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Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification

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Summary

1. Studies, mainly from the UK, show that many farmland birds have declined as a result of recent agricultural intensification. We tested this idea by analysing farmland bird population trends in Sweden, a country displaying less dramatic agricultural changes and less intensive agriculture. Specifically we investigated whether (i) farmland specialists have declined more than generalists, (ii) population declines in Sweden are less marked than in England and (iii) Swedish population trends are associated with changes in the amount of autumn-sown crops, and inputs of pesticides and fertilizers.
2. Data on population trends for 21 farmland bird species collected from the Swedish Breeding Bird Survey 1976–2001 were analysed in relation to agricultural changes in Sweden.
3. Fifteen (71%) farmland bird species declined significantly in number ($P < 0{\cdot}05$) over the 26 years. Farmland specialists displayed a significantly stronger average decline (55%) as a group than farmland generalists (7%). For seven species the declines were significantly steeper between 1976 and 1988 than between 1988 and 2001.
4. Farmland bird populations have declined at least as much in Sweden as in England. Several specialist species displayed similar temporal patterns in population change in both countries.
5. The area of autumn-sown crops has remained stable in Sweden, whereas use of pesticides and fertilizers has declined. There are no clear associations between these factors and observed farmland bird population declines.
6. The similarities in bird population trends in Sweden and England, despite large differences in patterns of agricultural change in Sweden and England, may be explained by: (i) common wintering grounds, (ii) similar negative effects of agricultural intensification (England) and intensification/abandonment (Sweden) and (iii) a simultaneous loss of landscape heterogeneity.
7. *Synthesis and applications.* Farmland birds in Sweden have declined by at least as much as in England, despite clear differences between the two countries in the degree of agricultural intensification over the last 30 years. We suggest that the marked declines in Swedish populations are caused by (i) the dual negative effects of intensification and abandonment of farmland at breeding grounds, and (ii) Swedish populations partly sharing wintering grounds with English populations. We conclude that agri-environmental schemes need to be flexible enough to address the negative effects both of intensification and the abandonment of farming. In addition, our results emphasize that farmland bird conservation is an issue without country borders.

Key-words: conservation, land abandonment, population change, population declines, set-aside, winter cereals

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Introduction

Many farmland birds in western Europe have suffered severe population declines since the 1970s (Tucker & Heath 1994; Fuller *et al*. 1995; Siriwardena *et al*. 1998; Donald, Green & Heath 2001), probably caused by agricultural intensification (Krebs *et al*. 1999; Aebischer *et al*. 2000; Chamberlain *et al*. 2000) or abandonment of farmland (MacDonald *et al*. 2000; Suarez-Seoane, Osborne & Baudry 2002; Laiolo *et al*. 2004).

Most studies relating agricultural intensification with population declines of farmland birds are from the UK (Ormerod & Watkinson 2000) and many suggested strategies for the conservation of farmland biodiversity are based on the situation in the UK (Aebischer *et al*. 2000; Vickery *et al*. 2004). However, in many parts of Europe the landscape and patterns of agricultural intensification are different. It is therefore important to determine whether farmland bird population trends display similar patterns between countries and whether the same explanation applies. Comparisons between countries may reveal whether (i) general relationships between specific components of agricultural intensification (e.g. the proportion of autumn-sown crops and inputs of fertilizer and pesticides) and population trends exist; (ii) population trends are temporally synchronized as a result of conditions in the non-breeding season; and (iii) the relative importance of specific components of agricultural intensification differs between countries or geographical regions. A recent study comparing population trends between Denmark and the UK suggested that bird trends and their relationships to components of agricultural intensification may vary across countries (Fox 2004).

Swedish farmland and the degree of agricultural intensification differs from that in the UK. This allowed us to examine the proposed link between bird population trends and agricultural change by contrasting Swedish data with data from the UK. First, farmland constitutes only 7% of the land area of Sweden vs. 70% of the UK (FAOSTAT 2005). Most of the farmland is concentrated on fertile soils in the lowland plains of southern Sweden, but even in these regions farmland occupies only 33% of the land area (Statistics Sweden 2001). In less productive parts of northern Sweden and the moraine highlands of southern Sweden, agricultural holdings are often small and separated by forests, creating a forest–farmland mosaic. Secondly, agricultural production has changed less dramatically in Sweden than in the UK (Fig. 1). This difference is partly caused by a recent divergence in Swedish farming related to regional conditions (Ihse 1995). In productive landscapes cereal production dominates, the proportion of mixed farms (farms with both cereal production and animal husbandry) has decreased rapidly (Statistics Sweden 1990; Clason & Granström 1992) and farming has become more intensive with, for example, removal of non-farmland habitats in order to enlarge fields (Statistics Sweden 1990; Ihse 1995). In contrast, in less productive areas (e.g. landscapes dominated by forest) farming has been partly abandoned or has become more extensive (Statistics Sweden 1990; Ihse 1995) and the agriculture landscape is dominated by improved cultivated grasslands (i.e. arable land used for hay, silage or grazing) and set-aside. Modern Swedish agriculture is characterized by a reduction in the area of arable land and semi-natural pastures, a decrease in the number of smallholdings and holdings with cattle, and an increase in the area of set-aside and relatively stable areas of improved cultivated grasslands (Fig. 2a–e). Thirdly, the use of autumn-sown crops (mainly winter wheat) has not increased in Sweden (Fig. 2f) whereas it has increased dramatically in the UK (Chamberlain *et al*. 2000). Fourthly, the inputs of inorganic fertilizers and pesticides have declined in Sweden (Fig. 2g,h) whereas they have increased in the UK (Chamberlain *et al*. 2000).

We used the 1976–2001 population trends of farmland birds in southern Sweden and compared them with corresponding figures from England (Crick *et al*. 2004). Based on findings mainly from lowland England, we predicted that: (i) the farmland bird population decline has been less severe in Sweden than in England because of the generally lower degree of agricultural intensification (cf. Chamberlain *et al*. 2000; Donald, Green & Heath 2001; Fig. 1); (ii) the decline has been most marked for farmland specialists (Siriwardena *et al*. 1998) because these species would be most sensitive to change in both countries independent of the degree of change (Shultz *et al*. 2005); (iii) the temporal

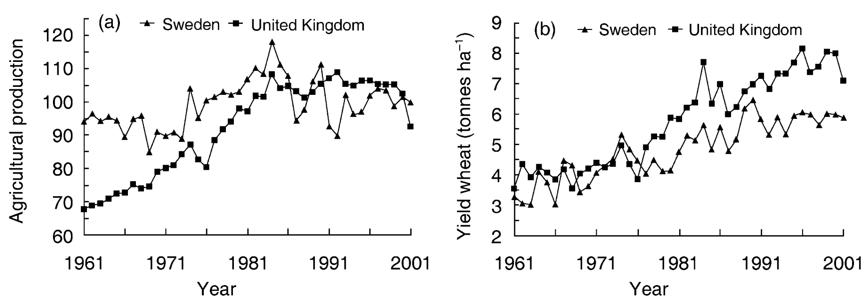

Fig. 1. (a) Country-specific indices of total agricultural production in Sweden and the UK. The total production is fixed to an average value of 100 in 1999–2001 for each country (FAOSTAT 2005). (b) Yield wheat (kg ha^{-1}) in Sweden and the UK (FAOSTAT 2005).

