

The Decline of Farmland Birds in Sweden

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Abstract

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Many farmland bird species have declined rapidly throughout Europe during the last 30 years and studies, mainly from the UK, suggest that these declines have been caused by agricultural intensification. However, since the conditions for farming vary considerably across Europe, the underlying causes of the population declines may also vary. The rate of agricultural intensification has been less dramatic since the mid 1970s in Sweden than in south-western Europe. Still, I show that population trends of farmland birds have declined at least as much in Sweden as in England between 1976 and 2001. Separating population trends in three Swedish landscape types with different patterns of agricultural change showed that the declines were most pronounced in the open plains characterised by intensification and in the forest farmland landscapes characterised by extensification or abandonment. Thus, the observed strong decline of farmland birds in Sweden was probably caused by the dual negative effects of intensification in productive regions and abandonment in marginal farmland. Several species displayed great temporal similarities in population trends within regions in Sweden and in comparison to England. These between population similarities may have been caused by large-scale effects of changing agricultural policies, as farmland bird population trend shifts were closely linked to agricultural policy shifts in Sweden and western Europe. However, it is also possible that reduced survival at wintering grounds may have had an additional effect because it was especially species that shared European wintering grounds that displayed the strongest between population synchrony in trends. Several farmland bird populations decreased less or even increased during the set-aside policy period (1987 to 1995) when agricultural became less intensive. However, a repeated census of farmland birds between 1994 and 2004 suggested that a general reduction of farming intensity, e.g. by increasing area of set-aside, leys and cultivated pasture, mainly benefit farmland birds in farmland-dominated landscapes where such land-use is rare, whereas a reduced farming intensity was negative for species richness in forest-dominated landscapes. In contrast, in forest-dominated landscapes farmland bird species seemed to benefit from an increased area of cereal production. My results of landscape-dependent patterns of relationships between farmland bird population changes and changes in land-use highlights the importance of developing new region-specific agri-environmental schemes. The results also suggest that an effective way of changing the present negative trends of farmland birds is a broad change in agricultural policy to reverse the geographical polarisation of farming activities.

Keywords: Agricultural intensification, farmland, abandonment, farmland birds, population declines, extensification, set-aside, Common Agricultural Policy, (CAP), winter wheat, semi-natural pastures, Agri-environmental scheme

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Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals:

- I. Wretenberg, J., Lindström, Å., Svensson, S., Thierfelder, T. & Pärt, T. 2006. Population trends of farmland birds in Sweden and England: similar trends but different patterns of agricultural intensification. *Journal of Applied Ecology* 43, 1110-1120
- II. Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. Wretenberg, J., Lindström, Å., Svensson, S., & Pärt, T. (Manuscript).
- III. Changes in local species richness of farmland birds in relation to land-use changes and landscape structure. Wretenberg, J., Pärt, T. & Berg, Å. (Manuscript).
- IV. Linking changes in local abundance of farmland bird species to changes in land-use. Wretenberg, J., Pärt, T. & Berg, Å. (Manuscript).

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Introduction

Many farmland bird species have declined rapidly throughout Europe during the last 30 – 40 years (Tucker & Heath 1994; Siriwardena *et al.* 1998; Donald, Green & Heath 2001; Donald *et al.* 2006) and these declines have generally been attributed to the intensification of agriculture (Chamberlain *et al.* 2000; Donald, Green & Heath 2001; Gregory *et al.* 2005). This agricultural change includes for example increased use of fertilizers and pesticides, simplified crop rotations, more homogenous and dense crops and loss of semi-natural grasslands and non-farmed habitats (Stoate *et al.* 2001; Robinson & Sutherland 2002; Newton 2004; Wilson, Whittingham & Bradbury 2005). Furthermore, many European countries have experienced extensive farmland abandonment (MacDonald *et al.* 2000; EEA 2004) and although less studied, abandonment is likely to affect farmland birds negatively as well (e.g., Suarez-Seoane, Osborne & Baudry 2002; Laiolo *et al.* 2004).

The conditions for farming differ across Europe because of differences in landscape structure, climate and agricultural policies. This has resulted in a cross-country variation from low to high intensity farming (Fig. 1a). Most clear are the differences between western Europe and eastern Europe, which partly reflect different agricultural policies. In the old EU countries, the Common Agricultural Policy (CAP) has encouraged production (Potter 1997; Sanderson, Donald & Burfield 2006), which has resulted in a considerable agricultural intensification. In contrast, because of a combination of lower agricultural subsidies and the break-up of the former Eastern Block in 1990, countries in eastern Europe have had a lower agricultural intensification during the last 15 years (Gregory *et al.* 2005; Sanderson, Donald & Burfield 2006). These differences in agricultural policies across Europe have been linked to large-scale differences in farmland bird population trends because declines of farmland birds in Europe have been more severe in western Europe compared with eastern Europe (Schifferli 2000; Donald, Green & Heath 2001; Gregory *et al.* 2005).

Although agricultural intensification may be a major underlying cause of the declines of farmland birds in Europe, intensification is only but a vague concept. However, individual species respond to specific changes in the landscape that are related to species-specific habitat requirements (Berg 1992; Berg, Lindberg & Kallebrink 1992; Aebischer *et al.* 2000). A complicating factor when searching for the specific causes to farmland bird declines is that many species use multiple habitats (Söderström & Pärt 2000; Vickery *et al.* 2004a). Although largely unknown for farmland birds, habitat preferences may differ between countries or regions because of differences in landscape structure and land-use. Because condition for farming vary considerably across Europe, the causes of the declines are also likely to be region-specific. An example of such a regional difference in land-use is the rapid increase in winter wheat in the UK, which has been linked to the decline of several farmland bird species (Newton 2004), whereas in Sweden, this crop has remained stable (Fig. 1b). However, even in regions with similar changes in land-use and landscape structure population trends may differ (Fox 2004).

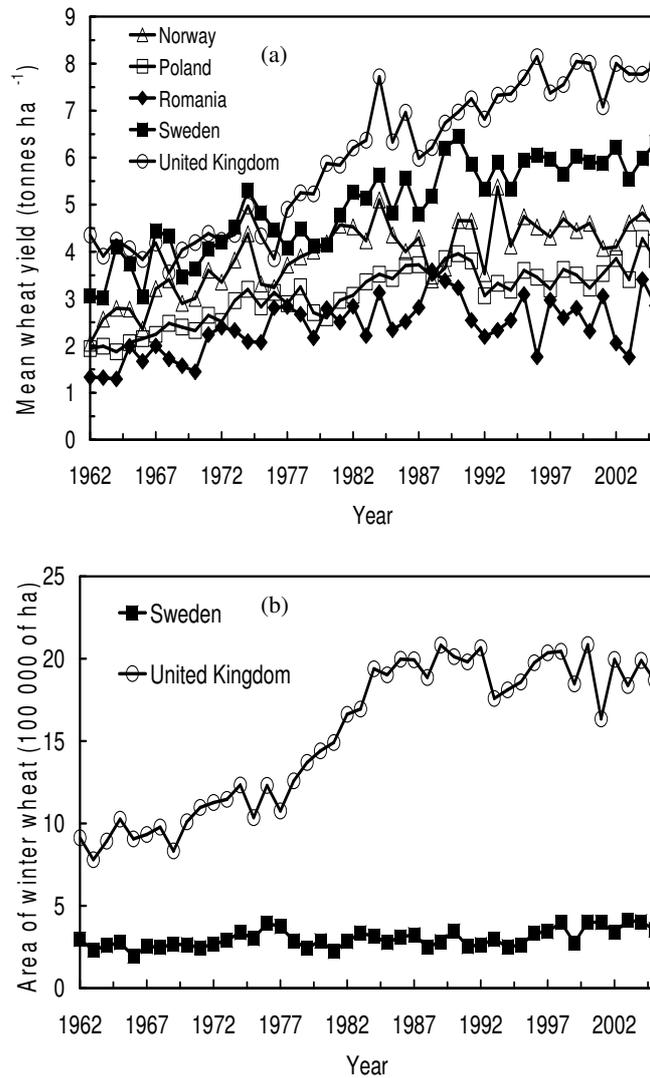


Fig. 1. Comparison of mean wheat yield (tonnes ha⁻¹) in five different European countries (a) and areas of winter wheat in Sweden and the UK between 1962 and 2005 (b). From FAOSTAT (2006).

Even in the UK, where most farmland birds studies have been performed (Ormerod *et al.* 2003; Newton 2004), there exist gaps in knowledge of the casual factors causing declines in some species (Newton 2004). In other parts of Europe the knowledge about farmland bird declines is more sparse or lacking. More studies from other European regions are therefore needed to test (i) the generality of the links between farmland birds and agricultural intensification and (ii) whether other important causes of farmland bird declines exist in other parts of Europe.

