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# Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales

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# **Summary**

- 1. Over the past three decades changes in agricultural management have resulted in increased crop and grass production. This intensification has been accompanied by population declines among farmland bird species and a decline in farmland biodiversity. We have analysed trends in agricultural management in order to quantify the degree of intensification, and have considered how they match change in the farmland bird community.
- 2. Changes in agriculture through time (1962–95) were examined quantitatively for 31 variables representing crop areas, livestock numbers, fertilizer application, grass production and pesticide use. The majority were highly intercorrelated because factors facilitating intensification simultaneously affected many management activities.
- **3.** Change in agriculture was measured using detrended correspondence analysis (DCA). The period 1970–88 saw most intensification, characterized by increases in the area of oilseed rape, autumn-sown cereals, and the use of pesticides and inorganic fertilizers. Spring-sown cereals, bare fallow and root crops declined.
- **4.** Indices of relative population change between 1962 and 1996 were determined for 29 bird species using data from Common Birds Census (CBC) plots on farmland in England and Wales. Principal components analysis (PCA) described a gradient from species that had declined most to those that had increased.
- 5. The ordinations of agricultural change and bird population change were broadly matching but with a time lag in the response of birds. The most accurately measured agricultural variables for the period 1974–91 matched the changes in farmland birds more closely.
- 6. We conclude that large shifts in agricultural management are a plausible explanation for the declines in farmland bird populations. We propose a threshold model relating to critical amounts of high-quality habitat or food resources that may be relevant in explaining the lag in response of birds, and propose it should be taken into account in predicting the effects of future agri-environment schemes. Identifying individual factors responsible for bird declines is not possible without detailed experimental work because many components of intensification are interdependent. Birds may be responding to a suite of interacting factors rather individual aspects of farm management. Holistic conservation strategy that encourages general extensification of farming practices will be most likely to benefit farmland bird communities.

Key-words: Common Birds Census, DCA, farm management, PCA, population declines.

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There have been great changes in the management of farmland in England and Wales over the last few decades. These changes have affected all aspects of the farmed landscape. Crop management and the type and relative abundance of different crops has changed markedly; grassland management has shifted away from hay to silage systems; chemical inputs on farmland have increased substantially; the timing of farming operations has changed; non-crop habitats such as hedgerows and farm ponds have been reduced; and there has been a reduction in the diversity of different types of agriculture per individual farm, with farms tending to specialize in either arable or livestock (O'Connor & Shrubb 1986; Grigg 1989; Stoate 1996). This 'intensification' of farmland has led to greatly increased yields. For example, wheat yields increased by 66% between 1970 and 1990 [Ministry of Agriculture, Fisheries and Food (MAFF), unpublished data]. Other crops and grass have shown similar increases in yield over the same period. Developments in farming technology in terms of machinery, development of new crop strains and development of pesticides and fertilizers, have probably been the main underlying causes behind the increased yields, although both social and economic factors have also contributed (Grigg 1989).

The coincidence of this period of intensification of farm management and the decline of many farmland bird species has led to suggestions of a causal link between the two (Fuller et al. 1995). The temporal relationship between changes in farming practices and changes in bird populations has not, however, been examined previously in a quantitative manner for the majority of farmland species. The proposed mechanisms by which agricultural changes in management have affected bird populations are diverse, but generally concern diminished food supplies (Potts 1986; Campbell et al. 1997; Evans et al. 1997; Brickle et al. 2000), less suitable nesting habitat (Wilson et al. 1997; Chamberlain et al. 1999) or direct mortality of birds by farming operations (Crick et al. 1994; Green 1995). Several studies indicate that there is an association between agricultural management and changes in bird populations. A number of these studies have considered differences in regional and habitat-specific population trends. For example, population declines of skylarks *Alauda* arvensis L. have been steepest in agricultural compared with upland and coastal landscapes (Chamberlain & Crick 1999), granivorous birds have declined most in arable farmland (Marchant & Gregory 1994), but corvids have increased the most on pastoral and mixed farmland (Gregory & Marchant 1996). Also, Donald (1997) found change in the relative population size of corn buntings Miliaria calandra L. to be correlated significantly with annual

variation in a number of agricultural variables which themselves were often intercorrelated.

Other potential causes of the population declines have been proposed, for example disease, climate and predation (Fuller *et al.* 1995). There is no evidence for disease causing long-term bird population change in the UK. Climate, however, has been shown to cause short-term changes in bird population size. For example, Baillie (1990) found that much variation in relative population change of a resident passerine, the song thrush *Turdus philomelos* L., could be explained by the number of freezing days in the preceding winter, although this effect was not sufficient to explain the most recent declines.

A number of predatory bird species have increased on farmland in recent years (Newton 1986; Gregory & Marchant 1996). There is evidence that breeding populations of game birds can be affected by predator numbers (Redpath & Thirgood 1997; Tapper, Potts & Brockless 1996), but there is little evidence to suggest that increased numbers of sparrowhawks *Accipiter nisus* L. (Newton 1993; Thomson *et al.* 1998) or magpies *Pica pica* L. (Gooch, Baillie & Birkhead 1991) affect breeding numbers of passerines.

Although the timing of the onset of population declines of a number of bird species has been examined in detail (Siriwardena *et al.* 1998), there has been no comparable examination of the detailed changes in agricultural practices. In this paper, we present a review of the main changes in agricultural management that have occurred over the past four decades. We examine the evidence that changes in bird abundance have coincided with changes in agricultural management by using ordination techniques to identify patterns of change in both bird abundance and agricultural management data. These analyses demonstrate the pattern of temporal association between bird population change and agricultural intensification.

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### Methods

#### HABITAT DATA

Annual changes in agricultural variables were derived from a number of sources: county-level summaries of MAFF June Census data; MAFF pesticide usage survey reports (Thomas 1997); Institute of Terrestrial Ecology (ITE)/Agricultural Development Advisory Service (ADAS) review of agricultural management (Wilkinson 1997); ADAS British Survey of Fertilizer Practice; and data presented by O'Connor & Shrubb (1986). The variables that were considered, the years from which data were available, data sources and abbreviations used in subsequent analyses are shown in Table 1. For some potentially important variables (e.g. areas of hay,

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**Table 1.** Agricultural variables considered in the analyses of annual changes. Data are for England and Wales unless stated. Sources: MAFF<sup>1</sup>, June census data adapted from parish summaries, provided by the University of Edinburgh Data Library; MAFF<sup>2</sup>, pesticide usage survey reports (e.g. Thomas 1997); ITE, review of agricultural management (Wilkinson 1997); ADAS, British Survey of Fertilizer Practice; O&S, O'Connor & Shrubb (1986). †Data for whole UK; other data are for England and Wales