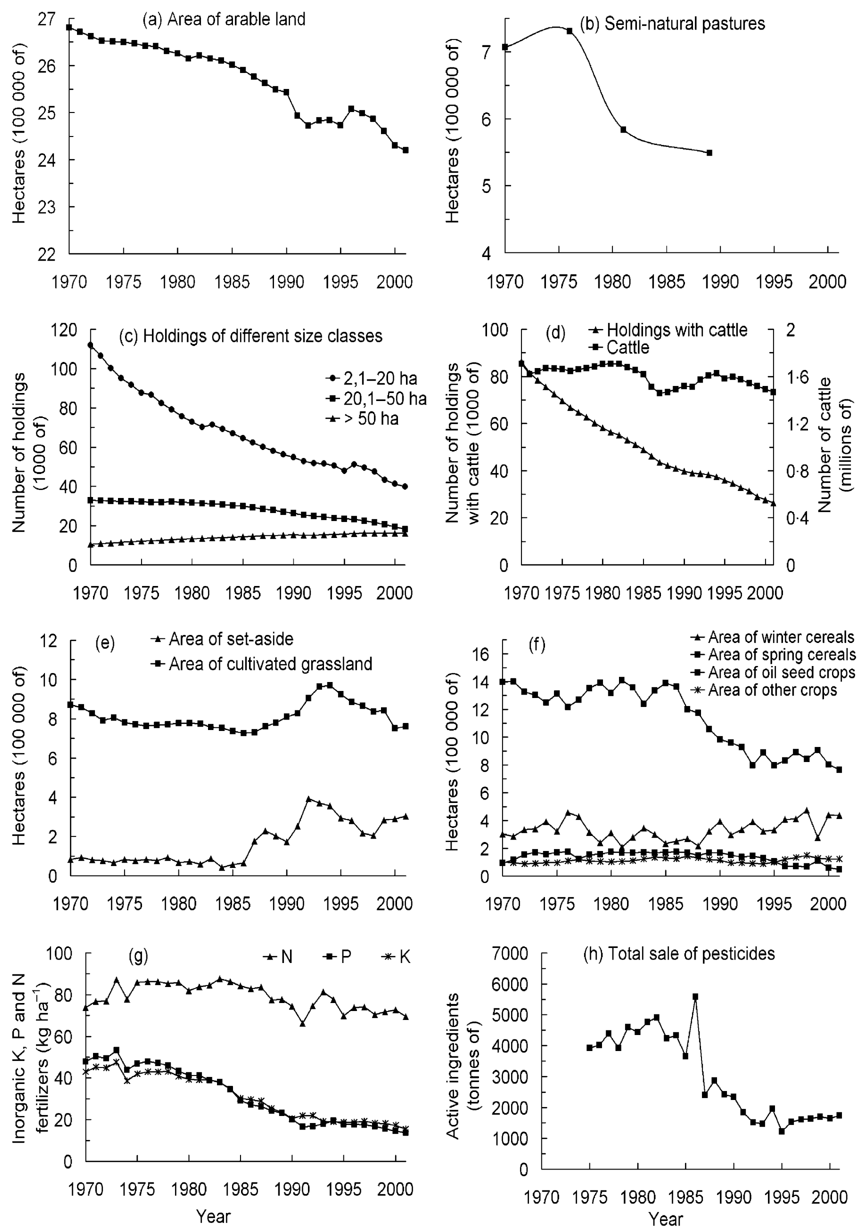

Fig. 2. Agricultural variables for Sweden. Data in (a, d, e, f) are from below latitude 61°, i.e. 90% of the Swedish farmland and where the birds were monitored. Data in (b, c, g, h) are from all of Sweden. Arable land (a) includes all crops (including improved cultivated grasslands) and set-aside. Other crops (f) include leguminous plants, potatoes and sugar beets. Data on fertilizers (total consumption divided by total arable land) from FAOSTAT (Rome, Italy) data. All other data from Statistics Sweden (Örebro, Sweden) annual reports. The high increase in pesticide consumption in 1986 was a result of a forthcoming price regulation, which made farmers rapidly increase their stocks.

patterns of the observed population changes in Sweden will be associated with changes in the use of autumn-sown crops and inputs of fertilizers and pesticides, because these factors have been identified as the cause of declines in England (Hudson, Tucker & Fuller 1994; Wilson *et al.* 1997; Burn 2000).

Methods

BIRD CENSUS DATA

We used data from the Swedish Breeding Bird Survey, which started in 1975 and consists of free-choice routes with 20 point counts (Lindström & Svensson 2005). At each point all birds heard or seen were counted during a 5-min period. The routes were censused once a year at route-specific days (± 5 days) and starting hour (± 30 min). Counts were made in the early morning between mid-May and mid-June. The geographical location of the routes and the exact position of the points were chosen by the observer. Routes abandoned by one observer were not taken over by a new observer. We used the total number of birds observed at the route level as independent observations in statistical analyses. Many routes were located in forest landscapes. As our aim was to study farmland birds in farmland

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Table 1. Trend estimates, standard errors and total percentage change with confidence intervals (CI) in Swedish populations of 21 farmland bird species between 1976 and 2001. The corresponding changes from Crick *et al*. (2004) for 17 species from England between 1975 and 2000 are also included

