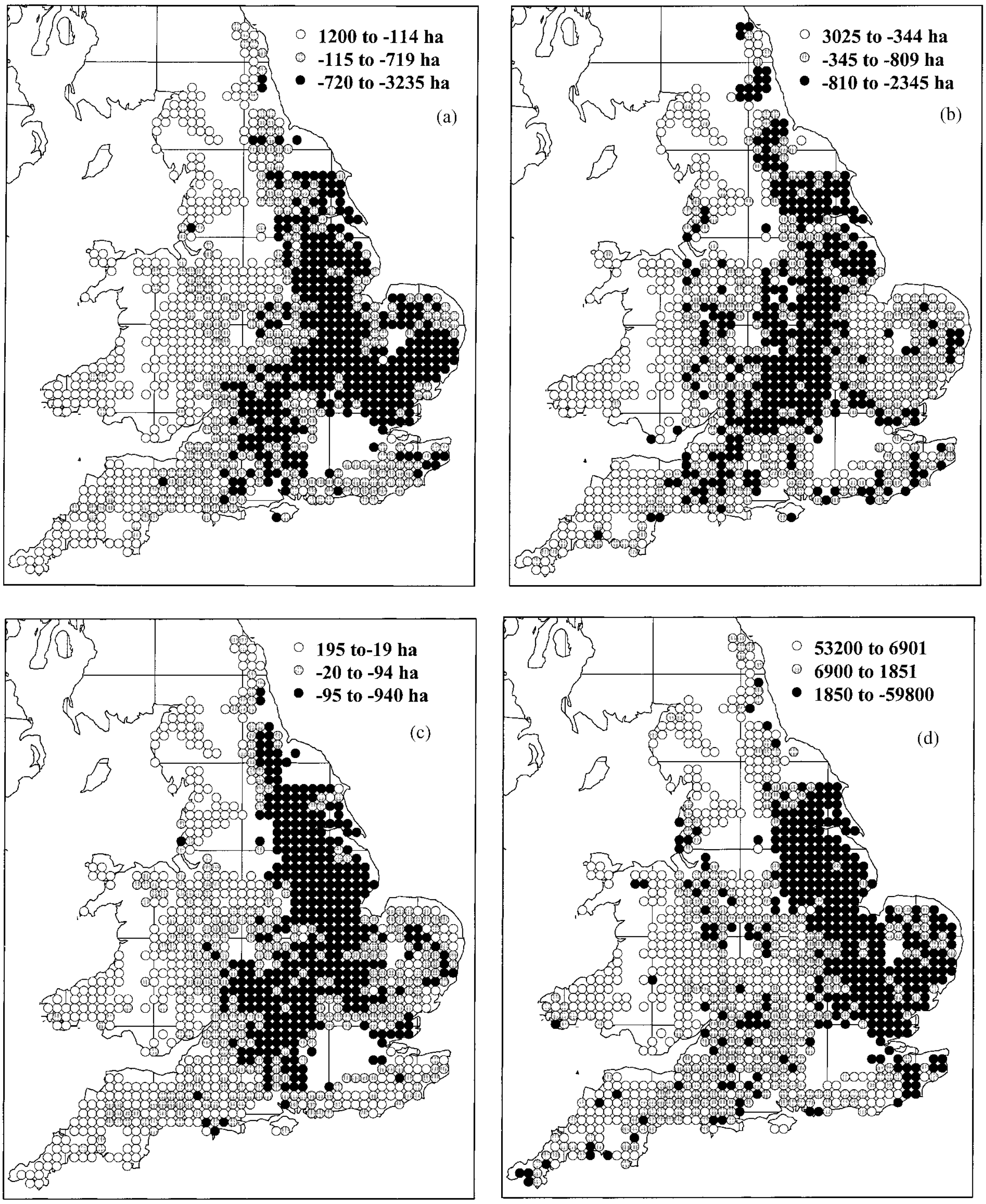

Fig. 3. Change in the 10 individual agricultural variables between 1988 and 1969 that had most influence on the first PCA axis (Table 2). Circles represent variables ranked according to the magnitude of change and placed into three groups of equal sample size. (a) Change in barley area (ha); (b) Change in improved grass area (ha); (c) Change in bare fallow (ha); (d) Change in numbers of sheep; (e) Change in numbers of cattle; (f) Change in rough grazing area (ha); (g) Change in area (ha) of tilled farmland; (h) Change in area (ha) of vegetables other than root crops; (i) Change in oilseed rape area (ha); (j) Change in wheat area (ha).