Variable	Years available	Source	Units
Bare fallow	1962–92	MAFF <sup>1</sup>	Area
Barley (total)	1962–92	$\mathrm{MAFF}^1$	Area
Barley (autumn-sown)	1962, 67, 69, 74–92, 94	$\mathrm{MAFF}^1$	Area
Barley (spring-sown)	1962, 67, 69, 74–92, 94	$\mathrm{MAFF}^1$	Area
Cattle	1977–86, 88	$\mathrm{MAFF}^1$	Total cattle + calves
Fertilizer application	1970–94	ITE	kg ha <sup>-1</sup>
Mown grass production†	1970-89	ITE	Tonnes dry matter
Permanent grass (> 5 or 7- years old)	1962–92	$\mathrm{MAFF}^1$	Area
Hay production†	1970–89	ITE	Tonnes dry matter
New grass (< 5 or 7-years old)	1962–92	$\mathrm{MAFF}^1$	Area
Linseed†	1989–95	$\mathrm{MAFF}^1$	Area
Oats	1962–92 (not 88)	$\mathrm{MAFF}^1$	Area
Oilseed rape	1962–92	$\mathrm{MAFF}^1$	Area
Rough grazing	1962–92	$\mathrm{MAFF}^1$	Area
Set-aside†	1989–95	$\mathrm{MAFF}^1$	Area
Sheep	1969, 77–92 (not 88)	$\mathrm{MAFF}^1$	Total ewes + lambs
Silage production†	1970–89	ITE	Tonnes
Slurry application	1969–91, 93 (not 86)	ADAS	Area
Potato	1962–92	$MAFF^1$	Area
Sugar beet	1962–92	$\mathrm{MAFF}^1$	Area
Total tilled land	1962–92	$MAFF^1$	Area
Turnip and swede	1962–92	$\mathrm{MAFF}^1$	Area
Wheat (total)	1962–92	$\mathrm{MAFF}^1$	Area
Wheat (autumn-sown)	1962, 67, 69, 74, 78, 82, 87, 94	$\mathrm{MAFF}^1$	Area
Wheat (spring-sown)	1962, 67, 69, 74, 78, 82, 87, 94	$\mathrm{MAFF}^1$	Area
Fungicides (total)	1974, 77, 82, 88, 90, 92, 94	$MAFF^2$	Spray hectares
Herbicides (total)	1974, 77, 82, 88, 90, 92, 94	$MAFF^2$	Spray hectares
Herbicides on cereals (pre-emergent)†	1960, 65, 70, 75, 80, 85	O & S	No. of chemicals
Herbicides on cereals (post-emergent)†	1960, 65, 70, 75, 80, 85	O & S	No. of chemicals
Insecticides (total)	1974, 77, 82, 88, 90, 92, 94	$MAFF^2$	Spray hectares
Seed dressings on cereals	1974, 77, 82, 88, 90, 92, 94	$MAFF^2$	Spray hectares

silage, stubbles and undersown cereals) no data sources were found. Data were obtained for England and Wales where possible to match up with the bird data (see below), although in some cases it was only possible to obtain data from the whole of the UK. In these cases, we assume that temporal changes show similar patterns in England and Wales to those from the whole UK, which was the case in a number of variables where data were available at both scales (e.g. similar percentage changes between 1970 and 1995).

### BIRD DATA

The Common Birds Census (CBC) is a long-term monitoring scheme, running since 1962, that provides estimates of annual population change for a large number of British bird species (Marchant *et al.* 1990). This scheme has, above all others, been responsible for drawing attention to the population declines of several farmland bird species (Fuller *et al.* 1995; Siriwardena *et al.* 1998). Estimates of relative

population change and change in breeding density were derived from CBC data for 29 selected species. Farmland CBC sites are not randomly distributed throughout the country, but show a south-eastern bias, so indices derived at the national level tend to be most representative of lowland habitats and predominantly arable farmland (Fuller, Marchant & Morgan 1985). Data were derived from lowland farmland CBC sites in England and Wales, the region and habitat of which CBC plots are most representative. The 29 species were identified by Fuller et al. (1995) as either farmland specialists or woodland generalists which commonly use farmland. The species, their population status and their predominant habitat according to Fuller et al. (1995) are shown in Table 2. Certain farmland species, although of great conservation concern, were too rare for any valid analysis (e.g. stone curlew Burhinus oedicnemus L. and cirl bunting Emberiza cirlus L.). Some common farmland species that are poorly censused were also not considered (e.g. pheasant Phasianus colchicus L., woodpigeon Columba

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**Table 2.** Species considered in the analysis. Population trends between 1969 and 1995 are based on the British Trust for Ornithology Alert Limit system (Crick *et al.* 1998) for decreasing species and significance tests in Siriwardena *et al.* (1998) for increasing species. Habitat is based on Fuller *et al.* (1995), where F = farmland specialist, W = primarily woodland species that commonly use farmland

Species	Population trend	Habitat
Kestrel Falco tinnunculus L.	Small decline	F
Grey partridge <i>Perdix perdix</i> L.	Severe decline	F
Lapwing Vanellus vanellus L.	Small decline	F
Turtle dove Streptopelia turtur L.	Severe decline	F
Stock dove Columba oenas L.	Increase	F
Skylark Alauda arvensis L.	Severe decline	F
Yellow wagtail Motacilla flava L.	Stable	F
Starling Sturnus vulgaris L.	Small decline	F
Jackdaw Corvus monedula L.	Increase	F
Rook C. frugilegus L.	Increase	F
Wren Troglodytes troglodytes L.	Stable	$\mathbf{W}$
Dunnock Prunella modularis L.	Small decline	$\mathbf{W}$
Whitethroat Sylvia communis L.	Stable	F
Latham Lesser whitethroat S. curruca Latham	Stable	$\mathbf{W}$
Robin Erithacus rubecula L.	Stable	$\mathbf{W}$
Blackbird Turdus merula L.	Small decline	$\mathbf{W}$
Song thrush <i>T. philomelos</i> L.	Severe decline	$\mathbf{W}$
Blue tit Parus caeruleus L.	Stable	$\mathbf{W}$
Great tit P. major L.	Stable	$\mathbf{W}$
Long-tailed tit Aegithalos caudatus L.	Stable	$\mathbf{W}$
Tree sparrow Passer montanus L.	Severe decline	F
Chaffinch Fringella coelebs L.	Increase	$\mathbf{W}$
Greenfinch Carduelis chloris L.	Stable	F
Goldfinch C. carduelis L.	Small decline	F
Linnet C. cannabina L.	Severe decline	F
Bullfinch Pyrrhula pyrrhula L.	Severe decline	$\mathbf{W}$
Corn bunting Miliaria calandra L.	Severe decline	F
Reed bunting Emberiza schoeniclus L.	Severe decline	F
Yellowhammer E. citrinella L.	Stable	F

palumbus L. and house sparrow Passer domesticus L.). Full CBC survey methods can be found in Marchant et al. (1990). The data were used primarily to calculate population indices, which reveal relative changes from year to year, hence providing an estimate of population change. Indices were determined from between 60 and 127 CBC farmland plots per year.

# ANALYSIS

For annual agricultural variables, data were obtained between 1962 and 1995 where possible, but in a number of cases data were available only for intermittent years within this period. For these variables, missing values were interpolated from a straight line drawn between years with actual data up to 1995. Data on the area of permanent grassland (at least n years old) and new grassland (seeded or reseeded within the previous n years) were a particular problem as the definition changed in 1974 from n=7 to n=5. In order to produce a run of

values, the difference between the means of the earlier and the later grassland definition was added onto every value after 1974 as a correction factor. We assume that the pattern of change is a good reflection of trends in grassland but acknowledge that the actual figures presented should not be taken as absolute values.

Many of the agricultural variables considered were strongly correlated with one another, which made interpretation of relationships between individual variables and bird abundance difficult. Therefore, we examined general gradients of agricultural change to allow an assessment of features that most strongly characterize those gradients. Agricultural variables were analysed by two ordination techniques: variables defined into categories were analysed using detrended correspondence analysis (DCA), and continuous variables using principal components analysis (PCA). For the DCA, underlying trends were identified using a smoothing procedure that uses a 4235H-twice running median (Velleman & Hoaglin 1981). Using the smoothing technique

allows the determination of continuous underlying temporal trends and has the advantage of few assumptions compared with alternative parametric methods. For each variable separately, annual values (including estimated values) were ranked across years and then divided equally into three groups of relatively high, medium and low ranks. These ranked groups were then recorded as attributes that were present or absent for each year and ordinated using DCA with the program DEC-ORANA (Hill 1979). Thus the data could be summarized in terms of attribute scores over years, giving an index of agricultural change. In this way, the category of the value rather than the actual value is important, so it matters less that certain values were estimated.