Testing the links between agricultural intensification and farmland birds trends in Sweden: background and aims of Paper I and II

Sweden has one of the longest monitoring surveys of breeding birds in Europe (Vorisek & Marchant 2003; Lindström & Svensson 2005) and the survey thus covers some major changes in Swedish agriculture. Below, I describe three possible ways to use the monitoring data to assess the hypothesis that agricultural intensification is the main driver of farmland bird declines, not only in western Europe, but also in Scandinavia.

Using comparisons between countries

Sweden represents a region of Europe where farming conditions differ in many aspects compared to western European countries. For example, Sweden has a different history of agricultural policy (Sweden joined the EU and the CAP in 1995), and farming intensity is intermediate compared with western Europe and eastern Europe (Fig. 1a). Furthermore, the landscape composition differ (the areas of farmland in Sweden and the UK are 7% and 70% of total land area, respectively; FAOSTAT 2006) and trends in some specific agricultural practices differ (Fig. 1b). This makes Sweden suitable to test whether difference in intensity and intensification between countries are reflected in different population declines of farmland birds as suggested by Donald, Green & Heath (2001). The aim of Paper I was to: (i) compare farmland bird trends between Sweden and England and (ii) relate changes in Swedish agriculture to farmland bird population trends in Sweden.

Using comparison between regions within Sweden

Furthermore, conditions for farming also vary between regions within Sweden. In southern Sweden, three relatively distinct agricultural regions can be identified (Fig. 2). These regions differ in landscape structure and farming intensity: (a) intensively managed arable land in the open plains with low proportion of grasslands (Fig. 3a), (b) less intensive farming in mosaic farmlands (Fig. 3b), and (c) infield farming in forest-dominated regions, which are characterised by low intensity and high proportion of grasslands (Fig. 3c). These regions have also experienced differences in intensification, (mainly in the open plains, but also in the mosaic farmlands) and extensification or abandonment (mainly in the forest regions; Statistic Sweden 1970-2004). Thus, by using data from the Swedish Breeding Bird Survey and comparing the regional population trends of farmland birds, it is possible to test whether agricultural intensification is the main driver of the declines of farmland birds also at smaller spatial scales. This was the first the aim in Paper II.

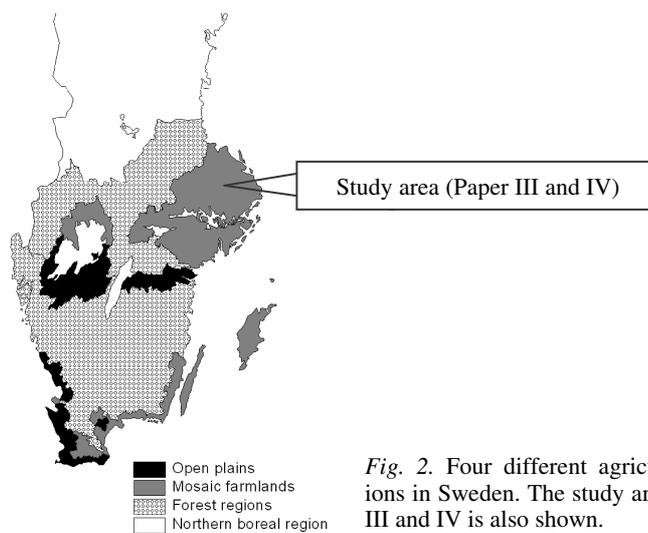


Fig. 2. Four different agricultural regions in Sweden. The study area of Paper III and IV is also shown.

Using comparisons between periods of different agricultural policy

The agricultural policy in Sweden has changed drastically two times since the early 1970s and three distinct phases can be identified. The first phase (the intensification period, pre-1970 to 1987) was dominated by intensified cereal production, high inputs of pesticides and fertilizers and a rapid increase in yield per hectare. Removal of non-crop habitats (e.g. ditches, stone walls and field roads) and amalgamation of small farms and fields into larger units was also a widespread phenomenon during this period (Statistic Sweden 1970-2004; Gerell 1988; Robertson, Eknert & Ihse 1990; Ihse 1995). The second phase (the set-aside period, 1987 to 1995) was caused by a huge surplus production of cereals in Sweden. As a result, Sweden initiated a set-aside programme in 1987, which was followed by additional programmes in 1990 (Swedish Board of Agriculture 2006a). During this period Sweden also launched the first agri-environment schemes and the use of fertilizers and pesticides decreased (Statistics Sweden 1990). The third phase started in 1995 when Sweden joined the EU and the Common Agricultural Policy (CAP). Production supporting subsidies were reintroduced and use of pesticides increased. Furthermore, during this period the area of farmland under agri-environment schemes increased rapidly (Swedish Board of Agriculture 1999, 2006a).

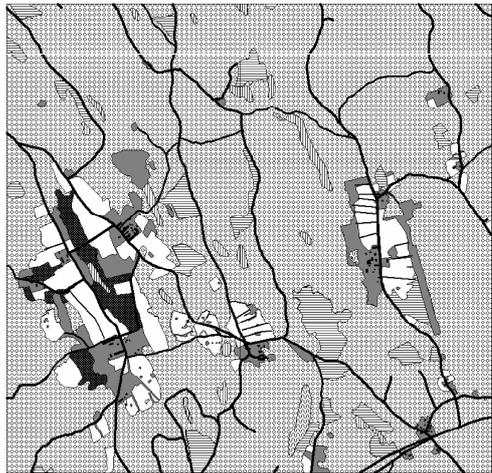
Agricultural policies during these three periods were likely to promote both intensification (during the first and third periods) and extensification (during the second period). Thus by linking population trends from the monitoring data to these three periods, it was possible to test the hypothesis that broad changes in agricultural policy affect population trends of farmland birds. This was the second aim in Paper II.



(a)



(b)



(c)

-  Arable land
-  Marsh
-  Coniferous forest
-  Clearing
-  Deciduous forest
-  River or lake
-  Garden and semi-natural pasture
-  Road
-  House and farmhouse

Fig. 3. Three different types of landscapes. (a) open plains, (b) mosaic farmlands and (c) forest regions. Thin lines are ditches. However, within each region the landscape composition varies considerably.

0 1 2 Kilometers

Assessing the effects of low intensity farming and habitat heterogeneity on farmland birds: background and aims of Paper III and IV

Because of the limited knowledge of the causal factors to species declines it has been difficult to develop effective countermeasures to reverse the declining population trends of farmland birds. Conservation actions are normally expensive and may be species-specific and the few successful cases that have been performed normally concern rare and very well-studied species (Aebischer, Green & Evans 2000). However, to reverse farmland bird declines we need measures on a large geographical scale, and the only practicable way will be through well designed agri-environmental schemes (Vickery *et al.* 2004a) although hitherto the positive effects of such schemes have yet been limited (Kleijn *et al.* 2001; Kleijn & Sutherland 2003; Kleijn *et al.* 2006).

One measure that is suggested to positively affect farmland biodiversity is a general reduction in farming intensity. This has also been the main objectives in many agri-environmental schemes (e.g. by reducing nutrient and pesticide emissions; Kleijn & Sutherland 2003). A second suggested measure, which is likely to have a broad positive effect on a number of species, would be to increase habitat heterogeneity, from the scale of fields (e.g. by increasing the number of crops grown per farm) to whole landscapes. In this way more species would be able to find suitable and alternative habitats (Benton, Vickery & Wilson 2003). It has also been suggested that increasing the area of set-aside and other low-intensity crops, e.g. short rotation coppice (Berg 2002a; Van Buskirk & Willi 2004) would benefit farmland birds and especially in intensively managed regions, where a few different crops dominate the production. This would not only reduce farming intensity, but also increase habitat heterogeneity.

The suggested countermeasures to reverse population declines of farmland birds discussed above have originated mainly from studies in western Europe. The Swedish farmland could therefore be used to test whether these countermeasures have a general positive effect across countries that (i) partly have experienced different changes in agricultural practices, (ii) differ considerably in landscape structure (e.g. amount of forest), and (iii) have a general lower degree of agricultural intensity. One way to test the effect of reduced farming intensity on farmland birds would be to repeat a census of farmland birds and take advantage of the crop-rotation systems that exist on farms. Such a semi-natural experiment would capture a number of transitions between low-intensity farming to high-intensity farming (e.g. from set-aside year one to winter wheat year two) and vice versa. Furthermore, a repeated census design implies that several potentially important non-crop habitats for farmland birds (e.g. amount of forest, length of ditches and structure of field-forest ecotones) are constant across years. Thus, correlations between changes in land-use and changes in farmland bird abundance would be a direct test of whether changes in land-use result in changes in farmland bird diversity.

To use repeated studies to estimate the effects of changes in habitat heterogeneity on farmland birds is more difficult because habitat heterogeneity is

often fairly constant on a short-term time scale. However, with repeated farmland bird censuses it is still possible to test whether sites with high level of habitat heterogeneity have a buffering effect against negative effects of land-use changes on changes in farmland bird abundance as would be expected if high habitat heterogeneity resulted in availability of high-quality alternative habitats.