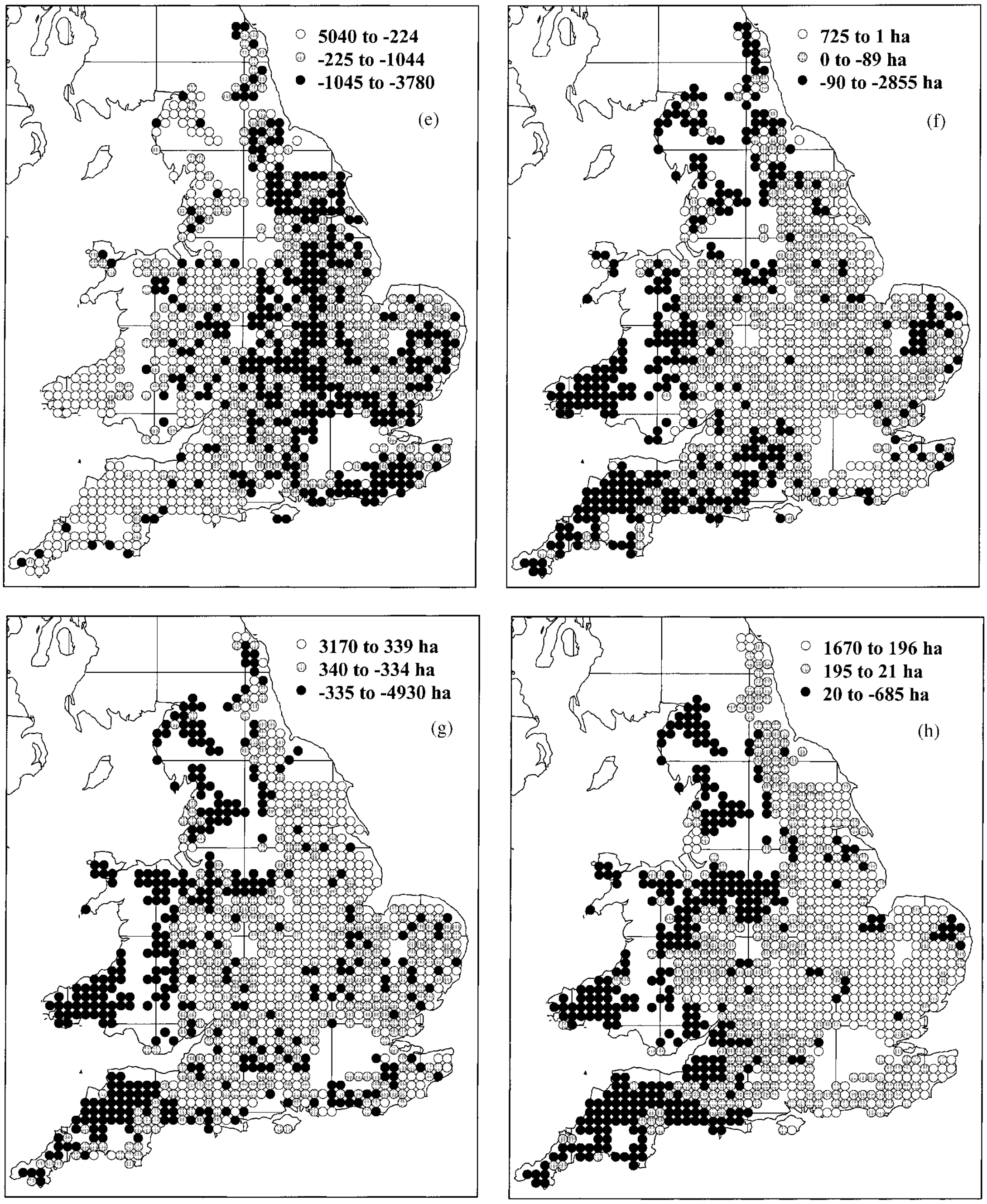

Fig. 3 (*Continued*).