For the PCA, variables with a large number of interpolated values (more than 2) were dropped from the analysis, so only variables with a continuous run of several years of actual data were considered. The majority of variables had generally poor data for both the earliest and latest years, so the analysis was carried out only on data between 1974 and 1991. PCA was carried out using the correlation matrix of (unsmoothed) variables, enabling variables measured on different scales to be included on the same axis (James & McCulloch 1990). Due to the 'gappiness' of the data, it was not possible to disregard all interpolated values in this analysis as this would have made the sample sizes small and, more seriously, would have meant that a number of important variables (especially autumn- and springsown barley) would not have been considered.

CBC population indices were determined using log-linear Poisson regression, modelling logarithms of bird counts using the software TRIM (ter Braak et al. 1994; Pannekoek & van Strien 1996). The model incorporated individual site and year effects, which revealed year-to-year changes in CBC index. Detailed patterns of change in CBC index are presented in Fuller et al. (1995) and Siriwardena et al. (1998). Model fit was examined using maximum likelihood methods, testing whether annual changes are homogeneous across sites (using likelihood ratio tests). Indices derived using the model incorporating site and year effects were analysed individually in relation to agricultural variables and by using PCA on a matrix of species index by year between 1962 and 1996. Use of PCA enabled the identification of general patterns of change within the farmland bird community.

General effects of agricultural change on bird populations were considered using axes of environmental variation from DCA and PCA. Principal axes derived from CBC indices (referred to as BIRDPCA) were plotted against axes of environmental variation derived from DCA and PCA of agricultural statistics (referred to as HABDCA and HABPCA, respectively) in order to identify coinci-

dence in general patterns of change in bird abundances and agricultural management.

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### Results

CHANGES IN AGRICULTURAL MANAGEMENT

Smoothed trends for 31 agricultural variables are shown in Fig. 1. The area of tilled land has increased by almost one million hectares since the early 1960s (Fig. 1a). There has been a slight decline recently, however, that may have been partly due to the introduction of set-aside (Fig. 1b). There have been substantial increases in wheat, oilseed rape and sugar beet, and decreases in oats, barley, potatoes, other root crops (turnips and swedes) and bare fallow (Fig. 1c-j), the latter two reflecting changes in crop rotations. A former feature of arable rotations was root crops, which had the function of cleaning the soil of weeds. This is no longer necessary with the development of pre-emergent herbicides (see below), and also the main use for the root crop as fodder no longer exists. Oilseed rape has replaced both of these crops in a typical rotation. We could find only recent data on the area of linseed, but we know that this crop has increased substantially since the late 1980s as it has become a more profitable industrial crop and also because it is often sown as a cover crop within the set-aside scheme. We thus assume that the increase in linseed has followed the trend for set-aside (Fig. 1k), although there will have been very small amounts grown prior to this.

Within cereal crops, there have been changes in the timing of sowing. The area of wheat and barley sown in the autumn increased substantially from the mid-1970s, with spring-sown cereals showing concomitant decreases in area (Fig. 11-o). One consequence of this is the decrease of winter stubble. Previously, a large proportion of harvested fields would have been ploughed and left until the spring. In some cases the stubble was left over winter to be ploughed in before planting the next crop. Undersowing of grass or clover was also a widespread practice that has declined with the increase in autumn sowing and the increasing separation of arable and pastoral enterprises. The majority of the wheat crop has been sown in the autumn since at least the early 1960s. By the mid-1980s, virtually all wheat was autumn-sown and currently less than 1% is sown in the spring. Spring-sown barley is still relatively common, accounting for 28% of the barley acreage in 1994 (MAFF, unpublished data).

Improved permanent and temporary grassland and rough grazing have all declined since the 1960s (Fig. 1p–r). However, the figures for total grass area are misleading because trends vary regionally, grass having decreased in arable regions and increased in pastoral regions due to a decrease in fodder crops

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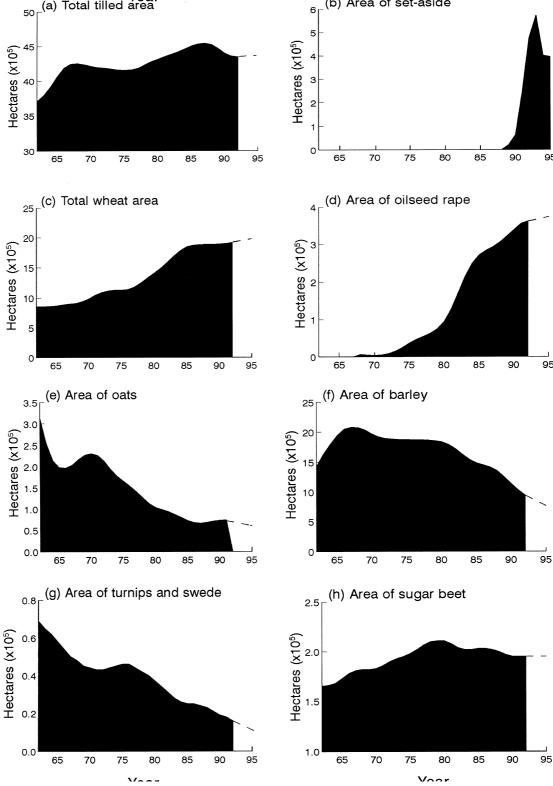


Fig. 1. Trends in agricultural variables for the whole of England and Wales or the whole UK (see Table 1 for variable definitions). Variables with continuous runs of annual data have been smoothed to reveal underlying trends. Solid black shading indicates annual smoothed data. Single lines joining crosses indicate data from intermittent years. Dashed lines indicate interpolated/extrapolated data.

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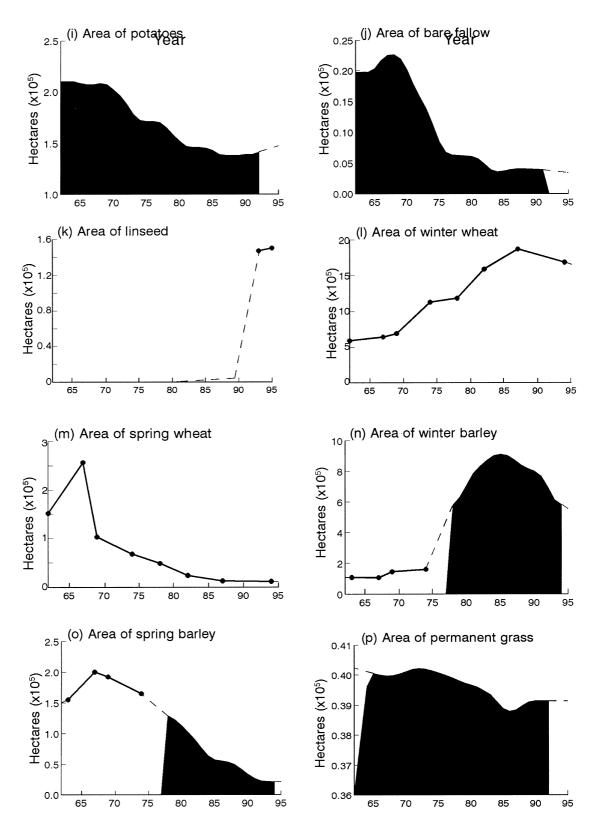