The aim of Paper III was to test whether temporal changes in local species richness of farmland birds were related to corresponding changes in the amount of low-intensity land-use (i.e. set-aside, leys, cultivated pastures and short rotation coppice) surrounding the site, and whether sites with high habitat heterogeneity had a buffering effect on changes in species richness. The aim of Paper IV was to assess the effects of changes in areas of different crops on changes in abundance of common farmland bird species, and as in Paper III, to test the importance of habitat heterogeneity.

Methods

Long-term trends of farmland birds in Sweden (Paper I and II)

Agricultural regions and changes in agricultural policy in Sweden

In Papers I and II, we selected routes from the Swedish Breeding Bird Survey that were located south of latitude 61° N (i.e. including approximately 90% of all Swedish farmland; Statistics Sweden 2002). Because of differences in soil, bedrock type, topography and climate the conditions for farming differ between regions in Sweden. This is reflected in for example amount of forest in the landscape, sizes of farms and fields, and productivity, which in turn affect agricultural intensity and production (cereal or cattle production). Based on these differences, southern Sweden has traditionally been divided into six regions (Statistics Sweden 2002). We used this classification in Paper II. However, because of relatively low sample sizes in the monitoring data, we pooled the regions into three agricultural regions, which in the text will be referred to as (1) open plains, (2) mosaic farmlands and (3) forest regions (Figs. 2 and 3). Of the censused routes, 55, 168 and 146 were located in the open plains, the mosaic farmland and forest regions, respectively.

As described in the Introduction, the agricultural policy in Sweden has changed drastically two times since the early 1970s and three distinct phases can be identified. It was therefore possible to divide the bird data into three time periods (i.e. 1976-1987 “the intensification period”, 1987-1995 “the set-aside period” and 1995-2003 the CAP period).

Agricultural data, bird censuses and statistical methods

Agricultural data for the whole of Sweden and for the three different regions were collected from Statistics Sweden (Statistic Sweden 1970-2004). The quality of these data differs between variables. For example, the accuracy of regional areas of different crops was very good, whereas annual data on levels of pesticides or

fertilizers only existed on a country level. Changes in areas of semi-natural pastures since the mid 1970s was also difficult to estimate (e.g. the classification semi-natural pastures was changed in 1981; Statistic Sweden 1970-2004).

The Swedish Breeding Bird Survey started in 1975 and consists of routes with 20 point counts (Lindström & Svensson 2005). Since the aim was to study farmland birds in farmland landscapes, we selected routes that contained at least some farmland. The first year of the Swedish Breeding Bird Survey, 1975, was omitted because disproportionately few routes were censused this year. We also excluded routes that were censused only one or two years. Paper I included routes censused between 1976 and 2001, whereas Paper II covered the period 1976 to 2003. The total number of routes included in the analyses was 355 (Paper I) and 369 (Paper II). All population trends were calculated using TRIM (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).

The importance of landscape structure, land-use and heterogeneity for farmland birds (Paper III and IV)

Agricultural statistics and habitat mapping

The bird censuses in Paper III and IV were restricted to the counties of Uppland and Västmanland (approximately 59° 40' N - 60° 07' N and 16° 30' E - 18° 10' E) in south-central Sweden (Fig. 2). Thus, all the census sites in Paper III and IV were located in the mosaic farmland region (Fig. 2). However, since the landscape in this region was highly variable, the sites could be located in landscapes with different amounts of forest at the scale of 600 m radius of the point centre (median 28%, range 0-92%).

All sites were located in farmland and the proportion of farmland within 100 m (i.e. the radius used for bird censuses) was high and 75% of the sites had more than 80% farmland within 100 m. The sites were mainly located in arable fields and the proportion of semi-natural pastures was low (87% had no semi-natural pasture within 100 m). Habitat mapping was made within 300 m of the point centres with the help of field visits, land-use maps (1:10 000) and aerial photographs. A detailed map was made and the proportions of different habitats and land-use types (crops) were estimated. In Paper III, we calculated the proportion of arable land consisting of low-intensity land-use (i.e. set-aside, short rotational coppice, leys and cultivated pastures, which are cultivated less often and treated with lower levels of pesticides and fertilizers than other high-intensity crops such as cereals, rape and pea), whereas in Paper IV, we analysed the amount of single crops. Furthermore, in both Paper III and IV, three different habitat heterogeneity indices were calculated: (i) length of linear habitats (i.e. total length (m) of all roads, ditches and grass strips between fields), (ii) landscape heterogeneity (i.e. number of transitions between arable land and farms, habitat islands within-fields, semi-natural pastures, coniferous forest, deciduous forest, young forest, gardens, rivers, lakes and a final class including other rare habitats) and (iii) land-use heterogeneity (includes short rotation coppice, leys, cultivated

pasture, non-rotational set-aside, rotational set-aside, spring-sown crops and autumn-sown crops). Land-use heterogeneity was calculated according to Hurlbert's (1971) diversity index (i.e. "PIE", see equation 1), where N equals the total number of land-use types and p(i) represents the proportion of the entire sample represented by land-use type (i)

$$PIE = \left(\frac{N}{N-1} \right) \left(1 - \sum_{i=1}^S p_i^2 \right) \quad \text{Equation 1}$$

At a larger distance (within 600 m radius from the census point) the proportion of the landscape that was covered by forests and arable fields were estimated to get a measure of the surrounding landscape composition. However, these two variables were strongly correlated ($r = -0.88$, $P < 0.001$) and we therefore only used proportion of the landscape covered by forest.

Farmland bird censuses

Birds were censused with point counts (Bibby, Burgess & Hill 1992) at 248 sites. All sites were visited six times in 1994 and five times in 2004 during early morning (mainly from sunrise to 10 am), once in each of the periods 15–30 April (only 1994), 1–10 May, 11–20 May, 21–31 May, 1–10 June and 11–20 June. The first period (15–30 April) was not included in the census of 2004 due to the low number of observations of many farmland bird species in this time period in 1994. Only a few species (greenfinch and yellowhammer) had their maximum abundances observed in this early time period at a few sites. Thus, any observed differences in species richness or abundance between the two years were not caused by the reduced effort in 2004. The observer noted all birds seen and heard within 100 m during five minutes. Birds that were flushed when approaching the point and observed within the distance limit were also included. No counts were made on mornings with strong wind or rain. Observations of singing males and pairs were used to estimate the number of pairs observed at the point at each visits. Flocks of obviously migrating birds were not included in the censuses. Estimates of species richness in Paper III included the total number of species with territories at each site. In Paper IV, the maximum number of territories recorded during the censuses was used as an estimate of abundance (see Berg 2002b).

Statistical methods

In Paper III, associations between species-richness and habitat variables were analysed with multiple linear regression models. As an estimate of changes in species richness between 1994 and 2004 we used the residuals of species richness from the regression of species richness of 1994 on that of 2004. This variable was uncorrelated to species richness in 1994 but strongly correlated to the difference in species richness between the two surveys ($r = 0.90$, $P < 0.0001$). In these models we included amount of forest, landscape heterogeneity and total length of linear habitats as constant variables since these variables did not display measurable changes between 1994 and 2004. Changes in non-crop habitats (for example removal of ditches and field roads) have previous been a widespread phenomenon

in the region. However, since 1994 removal of most such farmland habitat has been prohibited in Sweden. Changes in amount of low-intensity land-use were calculated as the difference between 2004 and 1994 [(proportion of arable land consisting of low-intensity land-use in 2004) – (proportion of arable land consisting of low-intensity land-use in 1994)]. Similarly, the difference between land-use heterogeneity between 2004 and 1994 was used as a measure of change in land-use heterogeneity.

Associations between changes in species abundance and the independent variables in Paper IV were analysed using ordinal logistic regression models. As an estimate for change in abundance of individual species we used the absolute difference of territories recorded in 2004 and 1994. In most cases the difference in abundance varied between -1 to +1. Thus, it was not possible to use the residuals as described above for Paper III. Only sites with occurrence in at least one year were included in analyses for each species. Amount of forest, landscape heterogeneity, linear habitats elements and changes in land-use heterogeneity were included in the same way as in Paper III. As an estimate of changes in amount of individual land-use types, the absolute difference between areas (ha) of each land-use type within sites [(land-use type X 2004) – (land-use type X 1994)] was used. Changes in area of spring-sown crops was correlated with changes in area of autumn-sown crops ($r = -0.52$; $P < 0.001$) and we therefore chose to exclude changes in area of autumn-sown crops in the analyses. Correlations between all other independent variables were low ($r < 0.30$).