Common name*	Number of routes†	Overall trend estimate‡	SE	% population change in Sweden (95% CI)	% population change in England (90% CI)
Lapwing	279	0·985	0·004	−32 (−45, −15)	−46 (−63, −28)
Curlew	124	0·930	0·009	−84 (−90, −74)	−40 (−80, 4)
Woodpigeon	355	0·987	0·002	−28 (−36, −20)	147 (61, 257)
Stock dove	218	0·970	0·006	−54 (−65, −38)	63 (26, 132)
Wryneck	193	0·940	0·006	−79 (−85, −71)	Extinct
Skylark	355	0·968	0·002	−55 (−59, −51)	−61 (−67, −54)
Barn swallow	313	0·999	0·005	−3 (−25, 24)	16 (−8, 48)
Pied wagtail	352	0·990	0·002	−22 (−30, −12)	−10 (−31, 24)
Whinchat	263	0·982	0·004	−37 (−48, −24)	No data
Northern wheatear	216	0·963	0·006	−61 (−72, −46)	No data
Whitethroat	333	1·000	0·003	1 (−13, 18)	49 (14, 90)
Red-backed shrike	249	0·989	0·006	−23 (−42, 1)	Extinct
Starling	353	0·978	0·003	−43 (−52, −33)	−71 (−78, −63)
Magpie	337	1·003	0·003	9 (−5, 25)	75 (52, 100)
Jackdaw	333	1·000	0·003	1 (−13, 18)	63 (12, 147)
Hooded/carrion crow	355	0·979	0·002	−42 (−48, −35)	60 (33, 94)
Tree sparrow	271	0·989	0·005	−25 (−41, −5)	−97 (−99, −94)
House sparrow§	225	0·949	0·005	−73 (−79, −65)	−69 (−78, −60)
Greenfinch	352	1·009	0·003	24 (9, 42)	13 (−12, 33)
Linnet	207	0·970	0·005	−53 (−64, −40)	−62 (−70, −52)
Yellowhammer	350	0·980	0·002	−40 (−46, −34)	−56 (−63, −48)

*Species in bold display significant trends in Sweden ($P < 0{\cdot}05$). Species in italics are classified as farmland specialists.
†The number of routes where each species was observed.
‡The overall trend estimates are overall yearly rate of change (< 1, decline; > 1, increase). A trend estimate of 0·95 equals an annual decline of 5%.
§Available data for house sparrow from England is 1977–2000 (Crick *et al*. 2004).

landscapes, we selected routes that contained at least some farmland. Information on the exact location of the census points was not collected in the first census years. Therefore, we used presence of skylark *Alauda arvensis* L. in at least 1 year as an indicator of occurrence of farmland habitats. The skylark is widespread and common in all farmland areas larger than 11·5 ha in Fennoscandia (Piha, Pakkala & Tiainen 2003). The first year of the survey, 1975, was omitted because disproportionately few routes were censused that year. We also excluded routes that had only been censused in 1 or 2 years. In total, we used data collected from 355 different routes below latitude 61° between 1976 and 2001. This part of southern Sweden covers approximately 90% of all Swedish farmland (Statistics Sweden 2001). Of these, 109 routes were surveyed for 10–28 years, 167 routes for 5–9 years and 79 routes for 3–4 years. The yearly number of routes censused varied between 62 and 169.

CLASSIFICATION OF FARMLAND BIRD SPECIES AND THEIR CHARACTERISTICS

We classified the bird species as farmland specialists or generalists using the classification in Siriwardena *et al*. (1998) (Table 1). Species classified as specialists in the UK were also classified as specialists in Sweden based on their broad habitat preferences. However, several species classified as farmland generalist in the UK (e.g. bullfinch *Pyrrhula pyrrhula* L., dunnock *Prunella modularis* L. and blackcap *Sylvia atricapilla* L.) are mainly confined to forest landscapes in Sweden. Therefore our selection of species slightly deviated from those published for other countries (Fuller *et al*. 1995; Siriwardena *et al*. 1998; Fox 2004) and included 21 species previously considered to be linked to farming in Sweden (Robertson & Berg 1992; Berg & Pärt 1994; Söderström & Pärt 2000). Seven species included in our analyses were not included in Siriwardena *et al*. (1998): curlew *Numenius arquata* L., house sparrow *Passer domesticus* L., red-backed shrike *Lanius collurio* L., northern wheatear *Oenanthe oenanthe* L., whinchat *Saxicola rubetra* L., woodpigeon *Columba palumbus* L. and wryneck *Jynx torquilla* L. We classified these as generalists or specialists based on their ecology and main habitat preferences in southern Sweden. Farmland bird species with scarce data were omitted (e.g. meadow pipit *Anthus pratensis* L., goldfinch *Carduelis carduelis* L., ortolan bunting *Emberiza hortulana* L. and yellow wagtail *Motacilla flava* L.). The pheasant *Phasianus colchicus* L. was also excluded as its population size is artificially maintained.

All species were classified according to phylogeny (Corvoidea/Muscicapoidea/non-passerine/Passeroidea/Sylvioidea; Sibley & Monroe 1990) and six ecological characteristics (Söderström & Pärt 2000; Cramp, Simmons & Perrins 1977–94), i.e. migration strategy (resident/temperate/tropical), main breeding farmland habitat (pasture/arable land), nesting site (ground/above ground/cavity), summer diet (plant/invertebrate/mixed diet), territory size (< 1 ha/> 1 ha) and foraging distance when foraging bouts extended outside territory (< 500 m/> 500 m) (see Table S1 in the supplementary material).

POPULATION TRENDS AND SPECIES-SPECIFIC INDICES

Yearly species indices for 1976–2001 were calculated using TRIM software (trends and indices for monitoring data; Pannekoek & van Strien 2001). TRIM analyses time series of counts with missing observations using Poisson regression (log–linear models; McCullagh & Nelder 1989). We used the linear trend model with all years as change points and all models were run with serial correlation taken into account. For each species we present yearly indices and an overall trend estimate (with 95% confidence intervals) calculated as the slope of the regression line through the logarithms of the indices over the whole study period. The 95% confidence interval for the overall trend estimate was used to test for significant population trends for each species (Pannekoek & van Strien 2001).

Following the procedure of Gregory *et al.* (2005), we combined indices of several species to produce three multispecies indices: (i) all farmland bird species, (n = 21) (ii) farmland specialists (n = 13) and (iii) farmland generalists (n = 8). Geometric means and their standard errors were calculated from the indices and standard errors of individual species.

BIRD TRENDS IN SWEDEN AND ENGLAND

Crick *et al.* (2004) present farmland bird population changes from England and the UK. We chose to use data from England only, because these data mainly came from farmland (Crick *et al.* 2004) and therefore corresponded better with our data. Crick *et al.* (2004) present data during the time period 1975–2000, roughly the same period as the Swedish data (1976–2001). To facilitate comparisons between the two countries, the Swedish bird data were transformed into values of percentage total change using the following procedure. The overall trend estimates, derived as described above, equalled the average annual change during this period. We calculated the total change during the 26 years of study as: (overall trend estimate^{25} – 1) × 100, with the lower and upper 95% confidence intervals converted into corresponding magnitude (Pannekoek & van Strien 2001). In this way the Swedish estimates of total change avoided the potential effects of divergent start and end years, and the same was true for the English data based on smoothed trends (Crick *et al.* 2004).