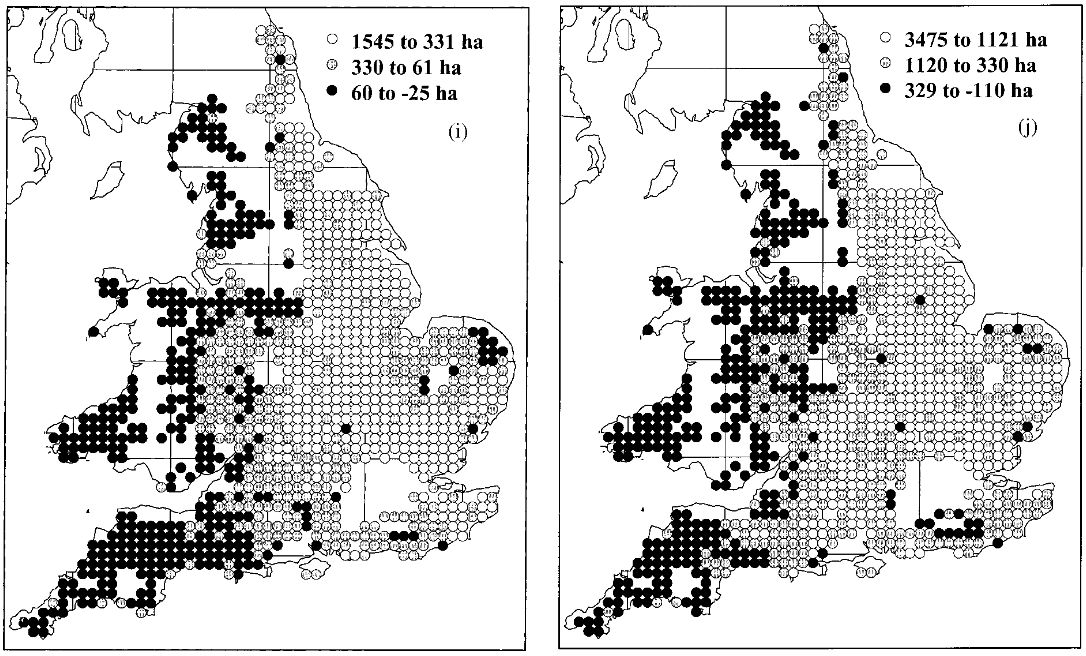

Fig. 3 (*Continued*).

increases in certain crop types (particularly wheat and oilseed rape) at the expense of barley, bare fallow and grass (Fig. 3) have high scores on this axis (Fig. 2). Ten kilometer squares towards the north and west of England and Wales have experienced less change in arable crops apart from a small increase in barley, but have increased in grass area (Fig. 3). Variables with intermediate scores on PRIN1 tended to show no clear geographical trends (total agricultural land) or showed only localised increases (sugar beet) or decreases (potatoes, other root crops and orchards).

The second axis, which explained 11.3% of variation in the data, was mainly associated with overall changes in the area of agricultural land (Table 2), and there were particularly high scores on this axis in central-eastern England (Fig. 4) indicating areas that had tended to decrease most in agricultural area, tilled land and sugar beet. PRIN3, which explained 9.5% of variation in the data (Table 2), was associated with changes in grassland and total farmland area (Fig. 5). PRIN3 showed no particular geographical pattern, with the exception of a large number of negative scores in 10 km squares in central-eastern England that had lost relatively large areas of grass and of total farmland between the two periods.

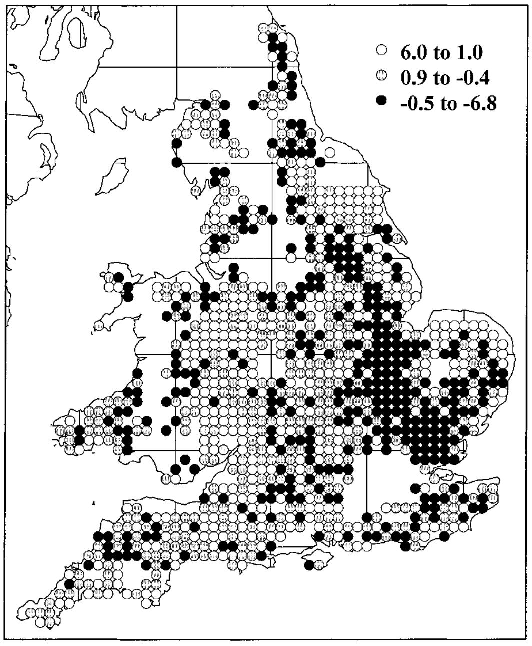

Fig. 4. Scores (arbitrary units) for 10 km squares in lowland England and Wales for the second principal component, PRIN2. Circles represent PCA scores ranked into three groups of equal sample size.

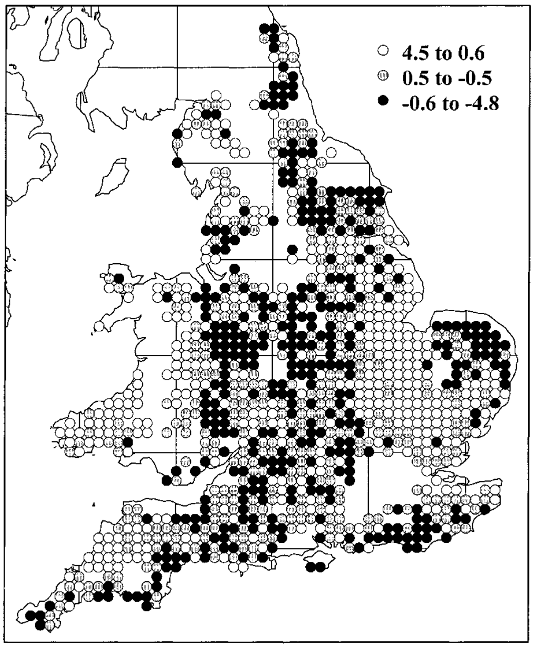

Fig. 5. Scores (arbitrary units) for 10 km squares in lowland England and Wales for the third principal component, PRIN3. Circles represent PCA scores ranked into three groups of equal sample size.