Selection and classification of species (Paper I, II, III and IV)

We classified the bird species as farmland specialists or generalists using the classification in Siriwardena *et al.* (1998), see Table 1. Species classified as specialists in the UK were also classified as specialists based on their broad habitat preferences in Sweden. However, several species classified as farmland generalist in the UK (e.g. bullfinch *Pyrrhula pyrrhula* L., dunnock *Prunella modularis* L., wren *Troglodytes troglodytes* L. and robin *Erithacus rubecula* L.; Fuller *et al.* 1995; Siriwardena *et al.* 1998; Chamberlain *et al.* 2000) are mainly confined to forest in Sweden. Therefore, the selection of species in the four studies slightly deviates from those published for other countries (e.g. Fuller *et al.* 1995; Siriwardena *et al.* 1998; Chamberlain *et al.* 2000; Fox 2004) and includes species previously considered to be linked to farming in Sweden (Robertson & Berg 1992; Berg & Pärt 1994; Pärt & Söderström 1999a, 1999b; Söderström & Pärt 2000; Berg 2002b).

The selection of farmland bird species differed between the four studies. In Paper I, II and IV, we only included common species with sufficient data to perform reliable analyses. Thus, in Paper I and IV, 21 and 16 common farmland bird species were included. In Paper II, where we focussed on farmland specialists that were either short distance migrants or residents, only seven species were included because sample sizes decreased rapidly when the data were separated into three regions and three time periods. In Paper III, where we focussed on species richness, all farmland bird species were included.

Results and discussion

Are differences in agricultural intensification between countries reflected in different population trends of farmland birds? (Paper I)

Based on findings mainly from lowland England (Aebischer *et al.* 2000; Newton 2004; Vickery *et al.* 2004b) and between country comparisons (Schifferli 2000; Donald, Green & Heath 2001), 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 expected to be most sensitive to agricultural changes in both countries independent of the degree of change (Shultz *et al.* 2005) and (iii) the temporal 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 population declines in England (Hudson, Tucker & Fuller 1994; Wilson *et al.* 1997; Burn 2000).

Of the 21 species associated with farmland in Sweden, 15 (71%) displayed a significant decline ($P < 0.05$) in numbers between 1976 and 2001 (Table 1). 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. 4). 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 *Numenius arquata* L., stock dove *Columba oenas* L., wryneck *Jynx torquilla* L., skylark *Alauda arvensis* L., northern wheatear *Oenanthe oenanthe* L., house sparrow *Passer domesticus* L. and linnet *Carduelis cannabina* L.; Table 1) of which the curlew experienced the greatest decline (average yearly decline of 7%).

There was a tendency for a stronger average decline of farmland birds in Sweden than England (Wilcoxon matched pairs test: $T = 45.0$, $n = 17$, $P = 0.14$). Our analyses showed that several farmland specialists have remarkably similar population trends in Sweden and England (e.g. skylark, linnet and yellowhammer *Emberiza citrinella* L.). However, other species show very different temporal trend patterns between the two countries (stock dove, carrion/hooded crow *Corvus cornix* L., magpie *Pica pica* L., woodpigeon *Columba palumbus* L. and tree sparrow *Passer montanus* L. (cf. Fig. 5 and Crick *et al.* 2004).

The 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. Second, we found declines mainly in farmland specialists, in common with results from the UK (Siriwardena *et al.* 1998). This supports the view that the cause of the decline is

connected to agriculture (Aebischer *et al.* 2000; Vickery *et al.* 2004b) and that species with specialist requirements are most sensitive to agricultural change (Siriwardena *et al.* 1998; Shultz *et al.* 2005). However, it is possible that

Table 1. Trend estimates, standard errors and total percentage change with confidence intervals 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 ¹	Number of routes ²	Overall trend estimate ³	S.E.	% population change in Sweden (95% CI)	% population change in England (90% CI)
<i>Lapwing</i>	279	0.985	0.004	-32 (-45, -15)	-46 (-63, -28)
<i>Curlew</i>	124	0.930	0.009	-84 (-90, -74)	-40 (-80, 4)
Woodpigeon	355	0.987	0.002	-28 (-36, -20)	147 (61, 257)
<i>Stock dove</i>	218	0.970	0.006	-54 (-65, -38)	63 (26, 132)
<i>Wryneck</i>	193	0.940	0.006	-79 (-85, -71)	Extinct
<i>Skylark</i>	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
<i>Northern wheatear</i>	216	0.963	0.006	-61 (-72, -46)	No data
<i>Whitethroat</i>	292	1.004	0.003	10 (-5, 28)	49 (14, 90)
<i>Red-backed shrike</i>	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)
<i>Tree sparrow</i>	271	0.989	0.005	-25 (-41, -5)	-97 (-99, -94)
<i>House sparrow</i> ⁴	225	0.949	0.005	-73 (-79, -65)	-69 (-78, -60)
Greenfinch	352	1.009	0.003	24 (9, 42)	13 (-12, 33)
<i>Linnet</i>	207	0.970	0.005	-53 (-64, -40)	-62 (-70, -52)
<i>Yellowhammer</i>	350	0.980	0.002	-40 (-46, -34)	-56 (-63, -48)

¹Species in bold display significant trends in Sweden ($P < 0.05$). Species in italics are classified as farmland specialists.

²The number of routes where each species was observed.

³The 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%.

⁴Available data for house sparrow from England is 1977-2000 (Crick *et al.* 2004).

generalist species also suffered detrimental effects of agricultural intensification but that this was masked by immigration (i.e. a buffer effect; Brown 1969a) from other source habitats, e.g. forests and urban areas. Our third prediction was not supported since the bird populations declined despite a reduction in the use of fertilizers and pesticides over the study period (Statistic Sweden 1970-2004), and the use of autumn-sown crops was not changing to a larger extent (Fig. 1b).

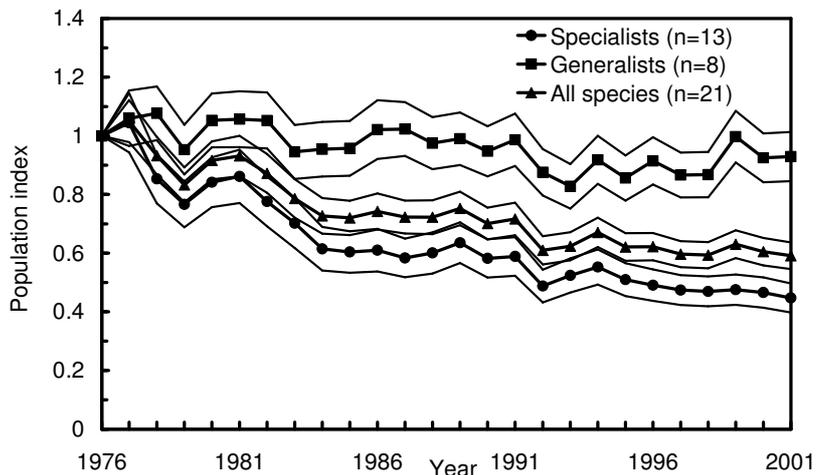


Fig. 4. Multi-species indices for farmland specialists, farmland generalists and all species pooled between 1976 and 2001 in Sweden. The upper and lower lines on indices show the 95% confidence intervals.

The results generated two hypotheses regarding the severe declines of farmland birds in Sweden. First, several species, especially short-distance migrants, share wintering grounds (i.e. western Europe) with British populations (The Swedish Bird Ringing Centre, T. Fransson pers. com.; 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.

Second, the conditions for farming differ between agricultural regions in Sweden. This has resulted in a polarization into cereal production in the open plains and cattle husbandry in the forest regions (Statistic Sweden 1970-2004), a common phenomenon also in other countries (Robinson & Sutherland 2002). The result has been pronounced agricultural intensification in productive regions, whereas in the forest regions, abandonment of arable land and semi-natural pastures has occurred. As a consequence, population declines in Sweden may have been caused by dual negative effects of intensification in the productive open plains and abandonment in the forest regions.