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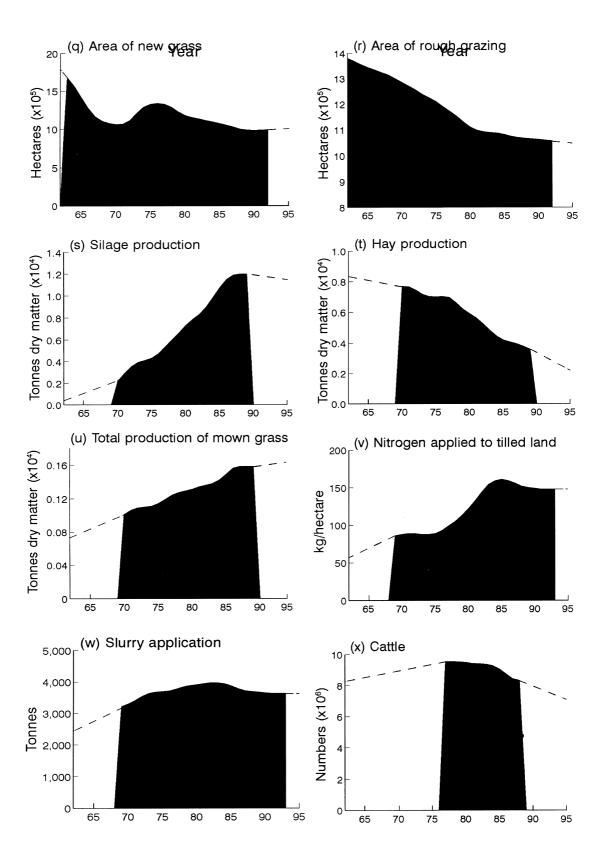


Fig. 1. continued.

and the conversion of marginal land to permanent improved pasture (Chamberlain & Fuller 2000). The decline of temporary grass has arisen due to the decline of traditional rotational and mixed farming systems and the increasingly widespread adoption of continuous tillage cropping. The type of temporary grass has also changed. In the late 1940s much would have been 1-year clover leys, but by the early

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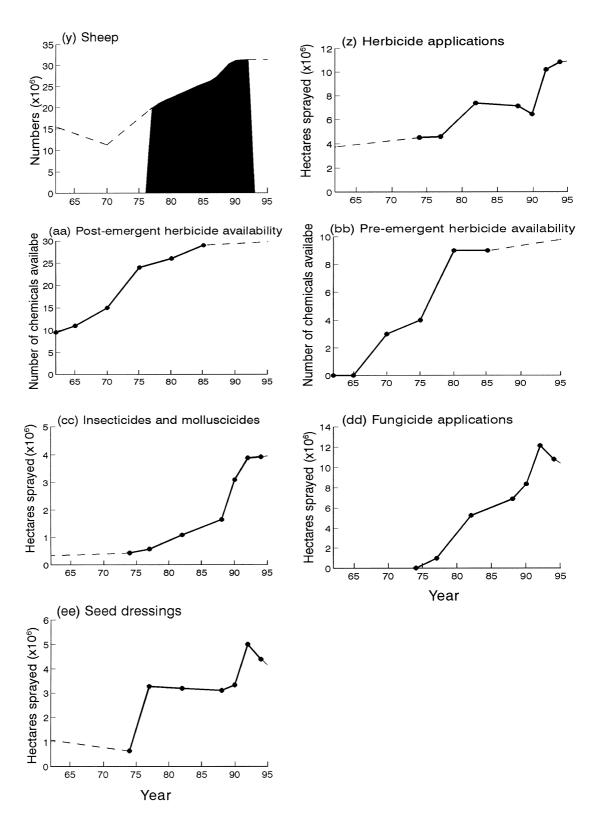


Fig. 1. continued.

1980s clover ley accounted for less than 1% of the area of all temporary grassland (O'Connor & Shrubb 1986). One of the main changes to have occurred in the post-war management of grassland has been the replacement of traditional hay meadows with grass grown for silage (Fig. 1s–t). Wide-

spread adoption of silage occurred from the 1960s onwards and by the 1980s this was the dominant form of grass feed production in the UK (Wilkinson 1997). Silage grass is often cut two or more times in a season compared with the single late cut of hay, and is typically cut too early for grass seed to set.

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The multiple cut of silage leads to increased yields over hay which has resulted in a great increase in grass yields (Fig. 1u).

Many changes in grass and crop management have been facilitated by increases in both artificial fertilizer and slurry inputs (Fig. 1v-w). Inorganic fertilizers have replaced farmyard manure as the major source of plant nutrients supplied to crops and grass. The development of concentrated artificial fertilizers has meant a much faster and easier application: 1 ton of inorganic fertilizer contains as much nutrient as 25 tons of manure (Grigg 1989). Although the majority of plant nutrients is now provided by artificial means, a large proportion (up to 25%) still comes from animal dung, in the form of either manure or slurry, particularly in grassland enterprises (Grigg 1989).

Since the 1970s there has been a decrease in cattle numbers (Fig. 1x), partly due to European Community (EC) dairy quotas, but probably also due to changing land use including the decline of mixed farming. This has been facilitated by the fact that farms no longer need to produce their own farmyard manure due to the use of chemical fertilizers. In the 1960s and early 1970s sheep numbers fell in central and eastern England due to the intensification of cereal farming, but since then there have been increases in both lowland and upland England and Wales (Fig. 1y). To some extent this may have been due to grassland improvement (e.g. drainage and reseeding), but the main reason is likely to be economic, the start of the increase in the mid-1970s coinciding with the introduction of the Hill Livestock Compensation Allowance. The figure presented may be misleading in the context of this analysis as these figures include uplands where increases have been much greater than on lowland farmland (Fuller & Gough 1999). Given that grass area is generally decreasing, there is likely to have been an even larger increase in the density of sheep (although this is not possible to determine accurately with MAFF statistics).

The area treated with all types of pesticide (herbicides, insecticides, molluscicides, fungicides and seed dressings) has increased since the early 1970s (Fig. 1z-ee). A further factor to consider is the increase in the diversity of chemicals, the number of different formulations on the official Agricultural Chemicals Approval Scheme list rising from 37 in 1955 to 199 in 1985 (O'Connor & Shrubb 1986). In the 1950s herbicides would have been mainly post-emergent, particularly acting on broad-leaved weeds in cereals. The development of pre-emergent and grass herbicides has been very important in facilitating changes in cropping practice, particularly the widespread adoption of autumn sowing. Grass weeds in particular are an obstacle to continuous cereal cropping and were previously dealt with by the two periods of cultivation per season experienced in rotation, when

grass that had germinated over winter was ploughed in before spring sowing. Pre-emergent herbicides remove competitive weeds and grasses at crop establishment and so have led to a serious reduction in their ability to set seed.

Several of the variables in Fig. 1 have shown similar trends or opposing trends over time and there was a high degree of collinearity in the data, with many variables significantly correlated with many others (Table 3), so changes in different aspects of agricultural management have tended to occur at the same time. A noticeable aspect of intensification is that changes are often closely interlinked. For example, technological advances in pesticides and fertilizers have facilitated changes in sowing regimes and, subsequently, changes in harvesting times and decreases in winter stubbles. Similarly, these developments have facilitated the polarization of British farmland into either pastoral or arable enterprises, as necessary resources that were previously produced on the farm itself (e.g. farmyard manure needed for arable crops, or cereals needed for animal feed) can now be supplied in artificial form (Grigg 1989).

### ORDINATION OF AGRICULTURAL DATA

DCA of temporal change in agricultural variables grouped into high, medium and low categories produced one strongly dominant axis that accounted for 82% of variation in the data (Table 4). At one end of this axis is a mixture of factors with low scores early in the time period in question (e.g. permanent grass, herbicides and winter cereals) and those with high scores at that time (e.g. spring wheat and hay production); at the other end are factors with low scores late in the time period (e.g. cattle, new grass and potatoes) and those with high scores then (e.g. oilseed rape, fungicide and silage production). Thus this axis summarizes the longterm trends in agricultural change, and the high proportion of the variance it explains confirms how coincident the various changes have been. HABDCA scores increased most rapidly between 1970 and 1988 (Fig. 2), the period when variables with the greatest effect on the axis were changing the most; 1962-70 and 1988-95 were periods of little change, especially in variables with most influence on the axis.