PCA analyses were repeated for arable and non-arable regions separately (Table 3). The axes, and in particular PRIN1, were similar to those in the overall analysis for each of the three regions, although change in the area of vegetables was of relatively greater importance in both mixed and pastoral regions. Change in total area of agricultural land and total tilled area had high scores on PRIN2 for each region, but decrease in sugar beet area showed similar geographic trends to these variables in arable and mixed regions. Rough grazing had the highest scores on PRIN2 in pastoral regions, showing similar geographic trends to losses in total tilled area. PRIN3 was the most variable axis across the regions. In the arable region, PRIN3 represented a gradient from squares that had decreased in grass and cattle to squares that had changed little in the former two variables (from low initial levels) but had decreased in potatoes and sugar beet. In the mixed region, PRIN3 represented a gradient from increasing grass and sheep to decreasing rough grazing. Finally, in the pastoral region, PRIN3 represented a gradient from decreases in total agricultural land and orchards to increases in potatoes.

The diversity index per 10 km square was determined for each period using the area of individual crop and grass variables from Table 1 (so not including total tillage, total agricultural land or livestock variables), but dividing total grass into permanent and temporary grass (the change in definition between the two years should matter little when considering land-use diversity). The absolute change in diversity index of crop types between 1988 and 1969 was determined per 10 km square (Fig. 6). The greatest increases in diversity were in the Midlands, the Welsh Borders, Kent, parts of East Anglia and north-west England. There was evidence of a decrease in diversity in a belt of 10 km squares in eastern England, south from the Humber Estuary through Lincolnshire and Cambridgeshire. This was probably due to a greater concentration on solely arable farming in these areas. There were also decreases in Wales and the south-west of England that may indicate the increasing specialisation of pastoral farms and the loss of arable crops in these regions. When considering the percentage change in diversity between the two time periods (i.e. relative to the original diversity of the square), a very similar pattern was evident.

3.2. Species distributions and individual agricultural variables

The variable that maximised the explained deviance in the logistic regression model for each species is shown in Table 4. A positive relationship indicated that an increase in the independent variable was associated with an increasing probability of local extinction, and a negative relationship indicated a decreasing probability of local extinction with an increase in the variable, so where the variables were differences in land-use type between the two periods (late–early), a positive relationship indicated that local extinction was associated with an increase in land-use area.

Considering all 10 km squares, local extinction increased in 10 km squares that had increased in cattle (Lapwing), increased in sheep (Reed Bunting), decreased or changed little in oilseed rape (Yellow Wagtail and Tree Sparrow) and wheat (Corn Bunting), and in 10 km squares that had increased in barley (Turtle

Table 3
PCA on the change in area of various agricultural land-use types per 10 km square between 1969 and 1988 in regions broadly defined by predominant agriculture in lowland England and Wales (Fig. 1), considering squares with a minimum farmland area of 5000 ha[a]

Agricultural variable	Arable			Mixed			Pastoral		
	PRIN1	PRIN2	PRIN3	PRIN1	PRIN2	PRIN3	PRIN1	PRIN2	PRIN3
Improved grassland	0.34	0.11	0.44	0.36	0.00	0.36	0.31	−0.01	0.40
Bare fallow	0.32	0.14	0.05	0.30	0.10	−0.15	0.34	−0.04	−0.18
Barley	0.28	0.25	−0.19	0.32	0.31	−0.16	0.29	0.19	−0.09
Cattle	0.21	0.22	0.37	0.22	0.18	−0.13	0.20	0.30	0.13
Sugar beet	0.15	0.41	−0.30	0.02	0.41	−0.08	−0.22	0.12	0.28
Sheep	0.10	0.08	0.12	0.27	−0.02	0.44	0.18	−0.20	0.30
Root crops	0.02	−0.11	0.24	−0.04	0.04	0.33	0.17	0.18	0.17
Potatoes	−0.01	0.18	−0.42	0.08	0.46	0.01	0.27	−0.09	−0.25
Vegetables	−0.12	0.17	0.19	−0.30	0.11	0.25	−0.28	−0.18	0.04
Total agricultural land	−0.15	0.59	0.19	0.06	0.48	0.44	0.04	0.47	0.49
Rough grazing	−0.18	0.15	0.27	−0.22	0.26	−0.33	−0.18	0.56	−0.09
Orchard and small fruit	−0.19	0.09	−0.28	0.02	0.02	0.01	−0.04	0.17	0.47
Total tilled land	−0.35	0.46	−0.06	−0.34	0.41	−0.07	−0.29	0.43	−0.17
Wheat	−0.44	0.03	0.25	−0.39	0.03	0.30	−0.38	0.02	0.06
Oilseed rape	−0.45	−0.14	0.08	−0.38	−0.02	0.20	−0.38	0.06	0.14
Eigenvalue	3.54	2.25	2.04	4.41	2.01	1.50	5.97	1.69	1.67
Variance explained	23.6	15.0	13.6	27.6	13.4	10.0	39.8	11.3	11.1