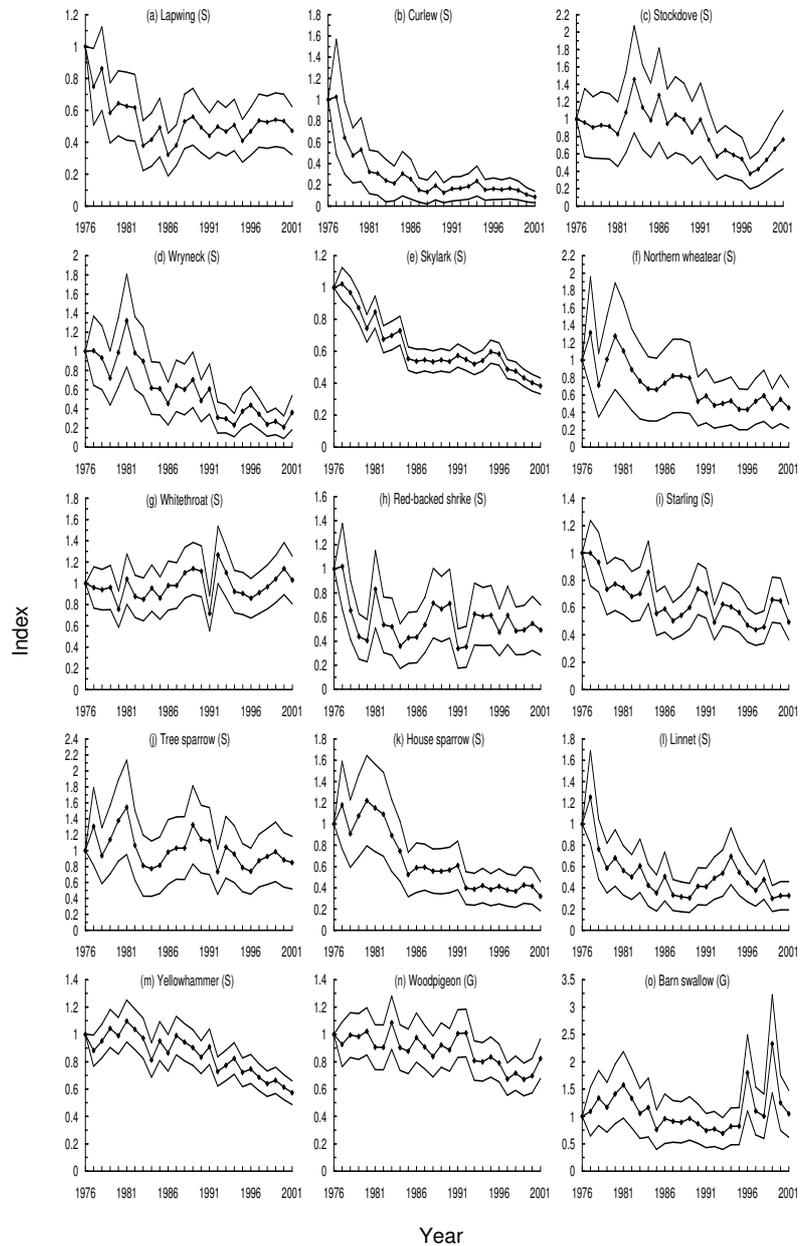


Fig. 5. TRIM indices for 21 farmland bird species (a-m are specialists (S) and n-u are generalists (G)) showing the changes in abundance in Sweden between 1976 and 2001. The upper and lower lines show the 95% confidence intervals. The first year is set to one and an index value of for example 0.80 any consecutive year is interpreted as a decrease to 80% compared with the first year.

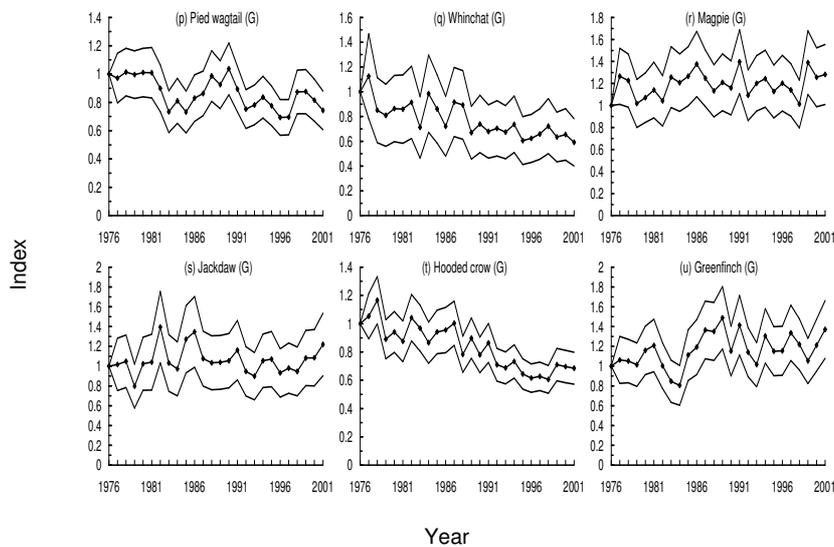


Fig. 5 (Cont.)

Are regional differences in agricultural intensification and changes in agricultural policy reflected in population trends of farmland birds? (Paper II)

In Paper II, we proceeded to test the hypothesis of the dual negative effects of intensification and abandonment, by analysing long-term population trends of four short-distance migrants (lapwing *Vanellus Vanellus* L, skylark, staling *Sturnus vulgaris* L. and linnet) and three resident species (tree sparrow, house sparrow and yellowhammer) and to relate these trends with agricultural changes in three agricultural regions in Sweden. We also tested the idea that time periods with different agricultural policies have promoted both agricultural intensification (the intensification period, 1976 to 1987, and the CAP period, 1995 to 2003 and extensification (the set-aside period, 1987 to 1995) and that these policy changes were reflected in population trends of farmland birds.

The analyses of agricultural variables showed that agricultural policy have had a considerable and rapid impact on agricultural practices in all three farmland regions (Fig. 6). For analyses of agricultural variables, see Appendix 1 in Paper II. The analyses showed that intensification was most pronounced during the first period (rapid increases in wheat yield per hectare and declines in proportion of mixed farms), whereas there was clear indication on extensification during the set-aside period (area of spring-sown cereal decreased rapidly, whereas leys, cultivated pastures and set-aside fields increased and the previous decline in proportion of mixed farms stopped in open plains and mosaic farmlands). In the CAP period, trend switches of agricultural variables were less clear. However, the introduction of the CAP in new EU members is normally associated with intensified production (Donald, Green & Heath 2001) and in Sweden production supporting subsidies were reintroduced and use of pesticides started to increase

(Swedish Board of Agriculture 1999, 2006a). During this period proportion of mixed farms again started to decline and the previous yearly decline in area of spring-sown cereals stopped.

The agricultural data also showed distinct regional differences in the level of farming intensity and intensification (Fig. 6). In the forest regions grasslands (leys, cultivated pasture and set-aside) dominated, whereas in the open plains, cereal production was most important. Wheat yield per hectare increased most in the open plains and least in the forest regions. Rate of abandonment of arable land differed between regions, with the most rapid decrease in the forest regions. The decline of mixed farms continued during all three time periods in the forest regions, whereas the proportion of mixed farms remained stable in the set-aside period in the open plains and mosaic farmlands. Finally, the area of set-aside increased most in the mosaic farmlands. Thus, both the time periods and the regions displayed different patterns of agricultural intensification making an ideal situation to test the general hypothesis that agricultural intensification and agricultural policy may affect farmland bird population trends.

The effect of changes in agricultural policy on farmland birds

The results from Paper II partly corroborate the prediction that farmland bird trends are linked to agricultural policy. Especially the four short-distance migrants displayed significantly different population trends in the intensification period (strongly declining), the set-aside period (more stable or increasing) and the CAP period (again declining, especially skylark and linnet; see Table 2). In contrast, the links between agricultural policy and population trends of the three resident species were more diverse (Table 2). One explanation for the differences between the short-distant migrants and the resident species may be that the migratory species are more closely confined to farmland habitats. Skylarks and lapwings are true field species and almost exclusively use farmland both for foraging and nesting, and linnets and starlings use farmland fields and pastures for foraging (Cramp, Simmons & Perrins 1977-1994). In contrast, parts of the populations of the three resident species also breed in non-farmland habitats (e.g. tree sparrow and house sparrow in urban areas and yellowhammer in forest clear-cuts; Svensson, Svensson & Tjernberg 1999) thus being less sensitive to changes in agricultural policy. Alternatively, as discussed above (Paper I), the short-distance migrants may be more affected by agricultural changes at the wintering grounds in western and south-western Europe. However, effects of common wintering grounds cannot explain why all four short-distance migrants showed significantly different trends in the three farmland regions of Sweden (see below). Clearly, at least a part of the explanation for the observed population trend shifts is likely to be found in agricultural changes at their Swedish breeding grounds.