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The above analysis was fairly simple in that it used categorical data based on ranks and had some variables (mostly pesticide data) where many values were estimated. A further, more rigorous, analysis using actual data was performed using PCA, considering only variables with a continuous run of smoothed data values and a maximum of two interpolated values from 1974 to 1991 (Table 5). The first axis explained 76% of variation in the data and represented a gradient from variables that had

Table 3. Correlation matrix of annual agricultural variables between 1962 and 1996 (defined in Table 2). Only years where actual data were available for each variable were used (i.e. no interpolated values).

	Barley	Barley Fertilizer	Permanent grass	New grass	Hay	Oats	Oilseed rape	Potatoes	Rough grazing	Root	Spring barley	Sheep	Silage	Slurry	Sugar beet	Winter barley	Wheat
Bare fallow	+++++		+++++	+	+++++	++		+++	++++++	+++++	+++++++++++++++++++++++++++++++++++++++				SZ	}	
Barlev	-		- +	+++++++++++++++++++++++++++++++++++++++	+++++++++++++++++++++++++++++++++++++++	+		+ + +	- + - +	+++++++++++++++++++++++++++++++++++++++	- + - +				SZ		
Fertilizer			-	:	-	.	+++++	-	-	-	:	++++	++++	: +	SZ	+++++	++++
Permanent grass				+	++++	+		+	++	+++	+++				SZ	-	
New grass					++++	SZ		+	+	++++	++				SZ	1	
Hay						++++		++++	++++	++++	++++				SN		
Oats								++++	++++	+++	++++						
Oilseed rape												++++	++++		SN	++++	+ + +
Potatoes									++++	++++	+++				1		
Rough grazing										++++	++++				1		
Root crops											++++	-			SZ		
Spring barley															SZ		
Sheep													++++		SZ	++++	+++
Silage															SZ	+++	++++
Slurry															++++	++	SZ
Sugar beet																+	SZ
Winter barley																	+ + +

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**Table 4.** Analysis of temporal change in agriculture by detrended correspondence analysis (DCA) scores of agricultural variables, showing only the 15 highest and lowest ranked variables on axis 1. Each variable has high, medium or low categories and has the prefixes H, M or L, respectively. A total of 93 variables (31 variables each with high, medium and low categories) was considered in the analysis

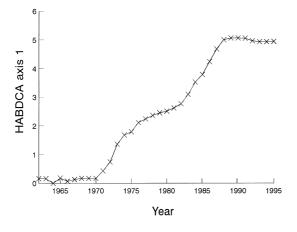
Low rank variables	DCA score (axis 1)	High rank variables	DCA score (axis 1)
L grass	-0.76	H insecticide	5.66
L post-emergent herbicide	-0.75	H silage production	5.66
L winter barley	-0.66	L potatoes	5.66
L winter wheat	-0.66	H set-aside	5.71
H spring wheat	-0.66	H linseed	5.71
H rough grazing	-0.52	L total barley	5.82
H oats	-0.52	L new grass	5.82
H hay production	-0.52	H total wheat	5.82
L grass production	-0.52	M set-aside	5.86
L sugar beet	-0.52	H fungicide	5.88
L pre-emergent herbicide	-0.50	L cattle numbers	5.89
L fertilizer application	-0.42	H oilseed rape	5.89
L slurry application	-0.26	M linseed	5.94
L sheep numbers	-0.20	L linseed	6.05
L seed dressing	0.29	L set-aside	6.05

shown rapid rises in more recent years, especially wheat, oilseed rape, sheep numbers, silage production and artificial fertilizer application, to variables that had shown a rapid decrease over the same period, such as spring barley, rough grazing, hay production and root crops (Table 5). The second axis explained 11% of variation in the data and was harder to interpret, but was dominated by sugar beet area and slurry application rates, which have shown fairly steady rates of change over time. A plot of axis 1 against year revealed similar patterns to that shown for HABDCA axis scores, with the period of greatest change between 1975 and 1986 for those variables having the greatest influence on

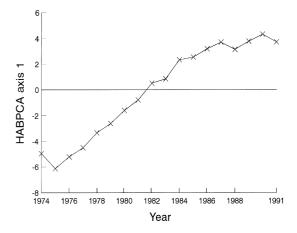
the gradient (Fig. 3). However, this pattern was more linear in form.

### ORDINATION OF CBC TRENDS

PCA analyses were carried out on CBC indices derived from a model incorporating year and site effects across years between 1962 and 1996. When including all 29 species, the first PCA axis represented a strong gradient from species showing evidence of increases (stock dove, rook and chaffinch) to species showing decreases. Tree sparrow, turtle dove, skylark, song thrush, linnet, blackbird, dunnock, bullfinch and corn bunting showed very similar axis scores (Table 6) and have similar patterns of decline (Siriwardena et al. 1998). Annual axis scores



**Fig. 2.** Annual scores from the first axis of detrended correspondence analysis of agricultural variables (Table 4) grouped into high, medium and low categories based on data in Fig. 1.



**Fig. 3.** Annual scores from the first axis of principal components analysis of agricultural variables, considering the 18 most accurately measured variables (Table 5).

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Table 5. PCA scores (axis 1 only) of smoothed annual agricultural variables between 1974 and 1991. Only data with a run of several years of annual data and a minimum of two interpolated values were

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Variable	Silage production	Total wheat	Oilseed rape	Nitrogen application	Sheep	Winter barley	Slurry application	Sugar beet	Bare fallow	Permanent grass	Total barley	Oats	New grass	Potatoes	Rough grazing	Turnips	Hay production	Spring barley
Axis 1 score	-0.27	-0.27	-0.27	-0.26	-0.26	-0.24	-0.01	60.0	0.19	0.19	0.24	0.25	0.26	0.26	0.26	0.27	0.27	0.27

were relatively stable up until the late 1970s (Fig. 4), apart from an outlier in 1963 caused by a population crash in most species after the exceptionally severe preceding winter. There was a rapid change in the PCA score of axis 1 between the late 1970s and mid-1980s, a period when the majority of species were showing the most rapid changes in abundance. Lower axes could not be meaningfully interpreted. Goodness-of-fit tests revealed that the model fit was questionable (significant  $\chi^2$ -tests) in nine species: lapwing, skylark (although this was only just significant at P < 0.05), starling, rook, jackdaw, whitethroat, tree sparrow, linnet and corn bunting. Indices are still produced for these species, and they may provide reasonable measures of population change, but confidence intervals cannot be estimated so nothing may be concluded about the precision of the indices or the significance of population change. When these species were removed, there was little difference in the eigenvalue of the 3652664, 2000, 5, Downloaded from https://besjournals

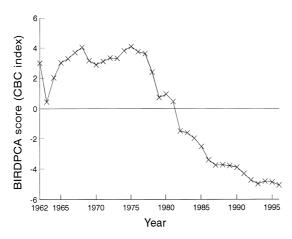
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**Table 6.** Principal components analysis scores from the first and second principal axis of Common Bird Census indices between 1962 and 1995 in order of scores on the axis for all data. Species with reliable indices are those with no significant heterogeneity between sites

	All species	Species with reliable indices
Species	Axis 1	Axis 1
Rook	-0.26	
Chaffinch	-0.23	-0.31
Stock dove	-0.21	-0.30
Great tit	-0.19	-0.28
Jackdaw	-0.16	
Blue tit	-0.13	-0.21
Long-tailed tit	-0.10	-0.18
Wren	-0.06	-0.13
Lesser whitethroat	-0.04	-0.07
Robin	0.00	-0.05
Kestrel	0.03	-0.02
Greenfinch	0.04	-0.02
Whitethroat	0.11	
Goldfinch	0.11	0.11
Yellow wagtail	0.12	0.17
Yellowhammer	0.12	0.15
Lapwing	0.14	
Reed bunting	0.15	0.15
Grey partridge	0.22	0.31
Starling	0.23	
Corn bunting	0.23	
Bullfinch	0.24	0.29
Dunnock	0.24	0.29
Blackbird	0.24	0.30
Linnet	0.25	
Song thrush	0.25	0.31
Skylark	0.25	
Turtle dove	0.26	0.32
Tree sparrow	0.26	
% variation	47.6	40.5

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**Fig. 4.** Annual scores from the first axis of Principal components analysis of Common Bird Census index of 29 farmland bird species.

first axis or the relative position of each species on the axis (Table 6), showing that inclusion of species with less reliable indices made no difference to the general community trends detected using PCA. All 29 species were therefore retained in the analysis.