At the species level we compared percentage total change and the corresponding confidence intervals. Four species were omitted from the comparison because of either a lack of data (whinchat and northern wheatear; Crick *et al.* 2004) or extremely low population numbers (wryneck and red-backed shrike) in England. The decline of the latter two species may have been affected by general factors related to small populations (e.g. demographic stochasticity and Allee effects). The data from England were reported with 90% confidence intervals, while our data were calculated with 95% confidence intervals. We considered the trends to be different when the confidence intervals did not overlap. Admittedly this is only a rough test at an α-level of approximately $P < 0{\cdot}10$, and with this in mind we only considered obvious differences and similarities in our comparisons.

AGRICULTURAL CHANGES AND BIRD POPULATION TRENDS IN SWEDEN

Agricultural variables were analysed using principal component analysis (PCA). We followed the procedure of Chamberlain *et al.* (2000) and Fox (2004) to allow direct comparisons between the studies. Twenty-one agricultural variables that described changes in the farmland between 1976 and 2001 were used (Table 3). PCA was performed with the statistical package CANOCO version 4.5 (ter Braak & Šmilauer 1997–2002). PCA on agricultural data was carried out using standardized PCA based on a correlation matrix, enabling variables measured on different scales to be included on the same axis (ter Braak & Šmilauer 2002). To derive general patterns of change within the farmland bird community, both Chamberlain *et al.* (2000) and Fox (2004) used PCA on a matrix of species indices by year. Because the interpretation of multispecies indices is more straightforward than species PCA indices, we used the multispecies indices including all 21 species in our presentation of the association of farmland bird population change and agricultural change. Results based on species PCA indices and our multispecies indices gave qualitatively very similar results. A second PCA on agricultural data was performed for the period 1970–2001, to examine whether there were any rapid changes in agriculture prior to the first year of bird trend data. The second PCA included all agricultural variables except pesticides because of lack of data before 1975.

Results

FARMLAND BIRD POPULATION TRENDS IN SWEDEN

Of the 21 species associated with farmland in Sweden, 15 (71%) displayed a significant decline ($P < 0{\cdot}05$) in numbers between 1976 and 2001 (Table 1; see Fig. S1 in the supplementary material). The total decline based on the geometric mean of all farmland species was 41% (Fig. 3), clearly different from that observed in other groups of bird in Sweden (e.g. forest species; Lindström

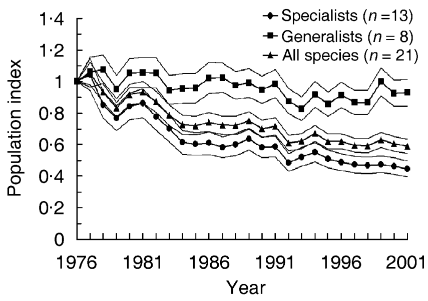

Fig. 3. Multispecies indices for farmland specialists, farmland generalists and all species pooled between 1976 and 2001. The upper and lower lines on indices show the 95% confidence intervals.

& Svensson 2005). Only the greenfinch *Carduelis chloris* L. increased significantly in numbers, whereas five species showed non-significant population trends (Table 1). Seven species experienced average population declines of more than 50% (curlew, stock dove *Columba oenas* L., wryneck, skylark northern wheatear, house sparrow and linnet *Carduelis cannabina* L.; Table 1), of which the curlew experienced the greatest decline (average yearly decline of 7%).

There were no significant differences in trends of birds categorized according to nesting site (Kruskal–Wallis test, H = 4·26, d.f. = 2, P = 0,12), phylogeny (Kruskal–Wallis test, H = 7,75, d.f. = 4, P = 0·10), summer diet (Kruskal–Wallis test, H = 0·50, d.f. = 2, P = 0·78), migration strategy (Kruskal–Wallis test, H = 3·75, d.f. = 2, P = 0·15), territory size (Mann–Whitney test, U = 40·0, N_1 = 12, N_2 = 9, P = 0·32), foraging distance (Mann–Whitney test, U = 47·5, N_1 = 10, N_2 = 11, P = 0·60) or main farmland habitat use (Mann–Whitney test, U = 46·5, N_1 = 9, N_2 = 12, P = 0·59). Only farmland specialists and generalists differed in their population trend estimates (Mann–Whitney test, U = 14·5, N_1 = 8, N_2 = 13, P = 0·007). The total declines based on the geometric mean for farmland specialists and generalists were 55% and 7%, respectively (Fig. 3). This difference was also evident (Mann–Whitney test, U = 6·5, N_1 = 6, N_2 = 8, P = 0·02) when we excluded the seven species not classified by Siriwardena *et al.* (1998).

It should be noted that among those few species that were rarely covered by the Swedish Breeding Bird Survey, there were both increasing species, such as corncrake *Crex crex* L., quail *Coturnix coturnix* L. and marsh harrier *Circus aeruginosus* L., and declining species, such as ortolan bunting (SOF 2003; Lindström & Svensson 2005).

COMPARISON OF BIRD TRENDS IN SWEDEN AND ENGLAND

There was a tendency for a stronger average decline of farmland birds in Sweden than England (Wilcoxon matched pairs test, t = 45·0, n = 17, P = 0·14). The main reason for this was that several species, notably hooded crow *Corvus corone cornix* L., magpie *Pica pica* L., jackdaw *Corvus monedula* L., woodpigeon and stock dove showed declining or stable populations in Sweden, whereas they have increased in numbers in England. However, several specialist species (e.g. lapwing *Vanellus vanellus* L., skylark, linnet, house sparrow and yellowhammer *Emberiza citrinella* L.) displayed similar negative trends in both countries (Wilcoxon matched pairs, only specialists, t = 26·0, n = 10, P = 0·88). The starling *Sturnus vulgaris* L. and the tree sparrow *Passer montanus* L. declined more in England than in Sweden (but see also yellowhammer; Table 1).

In the UK the major population declines occurred between the mid-1970s and the late 1980s (Siriwardena *et al.* 1998; Chamberlain *et al.* 2000). We tested whether the same pattern applied to Sweden by comparing bird trend estimates from 1976 to 1988 to those from 1988 to 2001. Eleven species displayed significantly different trends between these time periods, and for seven the decline was steeper in the first than in the second time period (lapwing, curlew, skylark, barn swallow *Hirundo rustica* L., starling, house sparrow and linnet; Table 2). Species displaying no trend shifts between the two time periods could be separated into two groups: (i) species displaying a continuous decline (wryneck, pied wagtail *Motacilla a. alba* L., whinchat, northern wheatear, hooded crow and tree sparrow) and (ii) species with more or less stable populations (whitethroat *Sylvia communis* Latham, magpie and jackdaw) throughout the whole period.