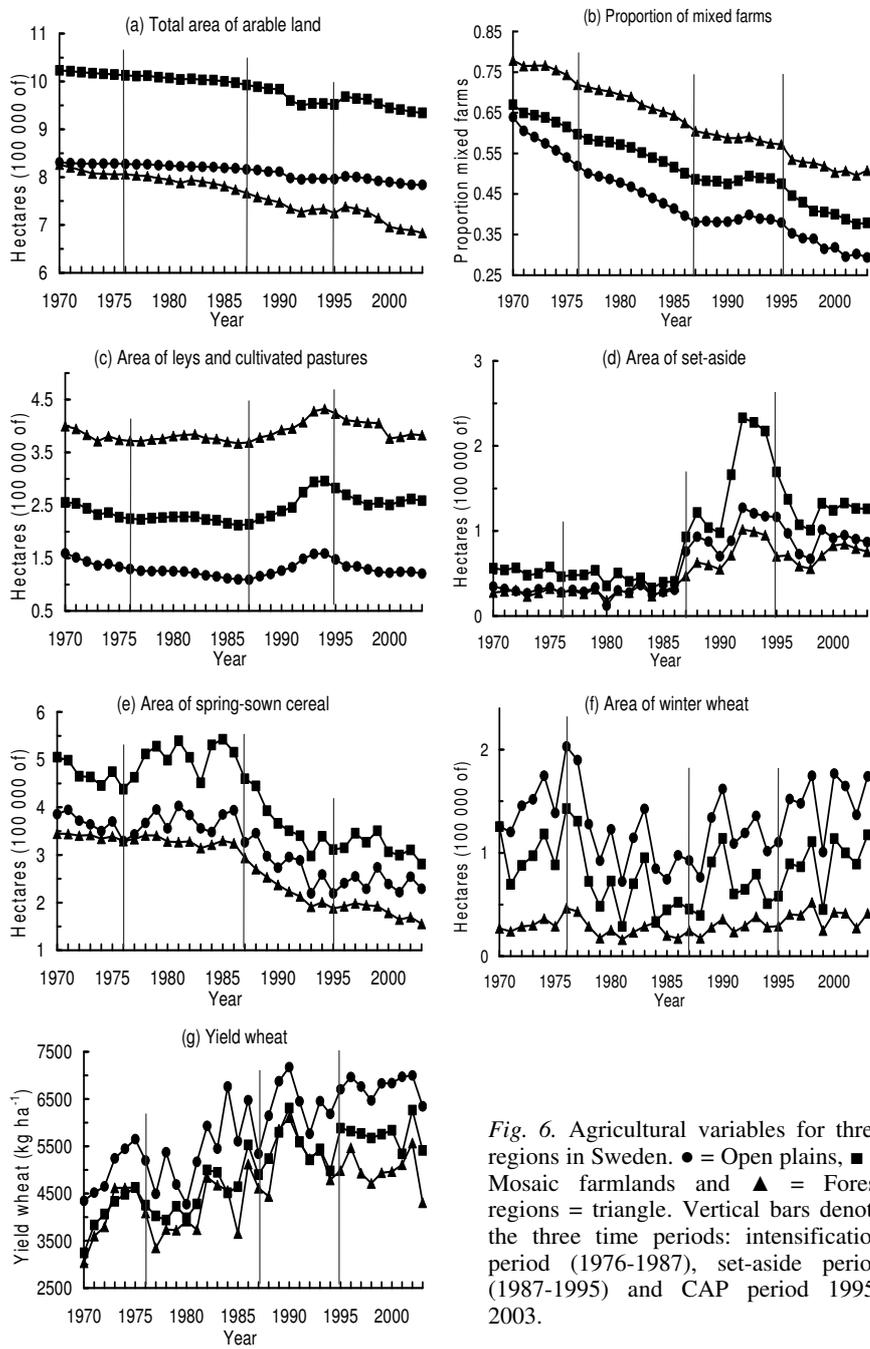


Fig. 6. Agricultural variables for three regions in Sweden. ● = Open plains, ■ = Mosaic farmlands and ▲ = Forest regions = triangle. Vertical bars denote the three time periods: intensification period (1976-1987), set-aside period (1987-1995) and CAP period 1995-2003.

Table 2. Annual population changes (in %) in three time periods and three regions (OP = open plains, MF = mosaic farmlands, FR = forest regions) with 95% confidence intervals (CI) of seven common farmland bird species. ($P > 0.05$) are in brackets, -, --, --- and +, ++, +++ equal P -values of <0.05 , 0.01 and <0.001 , respectively. For trends with P -value close to 0.05 , the actual values are given behind the sign.

Species	Intensification period 1976-1987			Set-aside period 1987-1995			CAP period 1995 – 2003					
	% annual population change	95% CI	Trend ¹	% annual population change	95% CI	Trend switch ²	% annual population change	95% CI	Trend switch ²			
Lapwing												
OP	-11.4	-15.7	-7.1	---	4.4	0.4	8.4	---	-5.8	-9.8	-1.8	--
MS	-4.5	-7.0	-1.9	---	1.9	-0.9	4.7	---	1.5	-1.1	4.1	(-)
FR	-7.2	-12.3	-2.0	---	-1.5	-5.3	2.3	---	0.6	-3.3	4.5	(+)
Skylark												
OP	-5.6	-7.4	-3.9	---	-0.2	-2.0	1.5	---	-9.2	-11.2	-7.2	---
MS	-5.9	-6.8	-5.0	---	1.4	0.1	2.6	---	-4.0	-5.4	-2.7	---
FR	-8.3	-10.3	-6.4	---	2.2	0.2	4.3	---	-8.7	-10.7	-6.7	---
Starling												
OP	-1.4	-5.1	2.3	(-)	-0.2	-3.7	3.4	(+)	-1.0	-5.0	3.1	(-)
MS	-5.7	-7.7	-3.7	---	-2.5	-4.6	-0.4	(+)0.08	0.5	-1.9	3.0	(+)
FR	-3.7	-6.7	-0.7	-	0.4	-2.1	2.8	(+)0.07	-1.0	-3.5	1.5	(-)

Table 2. (Cont.)

Linnet												
OP	-10.0	-13.7	-6.4	---	7.5	3.1	12.0	+++	-13.3	-18.3	-8.2	---
MS	-7.8	-11.5	-4.2	---	10.2	6.2	14.1	+++	-9.8	-12.8	-6.7	---
FR	-12.8	-18.2	-7.4	---	-1.9	-7.7	4.0	+	-5.7	-10.4	-1.0	(-)
Tree sparrow												
OP	-3.0	-7.5	1.5	(-)	-2.4	-6.7	1.8	(+)	6.6	1.2	12.0	+
MS	-1.6	-4.3	1.2	(-)	-3.3	-6.2	-0.4	(-)	2.0	-1.4	5.4	(+) 0.056
FR	4.6	-0.6	9.7	(-)	-3.0	-6.0	0.0	-	-0.8	-4.2	2.5	(+)
House sparrow												
OP	-7.2	-11.2	-3.2	---	-9.8	-14.5	-5.1	(-)	-6.2	-14.2	1.8	(+)
MS	-6.6	-9.0	-4.2	---	-3.1	-6.0	-0.1	(+)	-0.2	-4.2	3.8	(+)
FR	-8.1	-12.7	-3.4	--	-4.2	-7.8	-0.7	(+)	-3.4	-7.8	0.9	(+)
Yellowhammer												
OP	2.8	0.6	5.0	+	-1.9	-4.0	0.1	-	-3.9	-6.5	-1.4	(-)
MS	-0.4	-1.6	0.8	(-)	-5.3	-6.5	-4.0	---	-3.3	-4.8	-1.8	(+)
FR	-1.4	-3.3	0.5	(-)	-0.2	-1.9	1.5	(+)	-2.7	-4.4	-1.1	(-)

¹Signs and P -values describes a test of $H_0 = 0\%$ annual change.

²Signs and P -values describes a test of $H_0 =$ annual change of the preceding time period (i.e. a test of trend switches).

Table 3. Annual population changes (in %) between 1976 and 2003 in three regions (OP = Open plains, MF = Mosaic farmlands, FR = Forest regions) with 95% confidence intervals (CI) of seven common farmland bird species. Populations that have declined significantly in bold. Significant P-value shows that trends differ among regions. The last column shows the results from pair-wise tests, which were made in order to investigate between which regions population trends differed, e.g. OP; FR < MF means that populations in OP and FR have declined significantly more ($P < 0.05$) than in MF, but there was no significant difference between OP and FR

Species	OPEN PLAINS		MOSAIC FARMLANDS		FOREST REGIONS		P-value different trends	Regional comparisons
	% annual population change	95 % CI	% annual population change	95 % CI	% annual population change	95 % CI		
Lapwing	-2.5	-4.6, -0.3	-0.3	-1.3, 0.7	-3.0	-5.3, -0.7	0.014	OP; FR < MF
Skylark	-4.2	-5.0, -3.4	-2.5	-2.9, -2.1	-4.3	-5.2, -3.4	0.001	OP; FR < MF
Starling	-0.9	-2.3, 0.6	-3.1	-3.9, -2.4	-1.4	-2.7, -0.2	0.006	MF < OP; FR
Linnet	-4.2	-5.8, -2.5	-1.0	-2.4, 0.3	-8.3	-11.0, -5.6	0.007	FR < OP; MF ¹
Tree sparrow	-1.0	-2.9, 1.0	-1.5	-2.6, -0.4	0.5	-1.3, 2.4	0.630	OP; MF; FR
House sparrow	-7.9	-10.3, -5.4	-3.7	-4.9, -2.4	-5.4	-7.2, -3.5	<0.001	OP < FR; MF
Yellowhammer	-0.5	-1.5, 0.4	-3.1	-3.5, -2.6	-1.3	-2.0, -0.5	<0.001	MF < OP; FR

¹P-value = 0.068 for the comparison between OP and MF

Regional population trends

Regional long-term population trends of the seven species (1976-2003) were in most cases (15 of 21, 71%) significantly declining (Table 3). All species, except tree sparrow, had significantly different long-term population trends between regions. Four species (lapwing, skylark, linnet and house sparrow) showed the strongest decline in numbers in the open plains and the forest regions. The open plains were characterised by the most marked agricultural intensification and the forested region by extensification and abandonment of farming. Thus, the results support the hypothesis presented in Paper I, that at least for these species the overall negative population trends in Sweden may have been caused by dual negative effects of a simultaneous agricultural intensification and extensification / abandonment but in different regions.