# RELATIONSHIPS BETWEEN AGRICULTURAL INTENSIFICATION AND BIRD POPULATION TRENDS

A preliminary analysis was carried out that identified the single agricultural variable (from Table 1) that most closely matched the CBC trend for each species in Table 2 (i.e. the variable that had the highest  $r^2$  value). The majority of species (25 out of 29) showed a significant variable selection, and this was highly significant (P < 0.0001) in all but two of these species. There was a number of results that could have had underlying causal mechanisms. For example, variables associated with declines in stubble area (spring and winter barley area) were selected for five granivorous species particularly associated with farmland (greenfinch, goldfinch, linnet, corn bunting and reed bunting) but only with a time lag of 1 year in the agricultural data. Stubbles have been shown to be a preferred foraging habitat for a number of granivorous species (Wilson, Taylor & Muirhead 1996; Gillings & Fuller 1998) and their decline has led to suggestions of a possible effect of stubble loss on bird populations. Furthermore, as this effect would occur in the winter preceding a given breeding season, a lagged effect would be expected. However, there were also four generalist species (wren, dunnock, robin and blackbird) that showed similar relationships, but there was no a priori evidence for a preference for stubbles in these species. Due to the high degree of collinearity in the data (Table 3) and the fact that for many species it

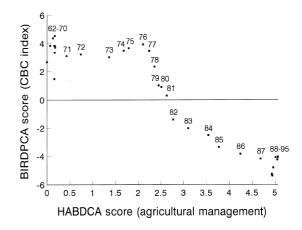
was difficult to identify likely causal mechanisms despite highly significant correlations, we feel that this approach is extremely limited in identifying specific potential factors that may have driven population declines in individual species. A more general approach will be taken relating a single measure of intensification to patterns of bird declines.

BIRDPCA scores for individual years derived from CBC indices for all 29 target species were plotted against HABDCA scores derived from agricultural variables between 1962 and 1995 (in Fig. 2). For both data sets, only the first axes were considered as these described gradients of most relevance to identifying effects of agricultural change on bird populations. There was a high correlation (Spearman rank correlation r = -0.87, n = 34, P < 0.0001) between the first axis scores of the bird and agricultural data, and most of the years tended to be in chronological order (Fig. 5). However, this was neither a linear nor a simple curved relationship. Attempts were made to transform the data, and although this reduced some of the curvature it was still not possible to fit a simple model. A decision was made not to fit a more complex model because the main aim was to describe the relationship rather than to develop predictive models, and it was felt the fitting of such a model would not further the interpretation.

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Between 1962 and 1970 there were small changes in BIRDPCA score, but little change in HABDCA score (Fig. 5), suggesting that bird numbers were fluctuating independently of agriculture. The lowest early BIRDPCA score was due to the crash in numbers of many resident species following the 1962–63 severe winter. Between 1971 and 1977 there was a steep increase in HABDCA score, but little change in BIRDPCA score, whilst between 1977 and 1982



**Fig. 5.** The relationship between the first axis of BIRDPCA (Common Bird Census indices) and the first axis from HABDCA (categorical agricultural variables; Table 4) between 1962 and 1995. Years corresponding to BIRD-PCA axis scores are given on the figure.

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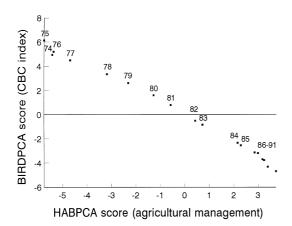
there was a more gradual increase in HABDCA score combined with a steep decrease in BIRDPCA score. Between 1982 and 1988 the HABDCA scores increased sharply and the BIRDPCA scores continued to decrease. Finally there was a period of minor fluctuations but little major change in both BIRDPCA and HABDCA scores between 1989 and 1995, indicating a period of relative stability. The nature of this relationship, with a period of major change in HABDCA score and little change in BIRDPCA scores followed by the converse, suggests that a time lag may be involved in the link between bird populations and agricultural change.

The above analyses were repeated, but using HABPCA scores for agricultural variables in place of HABDCA scores, which meant that fewer but more accurately measured agricultural variables from a smaller range of years (1974–91) were considered (Table 5). The relationship was similar to the previous analysis, with years tending to appear in order (Spearman correlation r = -0.97, n = 18, P < 0.0001), but it was more linear in form (Fig. 6). There was no indication of a time lag in bird population change relative to agricultural change, but this analysis was curtailed at either end relative to the more comprehensive DCA analysis, so most of the period of stability in bird populations was not included in this analysis.

## Discussion

# AGRICULTURAL INTENSIFICATION

The data presented here provide an overview of the nature and timing of changes in agricultural practices in lowland England and Wales. Many components of change in agriculture have followed the



**Fig. 6.** The relationship between the first axis of BIRDPCA (Common Bird Census index) and the first axis from HABPCA (continuous agricultural variables; Table 5) between 1974 and 1991. Years corresponding to BIRD-PCA axis scores are given on the figure.

same general pattern over the past three decades. The main underlying causes of these changes have been technological developments. The development of pesticides and fertilizers in particular, and also the increased efficiency of their application, has had widespread effects on farming practice, including changes in the timing of sowing of cereals, changes in crop rotations, and changes in the management and harvesting of grass. Changes in individual components of agricultural intensification have not therefore proceeded independently of one another. Rather, changes have been closely interlinked, a change in one aspect of management often facilitating change in other aspects.

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A number of agricultural variables showed consistent trends that enabled ordination analyses to produce axes of environmental variation that were good summaries of the major overall changes in agricultural management. Hence, annual axis scores are likely to be a good general index of agricultural intensification. The variables relating to crop and grass management used in these analyses include most of those likely to have potential effects on bird populations (O'Connor & Shrubb 1986). However, there were still some notable omissions. There were few data on spring and autumn cereals in the late 1960s and early 1970s, a crucial period of change. Time of sowing is likely to be important as spring sowing tends to be associated with overwinter stubbles, an important habitat for a number of bird species outside the breeding season (Wilson, Taylor & Muirhead 1996), while spring cereals provide an important nesting habitat for skylarks, particularly later in the breeding season when winter cereals are too tall and dense (Wilson et al. 1997; Chamberlain et al. 1999). There was no information on grass leys used in rotation. Crop rotations including grass levs tend to be associated with greater habitat diversity, which is likely to benefit at least skylarks (Chamberlain & Gregory 1999) and lapwings (Galbraith 1988) by providing a beneficial mix of habitats for nesting and feeding. Generally, changes in cropping and annual changes in pesticide and fertilizer use were fairly well covered by the data, with perhaps more detail for variables associated with arable farming. No adequate data were available on abundance and quality of non-crop habitats, particularly hedgerows, which are a major feature affecting the farmland bird community (O'Connor & Shrubb 1986), although Gillings & Fuller (1998) have argued that loss of non-crop habitat has been of secondary importance to reduction in habitat quality.