Visual inspections of the smoothed species curves from England (Crick *et al.* 2004) and Swedish indices (see Fig. S1 in the supplementary material) also suggested that several farmland specialists had remarkably similar population trends (e.g. skylark, linnet and yellowhammer). However, other species showed very different temporal trend patterns (e.g. stock dove, carrion/hooded crow, magpie, woodpigeon and tree sparrow).

RELATIONSHIPS BETWEEN AGRICULTURAL CHANGES AND BIRD POPULATION TRENDS IN SWEDEN

The first PCA axis (PC1) of agricultural data explained 59% of the variation. There was a clear gradient from variables with a decreasing trend between 1976 and 2001 (e.g. number of farm holdings and spring-sown crops) to those with a slightly increasing trend (set-aside, improved cultivated grassland and number of sheep; Fig. 2 and Table 3). In contrast to the UK (Chamberlain *et al.* 2000), both fertilizers and pesticides showed decreasing trends, whereas the area of autumn-sown crops increased only slightly, constituting no more than approximately 12% of all arable land in Sweden (Fig. 2f–h). The second PCA axis explained a further 17% of the variation, and was dominated by uncommon crops such as winter rape, beet, spring wheat and mixed grain. The annual scores on PC1 of agricultural variable PCA changed markedly throughout

Table 2. Trend estimates and standard errors for Swedish populations of 21 farmland bird species for the time periods of 1976–88 and 1988–2001, respectively. Wald-test for change point in 1988 describes the significance of a species' difference in trend estimate between the two time periods

Name	Overall trend estimate 1976–88	SE	Overall trend estimate 1988 –2001	SE	χ^2 (d.f. = 1)	*P*-value
Lapwing	0·951	0·009	1·011	0·006	21·13	< 0·001
Curlew	0·877	0·017	0·965	0·014	12·38	< 0·001
Woodpigeon	0·996	0·004	0·980	0·004	6·00	0·01
Stock dove	1·004	0·012	0·946	0·009	11·35	< 0·001
Wryneck	0·952	0·011	0·931	0·012	1·22	0·27
Skylark	0·951	0·004	0·981	0·003	29·41	< 0·001
Barn Swallow	0·956	0·011	1·047	0·007	32·94	< 0·001
Pied wagtail	0·989	0·005	0·990	0·004	0·01	0·90
Whinchat	0·983	0·008	0·981	0·006	0·05	0·82
Northern wheatear	0·953	0·012	0·970	0·010	0·77	0·38
Whitethroat	1·005	0·007	0·998	0·005	0·61	0·43
Red-backed shrike	0·972	0·011	0·999	0·010	2·42	0·12
Starling	0·962	0·007	0·995	0·005	10·64	0·001
Magpie	1·009	0·006	1·000	0·004	1·19	0·28
Jackdaw	1·005	0·007	0·998	0·005	0·61	0·43
Hooded crow	0·983	0·004	0·975	0·003	1·84	0·17
Tree sparrow	0·992	0·010	0·983	0·007	0·53	0·47
House sparrow	0·927	0·009	0·964	0·007	7·70	0·006
Greenfinch	1·022	0·006	0·997	0·004	9·52	0·002
Linnet	0·937	0·011	0·998	0·008	13·70	< 0·001
Yellowhammer	0·996	0·004	0·965	0·003	25·49	< 0·001

Table 3. PCA scores (axis one only) of the 21 agricultural variables used to summarize the changes in Swedish agriculture between 1976 and 2001

Variable	Units measured	PCA loading on axis 1
Holdings	Total number	–0·980
Potassium	kg (per ha)	–0·979
Holdings with cattle	Total number	–0·970
Phosphorus	kg (per ha)	–0·962
Spring oats	Area (ha)	–0·952
Mixed grain (spring-sown)	Area (ha)	–0·933
Total pesticides	Total kg active ingredients	–0·919
Spring barley	Area (ha)	–0·915
Potatoes	Area (ha)	–0·897
Nitrogen	kg (per ha)	–0·887
Spring oilseed rape	Area (ha)	–0·757
Winter rye	Area (ha)	–0·715
Cattle	Total number	–0·670
Spring wheat	Area (ha)	–0·548
Winter oilseed rape	Area (ha)	–0·362
Sugar beet	Area (ha)	0·329
Winter wheat	Area (ha)	0·348
Leguminous	Area (ha)	0·412
Improved cultivated grassland	Area (ha)	0·585
Sheep	Total number	0·724
Set-aside	Area (ha)	0·868

the period 1976–2001 (Fig. 4). As farmland birds also displayed a continuous decline during 1976–2001, there was a strong association between annual yearly PC1 scores and multispecies indices (Fig. 4).

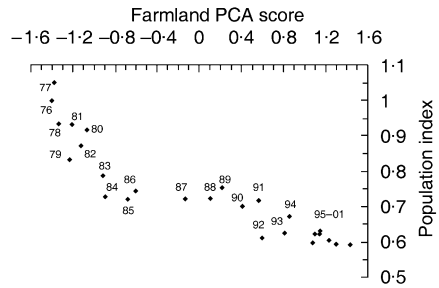

Fig. 4. Annual scores from the first axis of a PCA based on 21 agricultural variables between 1976 and 2001 plotted against the multispecies indices of 21 farmland bird species.

Several species declined more during the first half of the study period (Table 2). Chamberlain *et al.* (2000) suggested that delays might exist between the onset of agricultural changes and the onset of bird population declines. Therefore we performed a second PCA on agricultural variables including 6 years prior to the first year of bird data. Figure 5 plots the annual scores (1970–2001) on PC1 of agricultural variables and indicates that the changes in agriculture were relatively small from 1970 to 1982. Thus we could find no clear associations between changes in agriculture during the early 1970s and the sharp declines in many farmland bird species between 1976 and 1988.

Discussion

Many farmland bird species breeding in Sweden declined in numbers between 1976 and 2001 (Table 1)

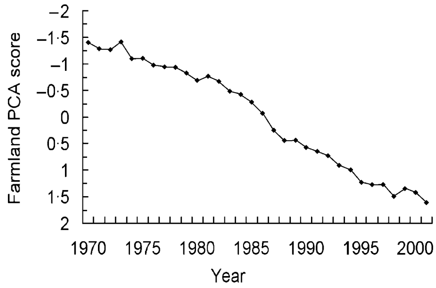

Fig. 5. Annual scores from the first axis of a PCA based on 20 agricultural variables between 1970 and 2001.

and this decline was most marked in the first part of this period (1976–88), broadly corresponding with findings from the UK (Fuller *et al.* 1995; Siriwardena *et al.* 1998). Our results only gave partial support to our predictions. First, in contrast to the prediction of less dramatic declines in Sweden than in England, Swedish farmland birds declined at least as much as those breeding in England. In addition, the Swedish bird declines were stronger in the first half of the study period, although farmland practices changed to a greater extent during the second half of the study period (Fig. 4). Secondly, we found declines mainly in farmland specialists, in common with results from the UK. This supports the view that the cause of the decline is connected to agriculture (Aebischer *et al.* 2000; Vickery *et al.* 2004) and that species with specialist requirements are most sensitive to agricultural change (Shultz *et al.* 2005). However, it is possible that generalist species also suffered detrimental effects of agricultural intensification but that this was masked by immigration (i.e. a buffer effect; Brown 1969) from other source habitats (e.g. forests and urban areas). Our third prediction was not supported because the bird populations declined despite a reduction in the use of fertilizers and pesticides over the study period and no change in the use of autumn-sown crops.