[a] The coefficients of the variables from each of the first three axes (PRIN1-3), in order of the first axis in the arable region, and the percentage of variation explained by each axis, are presented. Sample sizes: arable = 298 squares, mixed = 512 squares, pastoral = 279 squares.

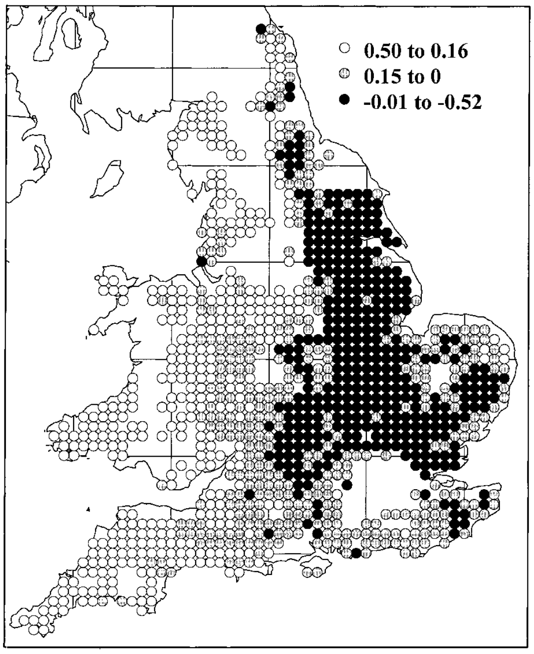

Fig. 6. The change in land-use diversity in 10 km squares in lowland England and Wales between 1988 and 1969. Circles represent diversity indices ranked into three groups of equal sample size.

Dove) and improved grass (Grey Partridge) (Table 4). The crop and livestock variables selected tended to show similar or complementary geographical patterns of change, with wheat and oilseed rape increasing in central and eastern 10 km squares and changing little in the west and north, cattle decreasing most in the west, and grass increasing in the north and west (Fig. 3). The original farm land-use diversity was a better predictor of Turtle Dove and Corn Bunting local extinction, woodland area was a better predictor of Grey Partridge and Tree Sparrow local extinction and altitude was a better predictor of Reed Bunting local extinction than individual crop or livestock variables.

Variables selected in the arable region were different from those selected for the full data set in each species (Table 4), and included sugar beet, rough grazing, wheat, cattle and orchards. A problem with these models is that local extinction rates were typically very low, and so they may not be very informative, particularly for Lapwing, Turtle Dove, Yellow Wagtail and Tree Sparrow, which showed changes of less than 5% in this region (Chamberlain et al., 1999). The mixed region showed different variable selection to

Table 4
The effect of agricultural land-use change between 1969 and 1988 on the probability that a species would not be recorded in a 10 km square in the later survey where it had been recorded in the early survey in all of lowland England and Wales and in three regions broadly defined by predominant agriculture (Fig. 1)[a]

Species	All squares	*n*	Arable	*n*	Mixed	*n*	Pastoral	*n*
Grey Partridge	Improved grass + (Woodland +)	1039	Sugar beet −	297	Sheep + (Woodland +)	502	Vegetables −(Woodland +)	241
Lapwing	Cattle +	1064	Rough grazing −	295	Root crops − (Change in diversity −)	512	Cattle +	257
Turtle Dove	Barley + (Original diversity −)	918	Wheat − (Altitude +)	297	Vegetables − (Original diversity −)	473	Wheat −	148
Yellow Wagtail	Oilseed rape −	777	Sugar beet +	245	Oilseed rape − (Woodland +)	400	Total tillage − (Altitude +)	132
Tree Sparrow	Oilseed rape − (Woodland +)	948	Cattle + (Original area −)	295	Oilseed rape − (Woodland +)	484	Total tillage −	169
Corn Bunting	Wheat − (Original Diversity −)	725	Orchards +	253	Barley + (Original diversity −)	355	Wheat − (Original diversity −)	117
Reed Bunting	Sheep + (Altitude +)	1044	Sugar beet + (Altitude −)	298	Sheep + (Altitude +)	488	Vegetables − (Woodland +)	258