# FARMLAND BIRD POPULATION CHANGES

Analysis of CBC indices using DCA showed that from 1977 onwards a major shift in bird populations began, continuing until the late 1980s. Trends for individual species are presented in Siriwardena *et al.* 

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(1998) and show clearly that many species started to decline markedly in the period 1974–76, and this is supported by analysis of turning points. A number of species show very similar patterns of decline. For example, Siriwardena et al. (1998) showed that song thrush, blackbird and skylark had similar patterns of decline and very similar turning points in the population trend. It is possible that this is due to these species being affected by the same factors. However, given their differing ecological requirements, this seems doubtful. Such coincidences in population trend are more likely to indicate that a large number of components of agricultural intensification changed at the same time, but the actual individual factors affecting population change differed from species to species. This also applies to increasing species such as chaffinch, rook and stock dove, and it is possible that in these species certain aspects of intensification have been beneficial.

The selection of the target species for these analyses was dictated largely by the quality of CBC data available. CBC indices can be derived only for the more common species, so this analysis does not include rare species of very high conservation concern, for example stone curlew and cirl bunting. It does, however, cover several declining farmland bird species, for example skylark, tree sparrow and linnet (Table 2). Also, the species best measured by CBC indices tend to be biased towards southern and eastern England (Fuller, Marchant & Morgan 1985). and so this analysis describes patterns of bird population change on lowland farmland. Marginal upland landscapes were not included in the analyses, yet intensification of pastoral farming in these regions and the consequences for bird populations are likely to have been as great as that seen in lowland regions, although this is likely to involve a different suite of species.

# POPULATION CHANGES AND INTENSIFICATION

Ordination of the CBC index showed that the axis describing bird population decline began to change in 1977. Ordination of agricultural variables showed that the period of most rapid change began in 1971, indicating that most species started to decline some 6 years after agricultural intensification really commenced. We suggest that the delay between the onset of agricultural change and the onset of bird population declines is exactly what would be expected if a causal link between the two operates through indirect mechanisms such as food reduction. There are several reasons for thinking this. Population effects could arise from reduced breeding productivity (Siriwardena et al. 2000), reduced survival outside the breeding season (Siriwardena, Baillie & Wilson 1998), or both. For a period of time, density-dependent factors may have compensated for

reduced breeding production or survival. Such a process may have been possible so long as both breeding production and survival outside the breeding season were not being affected simultaneously by changing habitat quality and provided that the initial effects on breeding output or productivity were not too great. These requirements would probably have been met because the pattern of agricultural intensification was a progressive phenomenon through the 1970s and 1980s (Fig. 1). Eventually, however, some critical threshold would have been exceeded when compensation was no longer possible and effects on population size would become apparent. A delayed response of population change to changes in agriculture would be expected if bird populations responded to threshold levels in agricultural management change. The relationship between BIRDPCA and HABDCA also implies that this threshold may be defined by a number of interacting factors, rather than a single causal agent.

Another factor likely to introduce a time lag is the functional response of bird populations to changing food supplies in the farmland environment. Typical forms of functional response involve an increase in consumption rate that is either initially linear or curvilinear but which rapidly decelerates often reaching a plateau with no change in consumption rate over a wide range in food density (Begon, Harper & Townsend 1990). A substantial decline in food resources, for example the density of seeds in winter, may have been necessary before foraging rates were affected. Coupled with this, many farmland birds are extremely gregarious and search for food over a wide area; this is especially true of granivorous species in winter. Consequently they may have been able to exploit alternative food supplies or increasingly patchy food supplies quite successfully for a period of time.

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## IMPLICATIONS FOR CONSERVATION

The apparent delayed response of bird populations to agricultural intensification may have important implications for predictive scenarios of the effects of future agricultural change. The time lag in the relationship implies that effects of change in habitat quality may not become apparent for several years. Conclusions on the effects of land use change on bird populations after only a few years are therefore unlikely to be valid. This may apply both to declining and increasing bird populations. For example, the introduction of set-aside has resulted in a relatively large area of farmland being converted into a habitat that is preferred by a number of farmland species (Henderson, Vickery & Fuller 2000), yet which has not had any great effect on farmland populations (Henderson et al. 2000). If a timelagged response is occurring, an effect of set-aside on national farmland bird populations may yet

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become apparent. Furthermore, if the time lag arises due to response to a critical threshold of high quality habitat, then that habitat may have to reach a certain area and a level of widespread distribution before there is any impact on bird populations.

Attempting to identify individual variables that may have been responsible for declines in individual species was difficult as so many variables showed similar timing in their patterns of change. Consequently, the individual agricultural management variables that were selected as explaining the most variation in CBC index were difficult to link to likely mechanisms causing an effect on the population of a given species. Given that we know that individual components of intensification are closely interlinked and for the most part highly correlated with each other, it is unlikely that general correlations at wide geographical scales could identify important factors driving population declines. Significant relationships detected between individual management variables and CBC indices are indicative of general intensification, but cannot be taken as evidence of potential causal effects. Further evidence is needed from intensive studies at the farm level before drawing firmer conclusions on the effects of changes in specific aspects of agricultural management on bird population change. However, given the complexity of the relationships between components of intensification, even intensive studies may struggle to isolate individual agricultural practices that have had most impact on a given bird species.

Manipulation of specific components of farming systems can sometimes bring really worthwhile benefits for wildlife under some circumstances. For example, the re-introduction of stubbles in parts of south Devon has been linked with an increase in cirl buntings (Lock 1999). However, the intensive, longterm, project required to identify the specific factors limiting the cirl bunting population is unlikely to be feasible for the majority of declining farmland birds. The likelihood that several interacting factors, rather than one single overriding factor, have driven population declines in a number of species has important implications for future agri-environmental management. As factors influencing intensification are strongly interlinked, we suggest that general extensification is likely to have the greatest range of benefits, as implied by the apparently beneficial effects of organic farming on local bird populations (Wilson et al. 1997; Chamberlain, Wilson & Fuller 1999).

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### References

- Baillie, S.R. (1990) Integrated population monitoring of breeding birds in Britain and Ireland. *Ibis*, **132**, 151–166.
- Begon, M., Harper, J.L. & Townsend, C.R. (1990) Ecology
   Individuals, Populations and Communities, 2nd edn.
   Blackwell Scientific Publications, Oxford, UK.
- ter Braak, C.J.F., van Strien, A.J., Meijer, R. & Verstrael, T.J. (1994) Analysis of monitoring data with many missing values: which method? *Bird Numbers 1992. Distribution, Monitoring and Ecological Aspects* (eds W. Hagemeijer & T. Verstrael), pp. 663–673. Proceedings of the 12th International Conference of the International Bird Census Council and European Ornithological Atlas Committee. Sovon, Beek-Ubbergen, Netherlands.
- Brickle, N.W., Harper, D.G.C., Aebischer, N.J. & Cockayne, S.H. (2000) Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. *Journal of Applied Ecology*, **37**, 742–755.
- Campbell, L.H., Avery, M.I., Donald, P., Evans, A.D., Green, R.E. & Wilson, J.D. (1997) A Review of the Indirect Effects of Pesticides on Birds. JNCC Report No. 227. Joint Nature Conservation Committee, Peterborough, UK.
- Chamberlain, D.E. & Crick, H.Q.P. (1999) Population declines and reproductive performance in skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom. *Ibis*, **141**, 38–51.
- Chamberlain, D.E. & Fuller, R.J. (2000) Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agriculture, Ecosystems and Environment*, **78**, 1–17.
- Chamberlain, D.E. & Gregory, R.D. (1999) Coarse and fine-scale habitat associations of breeding skylarks *Alauda arvensis* in the UK. *Bird Study*, **46**, 34–47.
- Chamberlain, D.E., Wilson, A.M., Browne, S.J. & Vickery, J.A. (1999) Effects of habitat type and management on the abundance of skylarks in the breeding season. *Journal of Applied Ecology*, **36**, 856–870.
- Chamberlain, D.E., Wilson, J.D. & Fuller, R.J. (1999) A comparison of bird populations on organic and conventional farmland in southern Britain. *Biological Con*servation, 88, 307–320.
- Crick, H.Q.P., Baillie, S.R., Balmer, D.E., Bashford, R.I., Beaven, L.P., Dudley, C., Glue, D.E., Gregory, R.D., Marchant, J.H., Peach, W.J. & Wilson, A.M. (1998) Breeding Birds in the Wider Countryside: their Conservation Status. British Trust for Ornithology, Thetford, UK.
- Crick, H.Q.P., Dudley, C., Evans, A.D. & Smith, K.W. (1994) Causes of nest failure among buntings in the UK. *Bird Study*, **41**, 88–94.