Agriculture in Finland is similar to that in Sweden in terms of land use (e.g. a low proportion of autumn-sown crops) and agricultural change (e.g. concurrent intensification and abandonment; Pitkänen & Tiainen 2001). Interestingly, Finnish farmland bird populations display similar trends to those observed in Sweden (Väisänen, Lammi & Koskimies 1998; Pitkänen & Tiainen 2001), suggesting that our results may be generalized to other similar north European agricultural landscapes. We believe, however, that our results indicate that there is no single straightforward method of predicting farmland bird population trends based on agricultural data at the country level (cf. Donald, Green & Heath 2001) and that the factors causing farmland bird populations to change may vary between countries.

Despite the marked differences in agriculture and its intensification between Sweden and England, several bird species displayed similar negative population trends, of which some species also showed temporal similarities (e.g. skylark and linnet). Other species displayed marked differences (e.g. woodpigeon, stock dove, hooded/carrion crow, jackdaw and tree sparrow; cf. Fig. S1 in the supplementary material and Crick *et al.* 2004). We suggest three possible explanations for the similarities: (i) population trends among countries are linked through a common shared population; (ii) populations share wintering grounds; (iii) the effects of intensive vs. reduced levels of farming (abandonment) have similar consequences for important features such as field layer structures and landscape heterogeneity.

Data on long-distance natal and breeding dispersal between countries are generally lacking, but it is unlikely that rates of dispersal between England and Sweden for most species included in our analyses are large enough to cause population trends to be as synchronous as observed here (Wernham *et al.* 2002). Although migration status was not significantly related to observed declines in Sweden (see also Siriwardena *et al.* 1998), four short-distance migratory species (lapwing, skylark, starling and linnet) displayed marked population declines. These species share wintering grounds (i.e. western Europe) with British populations (The Swedish Bird Ringing Center, T. Fransson, personal communication; Wernham *et al.* 2002). In this region of Europe the area of winter stubble has decreased dramatically, partly caused by an increased use of autumn-sown crops, and resources available to overwintering birds have therefore deteriorated (Lindström & Alerstam 1986; Moorcroft *et al.* 2002). For many farmland species changes in survival rates in the non-breeding season may be an important mechanism behind population changes (Siriwardena, Baillie & Wilson 1998, 1999). Thus the remarkably similar temporal trends for skylarks and linnets in Sweden and England could potentially be explained by agricultural changes at shared wintering grounds.

However, deterioration in overwintering conditions are probably not the only explanation for the declines in some species. For example, lapwings and linnets in the UK suffer from reduced productivity, probably because of changes in agricultural practices on their breeding grounds (Hudson, Tucker & Fuller 1994; Siriwardena, Baillie & Wilson 1999; Siriwardena *et al.* 2000). Furthermore, several farmland bird species (e.g. lapwings, skylarks and linnets) display different population trends in different agricultural regions within Sweden (J. Wretenberg, Å. Lindström, S. Svensson and T. Pärt, unpublished data).

Some factors are not easily captured by agricultural statistics, for example vegetation structure and landscape heterogeneity. Studies from the UK suggest that the decline of skylarks is partly a result of a reduced number of breeding attempts caused by changes in vegetation structure. The increasingly abundant autumn-sown crops simply become too dense and tall to be suitable as nesting habitat relatively early in the breeding season (Wilson *et al.* 1997). Although the use of autumn-sown crops has remained more or less stable in Sweden, two other habitats characterized by tall and dense field layers (non-rotational set-aside and improved cultivated grasslands) have increased at the expense of cereal fields, and particularly so in areas of low productivity (Clason & Granström 1992). Furthermore, the area of arable land decreased consistently throughout the study period, mainly because of abandonment in areas with low productivity (Ihse 1995). The area of spring-sown crops (mainly oats and barley) decreased rapidly by approximately 40% (550 000 ha) between the mid-1980s and mid-1990s (Fig. 2f). Therefore, the proportion of arable land with tall and dense vegetation, unsuitable as breeding habitat for skylarks and lapwings (Berg, Lindberg & Kallebrink 1992; Wilson *et al.* 1997), has increased in Sweden. It has been suggested that set-aside is beneficial for farmland birds (Berg & Pärt 1994; Henderson *et al.* 2000) but this concerns mainly natural regenerated rotational set-aside, whereas non-rotational set-aside is structurally more uniform and dense (Henderson *et al.* 2000). Furthermore, the reduction of arable habitats in regions with small-scale farming may have been detrimental to several farmland bird species, as cereal fields may have a positive effects on farmland bird abundance in regions dominated by other types of farming (Robinson, Wilson & Crick 2001).

The dual effects of the increased economic demands on agriculture resulting in intensification and abandonment have resulted in a loss of heterogeneity at the farmland landscape level in Sweden. In intensively farmed landscapes many residual habitats (e.g. stonewalls, ditches, grassy field boundaries and wetlands) have been removed and production at the farm level has specialized into either cereal production or animal husbandry (Robertson, Eknert & Ihse 1990; Statistics Sweden 1990; Ihse 1995). In landscapes of traditional small-scale farming (i.e. in forest-dominated landscapes), the loss of habitats with short field layers (e.g. grazed pastures and spring-sown crop fields), together with afforestation in some areas, has also reduced the landscape heterogeneity of these previously mosaic landscapes (Robertson, Eknert & Ihse 1990; Statistics Sweden 1990; Ihse 1995). This is likely to have serious effects on farmland birds (Benton, Vickery & Wilson 2003) and is in line with previous findings from Swedish farmland that surrounding landscape heterogeneity may be an important determinant for local bird abundance (Pärt & Söderström 1999; Söderström & Pärt 2000; Berg 2002).