The negative effects of agricultural intensification in the open plains (and to a lesser extent in the mosaic farmlands) and abandonment in the forest regions on farmland birds are probably similar to those found in western Europe (e.g. Suarez-Seoane, Osborne & Baudry 2002; Laiolo *et al.* 2004; e.g. Newton 2004). However, the negative effects of extensification are less obvious. In the forest regions, the rapid decrease in area of cereal production since the mid 1980s has created a landscape dominated by grasslands (leys, cultivated pastures and non-rotational set-aside fields; see Fig. 6). Today, it is possible that cereal is in shortage as a farmland habitat in the forest regions of Sweden. This possibility has also been discussed in Britain, where the importance of cereal habitats in grassland dominated landscape has been emphasized (Robinson, Wilson & Crick 2001). For example, lapwings prefer to put their nests on harrowed fields and avoid high and dense vegetation (Hudson, Tucker & Fuller 1994; Wilson, Whittingham & Bradbury 2005). Furthermore, cereal grains are important food resources for several granivorous species (e.g. yellowhammer, Fuller, Trevelyan & Hudson 1997; Kyrkos, Wilson & Fuller 1998; Stoate, Moreby & Szczur 1998) and there may be a threshold of cereal cultivation in farmland landscapes, below which some species cannot persist (Kyrkos, Wilson & Fuller 1998). This hypothesis is supported by the fact that the positive response in linnet and lapwing during the set-aside period was much weaker in forest regions compared with the open plains and the mosaic farmland (Table 3).

The increased farming intensity at the fertile soils in the open plains and the mosaic farmland, together with the conversion from annual crops to leys, cultivated pastures, non-rotational set-aside and abandoned fields in the forest regions, have all decreased farmland habitat heterogeneity in each region. In addition, mixed farms have declined in all regions. It is therefore possible that reduced habitat heterogeneity at both the landscape and local scale may also have affected the observed decline of lapwing, skylark, linnet and house sparrow (see Benton, Vickery & Wilson 2003). However, the population trends of the three other species (starling, tree sparrow and yellowhammer) are less clear and yellowhammer declined most in mosaic farmland, which experienced intermediate level of agricultural intensification and the highest level of increase in area of set-aside. This suggests that there is no single broad land-use change that affects all farmland bird species similarly.

To sum up, the results from Paper I and II suggest that farmland birds in Sweden have suffered from ongoing agricultural intensification in the open plains (and also to some degree in the mosaic farmlands) and extensification / abandonment in the forest regions. Furthermore, the results from Paper II are also in line with the hypothesis that differences in agricultural policies (promoting either intensification or extensification) have considerably affected farmland bird population trends (Donald, Green & Heath 2001; Gregory *et al.* 2005; Sanderson, Donald & Burfield 2006).

Are low-intensity crops and habitat heterogeneity beneficial for bird diversity in all types of landscapes? (Paper III)

The general suggestions that reduced farming intensity and high level of habitat heterogeneity benefit farmland birds were investigated in Paper III by using repeated large-scale censuses (in 1994 and in 2004). We tested whether temporal changes in species richness of farmland birds were related to corresponding changes in the amount of low-intensity land-use, and whether sites with high habitat heterogeneity had a buffering effect on temporal changes in species richness. Furthermore, we tested whether these relationships were consistent across sites surrounded by different amounts of forest (i.e. from farmland-dominated sites to forest-dominated sites).

A total of 42 and 41 farmland bird species were observed at the sites in 1994 and 2004, respectively. Most species were relatively uncommon and 57% and 59% of the species were found in less than 10% of the sites in 1994 and 2004, respectively. Local species richness declined significantly (mean \pm se) between 1994 (6.41 ± 0.18) and 2004 (5.58 ± 0.19 ; paired t-test: $N = 248$, $t = 4.44$, d.f. = 247, $P < 0.0001$). None of the heterogeneity indices were significantly related to changes in local species richness (Table 4). Thus, our results gave no support to the suggestion that heterogeneous landscapes may reduce population declines (see introduction).

Species richness declined more at sites surrounded by forest than those located in the open farmland and there was a weak general positive effect of an increase in amount of low-intensity land-use on changes in species richness (Table 4). The positive effect on local species richness at sites displaying a land-use transition from high- to low-intensity land-use is in line with many other studies. For example, a range of farmland bird species prefer set-aside fields (Berg & Pärt 1994; Wilson *et al.* 1997; Buckingham *et al.* 1999; Henderson *et al.* 2000; Henderson, Vickery & Fuller 2000) and short rotation coppice (Berg 2002a; Sage *et al.* 2005). However, the results of Paper III show that the effect of changes in amount of low-intensity land-use on changes in local species richness was significantly dependent on the amount of forest in the surrounding landscape (i.e. the interaction term was significant). Increasing the amount of low-intensity land-use had positive effects on local species richness in open landscapes consisting of low to intermediate amounts of forest, but negative effects in forest-dominated landscapes (Table 4 and Fig. 7).

Table 4. Multiple regression analysis of the effects of amount of forest (within 600 m), three heterogeneity indices (within 300 m) and changes in amount of low-intensity land-use (within 300 m) on the relative changes in local species richness (i.e. residuals of richness in 1994 regressed on richness in 2004)

Independents	Estimate	t-value	P-value
Intercept	1.63	2.65	0.008
Forest (A)	-2.42	-4.01	<0.001
Low intensity land-use (B)	1.90	2.60	0.010
Landscape heterogeneity	0.02	0.52	0.60
Linear habitats	0.00	-1.71	0.09
Change in land-use heterogeneity	-0.10	-0.16	0.87
A*B	-3.86	-2.58	0.010

Model; $r = 0.27$, $F = 3.25$, d.f. = 6, $p = 0.004$.

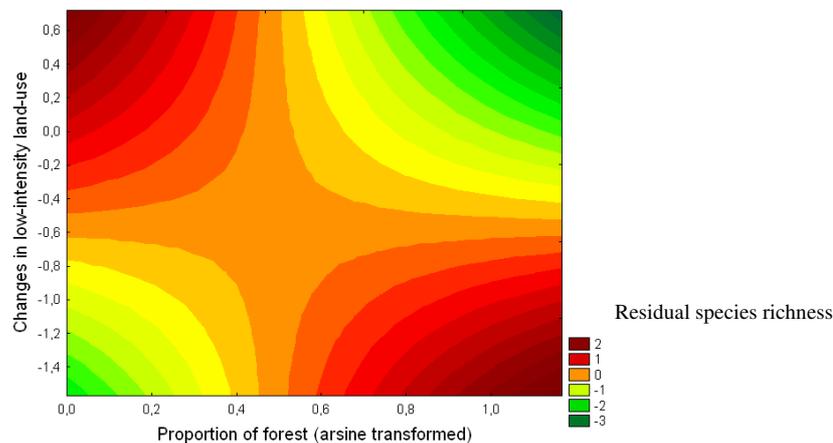


Figure 7. Contour plot showing the estimated interaction between proportion of forest (within 600 m) and changes in proportion of arable land with low-intensity land-use (within 300 m) on the relative changes in local species richness (i.e. residuals of richness in 1994 regressed on richness in 2004). Areas with dark red predict increases in species richness (i.e. in forest-dominated landscapes where amount of low-intensity land-use decreased and in farmland-dominated landscapes where amount of low-intensity land-use increased). Areas of dark green predict decrease in species richness.

The interaction between change in low-intensity land-use and forest could also be viewed as a “rare habitat effect”. This is because the effect of low-intensity land-use on species richness was positive at locations where this land-use was uncommon (at sites with < 20% forest, the average proportion of arable land with low-intensity land-use in 2004 was 27%) whereas the effect was negative at sites dominated by low-intensity land-use (at sites with > 60% forest the average proportion of arable land with low-intensity land-use in 2004 was 69%). Thus, Paper III is in line with Paper II, namely that cereal habitats are important for

farmland birds where this habitat is rare, and the two studies suggest that this effect on farmland birds is consistent both at the local (Paper III) and regional (Paper II) scale. Moreover, the same result was found by Robinson, Wilson & Crick (2001), i.e. cereal habitats were important in grassland dominated landscapes in Britain. These studies were performed in highly different landscapes, which suggest that the "rare habitat effect" may be a general phenomenon in agricultural landscapes.