[a] The single variables that explained the greatest amount of deviance were selected. Results in parenthesis include the additional variables of altitude, original area of agricultural land, the original land-use diversity of farmland, cover of woodland and cover of urban land, where variable selection differed from the original model. Regressions were weighted by observer effort in each 10 km square. The sign indicates the direction of the effect of a variable on the probability that a species was lost from a 10 km square. The deviance explained was significant at $p < 0.001$ in each case. Sample sizes show the number of 10 km squares where a species was recorded in the early survey.

Table 5
The effects of changes in various agricultural land-use types as represented by scores derived from 3 Principal Components axes (Table 2) on the probability that a species would not be recorded in a 10 km square in the later survey where it had been recorded in the early survey in all of lowland England and Wales and in three regions broadly defined by predominant agriculture (Fig. 1)[a]

Species	All squares	*n*	Arable	*n*	Mixed	*n*	Pastoral	*n*
Grey Partridge	PRIN1 + (Woodland +)	1039	PRIN3 +	296	PRIN1 +	502	PRIN1 + (Woodland +)	241
Lapwing	PRIN1 + (Change in diversity −)	1064	ns[b] (Change in diversity −)	295	PRIN1 +	512	PRIN1 + (Change in diversity −)	257
Turtle Dove	PRIN1 +	918	PRIN3 +	297	PRIN1 +	473	PRIN1 +	148
Yellow Wagtail	PRIN1 +	777	PRIN2 + (Change in diversity −)	245	PRIN1 + (Woodland +)	400	PRIN1 +	132
Tree Sparrow	PRIN1 + (Woodland +)	948	ns (Original area −)	295	PRIN1+ (Woodland +)	484	PRIN1 +	169
Corn Bunting	PRIN1 + (Original diversity −)	725	PRIN1 + (Change in diversity −)	253	PRIN1 + (Original diversity −)	355	PRIN1 +	117
Reed Bunting	PRIN1 + (Altitude +)	1044	PRIN3 + (Altitude +)	298	PRIN1 + (Altitude +)	488	PRIN1 + (Woodland +)	258

[a] Other details are as in Table 4.

[b] ns = no significant variables selected.

Table 6
The effects of agricultural change on change in species richness calculated over all species and for 21 target species only between the two atlas surveys in all of lowland England and Wales and in three regions broadly defined by predominant agriculture (Fig. 1)[a]

Number of 10 km squares	All squares	Arable	Mixed	Pastoral
	1089	298	512	279
(a) Changes in individual crop and livestock variables				
All species	Potatoes −−−	Orchards/fruit −− (Woodland −−−)	Cattle − (Suburban land ++)	ns (Altitude −−)
Target species	Oilseed rape −−−	ns (Woodland +)	Oilseed rape −−−	Bare fallow +++
(b) PCA axes				
all species	PRIN1 +++ (woodlaond +++)	PRIN3 +++	PRIN1 + (Suburban land ++)	PRIN1 + (Altitude −−
Target species	PRIN1 +++	ns (Woodland ++)	PRIN1 +++	PRIN1 +++

[a] The sign indicates the effect of a given variable on local extinction, where +/− $p < 0.05$, ++/−− $p < 0.01$, +++/−−− $p < 0.001$ (linear regression). Other details are as in Table 4.

the whole data set (Table 4), but variables typically showed similar geographical trends to those selected in the whole data set. However, in this region, variables other than individual crop or livestock variables were better predictors of local extinction in each species. For the pastoral region, local extinctions were generally associated with agricultural variables that had changed the most in west Wales and south-west England. Vegetables (associated with Grey Partridge and Reed Bunting local extinction), total tillage (Yellow Wagtail and Tree Sparrow), wheat (Turtle Dove and Corn Bunting) had decreased and cattle numbers (Lapwing) had increased most in these areas (Fig. 3).