Several farmland generalists (woodpigeon, hooded crow, magpie and jackdaw) and one specialist species (stock dove) have stable or declining populations in Sweden whereas they have increased rapidly in England (Table 1; see Fig. S1 in the supplementary material). Increases of the three corvid species in England have been associated with increased breeding performance, which may reflect their generalist and innovative feeding habits in the dynamic agricultural landscape (Crick *et al.* 2004). The increase of woodpigeon and stock dove, on the other hand, is thought to be a result of the increase in oilseed rape production and a recovery from the organochlorine seed dressings used in the 1950s and the 1960s (Inglis *et al.* 1990; Gibbons, Reid & Chapman 1993). None of these hypotheses explains why these species do not show the same trends in Sweden, as they share general food preferences and to some extent also wintering areas (Cramp, Simmons & Perrins 1977–94). A possible explanation could be the buffer effect (Brown 1969). For example, generalist species declining in Sweden (e.g. woodpigeon and whinchat) may do so because the farmland habitat is a sink habitat reflecting population changes in source habitat types (e.g. forests, bogs and clearings). Other differences in population trends are truly enigmatic, such as the dramatic decline of the tree sparrow population in UK but not in Sweden.

Farming has become more intensive across much of Europe, with associated negative effects on bird populations (Donald, Green & Heath 2001). However, a reduction in farming or complete abandonment is also widespread (MacDonald *et al.* 2000) and may affect farmland birds negatively (e.g. Italian Alps, Laiolo *et al.* 2004; northern Spain, Suarez-Seoane, Osborne & Baudry 2002; Hungary; Verhulst, Baldi & Kleijn 2004). Our results highlight the importance of developing dynamic agri-environmental schemes, not only to reduce the negative effects of intensive agriculture but also to prevent abandonment of farmland in less productive regions. In the UK, well-designed agri-environmental schemes have been successful in reversing the trends for at least four farmland bird species (Aebischer, Green & Evans 2000). Whether similar schemes can be successful in the northern European countries is difficult to predict because many species winter elsewhere. Furthermore, if a reduction in landscape heterogeneity as a result of abandonment is a major problem for populations inhabiting the forested farmland landscapes of northern Europe, agri-environmental schemes designed for the highly intensified farmland plains may be less effective in northern farmland landscapes. On the other hand, well-designed agri-environmental schemes from western Europe may also increase winter survival of populations breeding further north (e.g. through increasing the amount of winter-stubble fields; Gillings *et al.* 2005). This highlights the important fact that the conservation of farmland birds is an issue without country borders.

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References

Aebischer, N.J., Evans, A.D., Grice, P.V. & Vickery, J.A. (Eds) (2000) *Ecology and Conservation of Lowland Farmland Birds.* British Ornithologists' Union, Tring, UK.

Aebischer, N.J., Green, R.E. & Evans, A.D. (2000) From science to recovery: four case studies of how research has been translated into conservation action in the UK. *Ecology and Conservation of Lowland Farmland Birds* (eds N.J. Aebischer, A.D. Evans, P.V. Grice & J.A. Vickery), pp. 43–54. British Ornithologists' Union, Tring, UK.

Benton, T.G., Vickery, J.A. & Wilson, J.D. (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution*, **18**, 182–188.

Berg, Å. (2002) Composition and diversity of bird communities in Swedish farmland–forest mosaic landscapes. *Bird Study*, **49**, 153–165.

Berg, Å. & Pärt, T. (1994) Abundance of breeding farmland birds on arable and set-aside fields at forest edges. *Ecography*, **17**, 147–152.

Berg, Å., Lindberg, T. & Kallebrink, K.G. (1992) Hatching success of lapwings on farmland: differences between habitats and colonies of different sizes. *Journal of Animal Ecology*, **61**, 469–476.

ter Braak, C.J.F. & Šmilauer, P. (1997–2002) *CANOCO for Windows, Version 4·5.* Biometris–Plant Research International, Wageningen, the Netherlands.

ter Braak, C.J.F. & Šmilauer, P. (2002) *CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination* Version 4·5. Microcomputer Power, Ithaca, NY.

Brown, J.L. (1969) The buffer effect and productivity in tit populations. *American Naturalist*, **103**, 347–329.

Burn, A.J. (2000) Pesticides and their effects on lowland farmland birds. *Ecology and Conservation of Lowland Farmland Birds* (eds N.J. Aebischer, A.D. Evans, P.V. Grice & J.A. Vickery), pp. 89–104. British Ornithologists' Union, Tring, UK.

Chamberlain, D.E., Fuller, R.J., Bunce, R.G.H., Duckworth, J.C. & Shrubb, M. (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. *Journal of Applied Ecology*, **37**, 771–788.

Clason, Å. & Granström, B. (1992) *National Atlas of Sweden: Agriculture.* Almqvist & Wiksell International, Stockholm, Sweden.

Cramp, S., Simmons, K.E.L. & Perrins, C.M. (1977–94) *The Birds of Western Palaearctic.* Volumes I–IX. Oxford University Press, Oxford, UK.

Crick, H.Q.P., Marchant, J.H., Noble, D.G., Baillie, S.R., Balmer, D.E., Beaven, L.P., Coombes, R.H., Downie, I.S., Freeman, S.N., Joys, A.C., Leech, D.I., Raven, M.J., Robinson, R.A. & Thewlis, R.M. (2004) *Breeding Birds in the Wider Countryside: Their Conservation Status 2003*. BTO Research Report No. 353. BTO, Thetford, UK (http://www.bto.org/birdtrends2003, accessed 1 October 2005).

Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **268**, 25–29.

FAOSTAT (2005) *Agriculture*. Food and Agriculture Organization of the United Nations, Rome, Italy (http://faostat.fao.org, accessed 1 October 2005).

Fox, A.D. (2004) Has Danish agriculture maintained farmland bird populations? *Journal of Applied Ecology*, **41**, 427–439.

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.

Gibbons, D.W., Reid, J.R. & Chapman, R.A. (1993) *The New Atlas of Breeding Birds in Britain and Ireland*. Poyser, London, UK.

Gillings, S., Newson, S.E., Noble, D.G. & Vickery, J.A. (2005) Winter availability of cereal stubbles attracts declining farmland birds and positively influences breeding population trends. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **272**, 733–739.

Gregory, R.D., van Strien, A., Vorisek, P., Meyling, A.W.G., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W. (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B, Biological Sciences*, **360**, 269–288.

Henderson, I.G., Cooper, J., Fuller, R.J. & Vickery, J. (2000) The relative abundance of birds on set-aside and neighbouring fields in summer. *Journal of Applied Ecology*, **37**, 335–347.