- Donald, P.F. (1997) The corn bunting *Miliaria calandra* in Britain: a review of current status, patterns of decline and possible causes. *The Ecology and Conservation of Corn Buntings Miliaria calandra* (eds P.F. Donald & N.J. Aebischer), pp. 11–26. UK Nature Conservation No. 13. Joint Nature Conservation Committee, Peterborough, UK.
- Evans, A.D., Smith, K.W., Buckingham, D.L. & Evans, J. (1997) Seasonal variation in breeding performance and nestling diet of cirl buntings *Emberiza cirlus* in England. *Bird Study*, 44, 66–79.
- Fuller, R.J. & Gough, S. (1999) Changing patterns of sheep stocking in Britain and implications for bird populations. *Biological Conservation*, 91, 73–89.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R. & Carter, N. (1995) Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology*, 9, 1425–1441.
- Fuller, R.J., Marchant, J.H. & Morgan, R.A. (1985) How representative of agricultural practice in Britain are common birds census farmland plots? *Bird Study*, 32, 56–70.
- Galbraith, H. (1988) Effects of agriculture on the breeding ecology of lapwings *Vanellus vanellus*. *Journal of Applied Ecology*, 25, 487–503.
- Gillings, S. & Fuller, R.J. (1998) Changes in bird populations on sample lowland English farms in relation to loss of hedgerows and other non-crop habitats. *Oecolo*gia, 116, 120–127.
- Gooch, S., Baillie, S.R. & Birkhead, T.R. (1991) Magpie Pica pica and songbird populations, retrospective investigation of trends in population density and breeding success. Journal of Applied Ecology, 28, 1068– 1086
- Green, R.E. (1995) The decline of the corncrake *Crex crex* in Britain continues. *Bird Study*, **42**, 66–75.
- Gregory, R.D. & Marchant, J.H. (1996) Population trends of jays, magpies, jackdaws and carrion crows in the United Kingdom. *Bird Study*, **43**, 28–37.
- Grigg, D. (1989) English Agriculture. An Historical Perspective. Blackwell Scientific Publications, Oxford, UK.
- Henderson, I.G., Cooper, J., Fuller, R.J. & Vickery, J.A. (2000) The relative abundance of birds on set-aside and neighbouring fields in summer. *Journal of Applied Ecology*, 37, 335–347.
- Henderson, I.G., Vickery, J.A. & Fuller, R.J. (2000) Summer bird abundance and distribution on set-aside fields on intensive arable farms in southern England. *Ecography*, 23, 50–59.
- Hill, M.O. (1979) decorana: A fortran Program for Detrended Correspondence Analysis and Reciprocal Averaging. Section of Ecology and Systematics, Cornell University, Ithaca, NY.
- James, F.C. & McCulloch, C.E. (1990) Multivariate analysis in community ecology and systematics: panacea or Pandora's box? *Annual Review of Ecology and Systematics*, 21, 129–166.
- Lock, L. (1999) Saving the cirl bunting 1/4 and lots more. *British Wildlife*, 11, 17–22.
- Marchant, J.H. & Gregory, R.D. (1994) Recent population changes among seed-eating passerines in the United Kingdom? Bird Numbers 1992. Distribution, Monitoring and Ecological Aspects (eds W. Hagemeijer & T. Verstrael), pp. 87–96. Proceedings of the 12th International Conference of the International Bird Census Council and European Ornithological Atlas Commit-

- tee. International Bird Census Council and European Ornithological Atlas Committee, Sovon, Beek-Ubbergen.
- Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P.A. (1990) Population Trends in British Breeding Birds. British Trust for Ornithology, Tring, UK.
- Newton, I. (1986) The Sparrowhawk. Poyser, Calton, UK.
- Newton, I. (1993) Predation and limitation of bird numbers. *Current Ornithology*, **11**, 143–194.
- O'Connor, R.J. & Shrubb, M. (1986) Farming and Birds. Cambridge University Press, Cambridge, UK.
- Pannekoek, J. & van Strien, A.J., (1996) TRIM (Trends and Indices for Monitoring Data). Statistics Netherlands, Voorburg, the Netherlands.
- Potts, G.R. (1986) *The Partridge: Pesticides, Predation and Conservation*. Collins, London, UK.
- Redpath, S.M. & Thirgood, S.J. (1997) *Birds of Prey and Red Grouse*. HMSO, London, UK.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. (1998) Trends in the abundance of farmland birds: a quantitative comparison of smoothed common birds census indices. *Journal of Applied Ecology*, 35, 24–43.
- Siriwardena, G.M., Baillie, S.R., Crick, H.P.Q. & Wilson, J.D. (2000) The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *Journal of Applied Ecology*, 37, 128–148.
- Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (1998) Variation in the survival rates of some British passerines with respect to their population trends on farmland. *Bird Study*, 45, 276–292.
- Stoate, C. (1996) The changing face of lowland farming and wildlife. II. 1945–1995. *British Wildlife*, 7, 162–172.
- Tapper, S.C., Potts, G.R. & Brockless, M.H. (1996) The effect of an experimental reduction in predation pressure on the breeding success and population density of grey partridges *Perdix perdix Journal of Applied Ecol*ogy, 33, 965–978.

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- Thomas, M.R. (1997) Review of Usage of Pesticides in Agriculture and Horticulture Throughout Great Britain 1984–94. Pesticide Usage Report 100. MAFF, London, UK.
- Thomson, D.L., Green, R.E., Gregory, R.D. & Baillie, S.R. (1998) The widespread declines of songbirds in Britain do not correlate with the spread of avian predators. *Proceedings of the Royal Society of London*, Series B, 265, 2057–2062.
- Velleman, P.F. & Hoaglin, D.C. (1981) Applications, Basics and Computing of Exploratory Data Analysis. Duxbury Press, Boston, MA.
- Wilkinson, M. (1997) A Review of Changes in Farm Management Practice Since 1970. ADAS Contract Report to ITE. ADAS, Huntingdon, UK.
- Wilson, J.D., Evans, J., Browne, S.J. & King, J.R. (1997) Territory distribution and breeding success of skylarks Alauda arvensis on organic and intensive farmland in southern England. Journal of Applied Ecology, 34, 1462–1478.
- Wilson, J.D., Taylor, R. & Muirhead, L.B. (1996) Field use by farmland birds in winter: an analysis of field type preferences using resampling methods. *Bird Study*, 43, 320–332.