3.3. Species distributions in relation to PCA axes

Over the whole of England and Wales, the first PCA axis (PRIN1) was selected for each species (Table 5). This showed that generally, species tended to be lost from 10 km squares that had increased in grass and barley and decreased or changed little in other crops such as wheat and oilseed rape which had a large influence on PRIN1 (positive PCA scores on Fig. 2), and tended to be retained in 10 km squares that had increased in the area of rape and wheat and decreased in the area of barley and grass (negative PCA scores). However, other variables, including woodland area (Grey Partridge and Tree Sparrow), original land-use diversity (Corn Bunting), change in land-use diversity (Lapwing) and altitude (Reed Bunting) were better predictors of local extinction than PCA axes. In both mixed and pastoral regions, PRIN1 was also selected in each species (Table 5), using PCA axes derived separately for each region. In the arable region, however, lesser PCA axes were better predictors of local extinction. PRIN3, which was mainly associated with grassland and potato area, was selected for Grey Partridge, Turtle Dove and Reed Bunting, implying that these species were more likely to have been lost in 10 km squares that had increased in grass area and cattle numbers. Yellow Wagtail showed a negative association with PRIN2, implying local extinction was lower in 10 km squares that have increased most in total agricultural area, total tilled area and sugar beet area. No significant effects of PCA axes were detected in Lapwing or Tree Sparrow.

3.4. Species richness and agricultural land-use

The land-use variables that showed the best fit (the highest r^2 value) to change in species richness between the two atlas surveys are shown in Table 6. For all farmland 10 km squares in England and Wales, the area of potatoes was the variable most closely associated with total species loss, with local extinction increasing in 10 km squares in East Yorkshire, Lincolnshire, The Fens and eastern East Anglia, which had decreased the most in potato area. In regional terms, species loss was higher in the arable region which had changed most in orchards and fruit and in the mixed region which had decreased in cattle. However, species loss was more closely associated with smaller areas of woodland and larger areas of suburban land, respectively. Species richness in the pastoral region tended to decline more in 10 km squares of lower altitude. When considering the 21 target species only, species loss was closely associated with areas of little change in oilseed rape (all 10 km squares and the mixed region) and bare fallow (pastoral region) and larger areas of woodland (arable region). Note that this latter result contradicts that for all species in the same region.

When PCA axes were used instead of individual variables of change, PRIN1 was selected in most cases, with loss of all species and target species increasing in 10 km squares that had undergone relatively little change in cropping for all squares and for mixed and pastoral regions. However, non-agricultural variables were more closely correlated with the change in total species. In the arable region, total species loss was positively associated with PRIN3, indicating increased local extinctions in 10 km squares that have lost most grass and increased in the area of potatoes. Local extinction of target species in this region increased in 10 km squares with a larger area of woodland, but were not significantly related to any PCA axis.

4. Discussion

Generally, the individual species considered showed similar patterns of decline. Arable-dominated 10 km squares that had generally increased in oilseed rape and decreased in barley were more likely to retain species, and pastoral 10 km squares that had generally changed little in wheat and rape (typically from very low initial levels), but that had increased in the area of barley and improved grass were more likely to have lost species. These variables had a large influence on the first axis derived from PCA, and this was significantly related to the probability of local extinction over all 10 km squares in each of the seven species considered. Relationships between specific agricultural change variables and local extinction showed the same general patterns, with the probability of local extinction being associated with agricultural variables that showed strong regional trends. Species richness also showed similar general relationships, reflecting similar geographical patterns of change to individual species.

Whether any of these associations represented causal relationships seems doubtful as in the majority of cases it was difficult to envisage how selected variables could have affected change in species' distributions, given previous knowledge of habitat associations and the ecology of the species involved. It seems most likely that closely correlated variables were selected that may have been merely representative of the wider pattern of decline, or the variables selected in the analysis may have been substituting for closely correlated variables that we could not estimate at the 10 km level. The main exception to this was the Lapwing and its associations with grassland habitat. Local extinction of this species was associated with increases in cattle (all 10 km squares and the pastoral region) and decreases in rough grazing (arable region). Increasing disturbance, nest destruction and creation of less suitable habitat due to higher stocking rates have been suggested as possible reasons for the decline of the Lapwing, as has the 'improvement' of pasture land and consequent loss of rough grazing (Shrubb, 1990; Hudson et al., 1994).

In many cases, variables describing change in individual crop or livestock components were less closely associated with local extinction than other variables describing non-agricultural habitat. Larger areas of woodland in particular tended to increase the probability of local extinction from a 10 km square in a number of species. Similarly, species tended to be lost from 10 km squares at higher altitude and with a lower original diversity of farm land-use. All of these variables still tended to show similar geographical patterns to those agricultural variables selected in other models. Loss of land-use diversity was associated with increased local extinction rates in a number of species. This has been a potential factor in species declines, including the Lapwing (Hudson et al., 1994), but change in diversity was typically not the variable most closely associated with local extinction, and tended to be selected only in comparison with PCA axes (Table 5).