Hudson, R., Tucker, G.M. & Fuller, R.J. (1994) Lapwing *Vanellus vanellus* populations in relation to agricultural changes. *The ecology and conservation of lapwing Vanellus vanellus* (eds G.M. Tucker, S.M. Davies & R.J. Fuller), pp. 1–33. UK Nature Conservation No. 9. Joint Nature Conservation Committee, Peterborough, UK.

Ihse, M. (1995) Swedish agricultural landscapes: patterns and changes during the last 50 years, studied by aerial photos. *Landscape and Urban Planning*, **31**, 21–37.

Inglis, I.R., Isaacson, A.J., Thearle, R.J.P. & Westwood, N.J. (1990) The effects of changing agricultural practice upon woodpigeon *Columba palumbus* numbers. *Ibis*, **132**, 262–272.

Krebs, J.R., Wilson, J.D., Bradbury, R.B. & Siriwardena, G.M. (1999) The second silent spring? *Nature*, **400**, 611–612.

Laiolo, P., Dondero, F., Ciliento, E. & Rolando, A. (2004) Consequences of pastoral abandonment for the structure and diversity of the alpine avifauna. *Journal of Applied Ecology*, **41**, 294–304.

Lindström, Å. & Alerstam, T. (1986) The adaptive significance of reoriented migration of chaffinches *Fringilla coelebs* and bramblings *F. montifringilla* during autumn in southern Sweden. *Behavioral Ecology and Sociobiology*, **19**, 417–424.

Lindström, Å. & Svensson, S. (2005) *Övervakning Av Fåglarnas Populationsutveckling. Årsrapport för 2004.* Ekologiska institutionen, Lunds universitet, Lund, Sweden.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models*, 2nd edn. Chapman & Hall, London, UK.

MacDonald, D., Crabtree, J.R., Wiesinger, G., Dax, T., Stamou, N., Fleury, P., Lazpita, J.G. & Gibon, A. (2000) Agricultural abandonment in mountain areas of Europe: environmental consequences and policy response. *Journal of Environmental Management*, **59**, 47–69.

Moorcroft, D., Whittingham, M.J., Bradbury, R.B. & Wilson, J.D. (2002) The selection of stubble fields by wintering granivorous birds reflects vegetation cover and food abundance. *Journal of Applied Ecology*, **39**, 535–547.

Ormerod, S.J. & Watkinson, A.R. (2000) Birds and agriculture: editors' introduction. *Journal of Applied Ecology*, **37**, 699–705.

Pannekoek, J. & van Strien, A.J. (2001) *TRIM 3 Manual. Trends and Indices for Monitoring Data.* Research Paper No. 0102. Statistics Netherlands, Voorburg, the Netherlands.

Pärt, T. & Söderström, B. (1999) The effects of management regimes and location in landscape on the conservation of farmland birds breeding in semi-natural pastures. *Biological Conservation*, **90**, 113–123.

Piha, M., Pakkala, T. & Tiainen, J. (2003) Habitat preferences of the Skylark *Alauda arvensis* in southern Finland. *Ornis Fennica*, **80**, 97–110.
Pitkänen, M. & Tiainen, J. (2001) *Biodiversity of Agricultural Landscapes in Finland.* BirdLife Finland Conservation Series No 3. BirdLife Finland, Helsinki, Finland.
Robertson, J. & Berg, Å. (1992) Status and population changes of farmland birds in southern Sweden. *Ornis Svecica*, **2**, 119–130.
Robertson, J.G.M., Eknert, B. & Ihse, M. (1990) Habitat analysis from infrared aerial photographs and the conservation of birds in Swedish agricultural landscapes. *Ambio*, **19**, 195–203.
Robinson, R.A., Wilson, J.D. & Crick, H.Q.P. (2001) The importance of arable habitat for farmland birds in grassland landscapes. *Journal of Applied Ecology*, **38**, 1059–1069.
Shultz, S., Bradbury, R.B., Evans, K.L., Gregory, R.D. & Blackburn, T.M. (2005) Brain size and resource specialization predict long-term population trends in British birds. *Proceedings of the Royal Society of London Series B, Biological Sciences.*
Sibley, C.G. & Monroe, B.L. (1990) *Distribution and Taxonomy of the Birds of the World*. Yale University Press, New Haven, CT.
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.Q.P., Wilson, J.D. & Gates, S. (2000) The demography of lowland farmland birds. *Ecology and Conservation of Lowland Farmland Birds* (eds N.J. Aebischer, A.D. Evans, P.V. Grice & J.A. Vickery), pp. 117–133. British Ornithologists' Union, Tring, UK.
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.
Siriwardena, G.M., Baillie, S.R. & Wilson, J.D. (1999) Temporal variation in the annual survival rates of six granivorous birds with contrasting population trends. *Ibis*, **141**, 621–636.
Söderström, B. & Pärt, T. (2000) Influence of landscape scale on farmland birds breeding in semi-natural pastures. *Conservation Biology*, **14**, 522–533.
SOF (2003) *Fågelåret 2002*. SOF, Stockholm, Sweden.
Statistics Sweden (1990) *The Natural Environment in Figures*, 3rd edn. Statistics Sweden, Stockholm, Sweden.
Statistics Sweden (2001) *The Yearbook of Agricultural Statistics 2001.* Statistics Sweden, Örebro, Sweden.
Suarez-Seoane, S., Osborne, P.E. & Baudry, J. (2002) Responses of birds of different biogeographic origins and habitat requirements to agricultural land abandonment in northern Spain. *Biological Conservation*, **105**, 333–344.
Tucker, G.M. & Heath, M.F. (1994) *Birds in Europe: Their Conservation Status.* BirdLife International, Cambridge, UK.
Väisänen, R.A., Lammi, E. & Koskimies, P. (1998) *Distribution, Numbers and Population Changes of Finnish Breeding Birds.* Otava, Keuruu, Finland.
Verhulst, J., Baldi, A. & Kleijn, D. (2004) Relationship between land-use intensity and species richness and abundance of birds in Hungary. *Agriculture Ecosystems and Environment*, **104**, 465–473.
Vickery, J.A., Evans, A., Grice, P., Brand-Hardy, R. & Aebischer, N.A. (Eds) (2004) Ecology and conservation of lowland farmland birds. II. The road to recovery. *Ibis*, **146** (Supplement 2).
Wernham, C.V., Toms, M.P., Marchant, J.H.C., Lark, J.A., Siriwardena, G.M. & Baillie, S.R. (2002) *The Migration Atlas: Movements of the Birds of Britain and Ireland.* T. & A. D. Poyser, London, 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.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from http://w.w.w.blackwell-synergy.com.

Table S1. Phylogeny and ecological characteristics of 21 farmland bird species.

Figure S1. TRIM indices for 21 farmland bird species showing the changes in abundance in Sweden between 1976 and 2001.