The majority of species considered in this analysis are closely associated with lowland farmland, particularly arable and mixed farms (O'Connor and Shrubb, 1986), the most notable exception being the Lapwing, which is a common (but declining) breeder in pastoral farmland in marginal uplands (Hudson et al., 1994). This was the only species where individual agricultural change variables were consistently more closely associated with local extinction than non-agricultural land-use variables across all regions. Aside from Lapwing, the associations between broad land-use and local extinction may indicate that local extinctions occurred in generally less favoured habitat, characterized by pastoral farming, relatively high altitude, large areas of woodland and low land-use diversity. This contention is supported by Gates and Donald (1999), who found that species tended to be lost from 10 km squares that were more similar to 10 km squares where they had never been recorded, than to those where they were retained.

When analysing atlas data in relation to land-use change, the scale of the analysis should be appropriate to the issues being addressed (Donald and Fuller, 1998). This study has considered bird declines at a fairly coarse scale. Analyses of declines at smaller sampling units have revealed that many species are undergoing significant population changes (Siriwardena et al., 1998), yet few species have disappeared from more than a few percent of 10 km squares, so the present analysis can only consider the most severely declining species. At this level, the land-use data can detect only very broad-scale relationships with land-use area and livestock number, thus factors that operate at a finer scale will not be detected. There were also a number of potentially important variables that were not available at the 10 km square level. For example: there was no information on spring-sown crops in the early period that are potentially important breeding habitat for Lapwing (Hudson et al., 1994) and winter habitat in the form of stubbles for granivorous species Tree Sparrow, Corn Bunting and Reed Bunting (Wilson et al., 1996); no information on the management of grassland (e.g. for silage or hay) which may affect ground nesting species, particularly Lapwing (Shrubb, 1990); and, no information on changes in hedgerow length, which may be important nesting habitats for Tree Sparrow and Reed Bunting (Lack, 1992; Green et al., 1994).

It is possible that range contraction recorded in atlas surveys may not be associated with changes in the immediate habitat, but is affected by land-use changes in other areas where the species persists (Donald and Fuller, 1998). This could arise through source-sink effects, where habitat changes in the source population result in lower productivity that has subsequent effects on the size of sink populations in less favoured habitats (Pulliam, 1988). In a number of species considered here, there were indications that local extinctions occurred in 10 km squares that were predominantly pastoral, relatively well wooded and of a higher altitude. It is possible that for species that are known to prefer lowland arable landscapes such as Corn Bunting (Donald et al., 1994) and Grey Partridge (Potts, 1986), these local extinctions represent source-sink effects. Gates and Donald (1999) also suggested that local extinctions occurred in less suitable habitats in a number of species. However, there is as yet little evidence for source-sink effects in any bird species and such effects would be extremely difficult to prove (Pulliam, 1988; Watkinson and Sutherland, 1995).

The analyses of the change in both the distribution of individual species and of species richness (particularly of the target species) have shown that reductions in range had occurred most frequently in non-arable (i.e. grass-dominated) regions. This appears to conflict with the hypothesis that recent declines in farmland birds are linked to the increased intensification of arable farmland (Fuller et al., 1995). Many species that we have considered appear to occur at lower densities in non-arable regions, and may be at the edge of their geographical range, especially in predominantly pastoral counties (Gibbons et al., 1993). If densities have declined by similar amounts throughout the whole region, then those squares with initially low density are more likely to lose species than those of high density, thus species may be more likely to be lost at the edge of their range. Analysis of annual bird abundance data show that generally, species have decreased in density by similar proportions in arable and non-arable (particularly mixed) regions (Chamberlain et al., 1999), yet absolute losses from 10 km squares differ, so an edge of range effect seems plausible.

5. Conclusions

The majority of relationships between local extinction and change in individual agricultural variables were unlikely to represent causal relationships, with the possible exception of Lapwing which was consistently related to variables associated with grassland management. However, local extinctions tended to occur in regions of similar agricultural change, probability of loss in all species being related to a PCA axis that represented a polarization of farming, with increases in livestock, grass and barley in the west and increases in wheat, oilseed rape and vegetables in the east. The greater local extinction rates in western England and Wales raise some interesting questions. If arable intensification has had a major impact on bird populations as suggested by a number of authors (O'Connor and Shrubb, 1986; Fuller et al., 1995; Chamberlain et al., 1999), then why are local extinctions prominent in areas of predominantly pastoral agriculture? The answer may lie in source-sink effects, as sink populations are likely to be characterised by lower densities (e.g. Krebs, 1971). Alternatively, these general patterns of change may be associated with agricultural and non-agricultural factors that were not addressed in this study. For example, the data considered here had much detail on land-use associated with arable farmland, but relatively little on grassland management components that could be potentially crucial, such as the amount of silage grass compared to hay or pasture. In comparison with arable farms, the factors affecting bird populations on pastoral farms are poorly understood, and this is an area in which further research would contribute greatly to our understanding of the patterns of decline in species distributions and species richness.

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