The latest reformation of the CAP has decoupled payments from production and thus has promoted especially small-scale farmers in Sweden to use their land in an extensive way since 2005 (EU Commission 2003; Statistics Sweden 2006). As a consequence, the area of low-intensity land-use in Sweden has increased rapidly during the last two years. For example, between 2004 and 2005 the area of set-aside increased by 20%, and the area of leys and cultivated pastures by 10% (Statistics Sweden 2006). In 2006, the smallest area of cereal production ever in Sweden was recorded (Swedish Board of Agriculture 2006b). The most recent trend, after the decoupling of payments, clearly indicates that extensification continues in forest-dominated surroundings, whereas in the farmland-dominated landscapes farming is likely to be intensified. The results from Paper III, based on species richness of farmland birds suggest that this polarisation will further decrease farmland bird diversity in Sweden.

Effects on land-use changes on changes in local abundance (Paper IV)

Although we did not experimentally manipulate farmland landscapes, the repeated census design implied that several potentially important non-crop habitats for farmland birds (e.g. amount of forest, total length of ditches and structure of field-forest ecotones) were constant across years whereas land-use changed considerably at the site level. Thus, the main change between years was the transitions between different crops, which enabled tests of whether changes in land-use resulted in changes in abundance of 16 common farmland bird species. Furthermore, because different species either showed a decline or an increase in population numbers across the whole study area it was also possible to test whether these changes in abundance were more marked in certain landscapes (e.g. in relation to amount of forest and landscape heterogeneity).

Due to crop rotation most sites experienced increases or decreases in the different land-use types across years (Fig. 8). The major land-use changes were an increase in autumn-sown crops (mainly winter wheat) and a decrease in cultivated pasture. Other land-use types were relatively stable in total, but showed a great variation at the site level (Fig. 8).

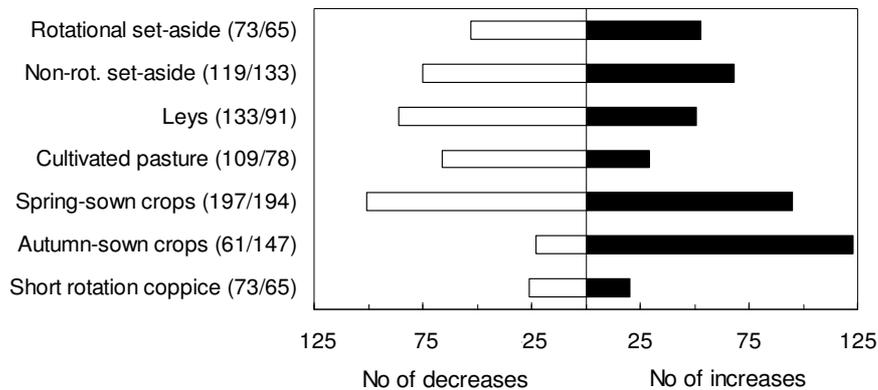


Fig. 8. Number of sites with increases and decreases in area of different land-use types within 300 m from the censused plots. Values in parentheses are the number of sites in which each land-use type was found in 1994 and 2004, respectively.

Of the 16 species, 8 species decreased and 3 species increased significantly between 1994 and 2004 (Table 5). Skylark was the dominant species and was found on 83% and 70% of the sites in 1994 and 2004, respectively, indicating a relatively small range contraction. In contrast, the abundance of skylarks decreased drastically from 644 to 367 territories (-43%) across years. In addition to skylark, five species (yellowhammer, linnet, reed bunting, *Emberiza schoeniclus* L., pheasant *Phasianus colchicus* L., and red-backed shrike *Lanius collurio* L.) decreased by at least 40% between 1994 and 2004. Three species (woodpigeon, white wagtail *Motacilla a. alba* L. and common starling) increased with more than 40% (Table 5).

In contrast to earlier studies of habitat preferences our results suggest that neither amount of forest (e.g. Söderström & Pärt 2000; e.g. Berg 2002b) nor habitat heterogeneity (e.g. Böhning-Gaese 1997; Tryjanowski 1999; Aauri & de Lucio 2001; Herzon & O'Hara in press) were linked to local change in abundance, except in a few species (Fig. 9). Thus, as in Paper III, our suggestion that high habitat heterogeneity at censused sites should have a buffering effect on declining species was again not supported. However, the link between habitat heterogeneity and farmland birds is complex. For example, Gillings & Fuller (1998) found no evidence for larger population declines of farmland birds on farms where important non-crop habitats had disappeared compared to those where such structures had remained. They instead suggested that changes in quality of non-crop habitats, along with parallel changes in crop quality, had caused population declines in lowland English farms. Furthermore, curl bunting *Emberiza cirrus*, a species strongly linked to hedgerows, disappeared from areas where hedgerow loss was minimal in the UK (Evans 1997).

However, a general problem of testing relationships between changes in local abundance and constant habitat variables in species displaying a general decline is that these relationships are partly confounded by initial levels of abundance. For example, species avoiding forest-dominated farmlands initially had lower local

densities (or were absent) at sites located in forest dominated landscapes compared to sites in open farmland landscapes. For such species data on change in abundance may become less clear in forest-dominated landscapes than in open farmland landscapes. The same explanation may also apply to relationships between heterogeneity indices and changes in local abundance. Therefore, the power of detecting such relationships may have been low for several species. Similarly, the power of detecting interactions between amount of forest and change in land-use on changes in abundance was low. To detect such interaction with a skewed ordinal response data (in our case the responses in changes of abundance were mainly -1 and 0) require large sample sizes.

Most species (13 of 16) displayed some relationships between change in land-use and change in abundance (Fig. 9). These associations were largely species-specific (see also Siriwardena *et al.* 2000), although changes in area of non-rotational set-aside were linked to population changes in 38% of the species. In general increased area of low-intensity crops (i.e. short rotation coppice, leys, cultivated pasture and set-aside) benefited several species (pheasant, skylark, whinchat *Saxicola rubetra* L., whitethroat *Sylvia communis* Latham, common starling and reed bunting (see also Berg 2002a; Berg & Kvarnäck 2005). However, nine species were negatively affected by increases in area of low-intensity crops (or showed different associations to different low-intensity crops; Fig. 9). Thus, these crops may not be beneficial for all species, for instance species associated with short vegetation or disturbed sites (lapwing, northern wheatear, white wagtail) or species feeding on crops (woodpigeon and yellowhammer). Only two species (yellowhammer and starling) benefited from increased areas of the dominating land-use type spring-sown crops (i.e. mainly oat and barley). Several previous studies have shown that yellowhammers prefer cereal habitats (e.g. Kyrkos, Wilson & Fuller 1998; Robinson, Wilson & Crick 2001), whereas common starling normally prefer grasslands (pastures and mowed hay fields), but also may use newly cultivated fields, especially early in the breeding season (Cramp, Simmons & Perrins 1977-1994).

In conclusion, Paper IV shows that changes in land-use are linked to changes in local abundance of many species. The study also shows that farmland birds display a great inter-specific variation in preferences for certain land-use types, suggesting that a mixture of land-use types benefit the local diversity of farmland birds.

Table 5. Number of occupied sites and territories of the 16 farmland bird species included in the survey. In total 248 sites were censused in 1994 and 2004. Species are presented in order of number of occupied sites in 1994. The difference in abundance between years was analysed with a paired t-test.

Species	Scientific name	No of sites occupied in 1994	No of sites occupied in 2004	No of territories in 1994	No of territories in 2004	% change in abundance	P-value [†]
Skylark	<i>Alauda arvensis</i> L.	207	173	644	367	-43	***
Yellowhammer	<i>Emberiza citrinella</i> L.	195	141	259	141	-46	***
Greenfinch	<i>Carduelis chloris</i> L.	129	93	182	129	-29	**
Whinchat	<i>Saxicola rubetra</i> L.	121	98	156	107	-31	***
Linnet	<i>Carduelis cannabina</i> L.	103	51	111	67	-40	***
Whitethroat	<i>Sylvia communis</i> Latham	94	81	107	91	-15	NS
Common starling	<i>Sturnus vulgaris</i> L.	78	93	115	210	83	***
White wagtail	<i>Motacilla a. alba</i> L...	71	101	71	108	52	***
Reed bunting	<i>Emberiza schoeniclus</i> L.	56	31	68	36	-47	**
Pheasant	<i>Phasianus colchicus</i> L.	49	9	53	9	-83	***
Fieldfare	<i>Turdus pilaris</i> L.	45	45	67	75	12	NS
Woodpigeon	<i>Columba palumbus</i> L.	40	75	48	101	110	***
Lapwing	<i>Vanellus Vanellus</i> L.	39	45	81	64	-21	NS
Magpie	<i>Pica pica</i> L.	36	29	37	31	-16	NS
Northern wheatear	<i>Oenanthe oenanthe</i> L.	31	37	32	37	16	NS
Red-backed shrike	<i>Lanius collurio</i> L.	29	14	30	16	-47	*

[†]*P < 0.05, **P < 0.01, ***P < 0.001.

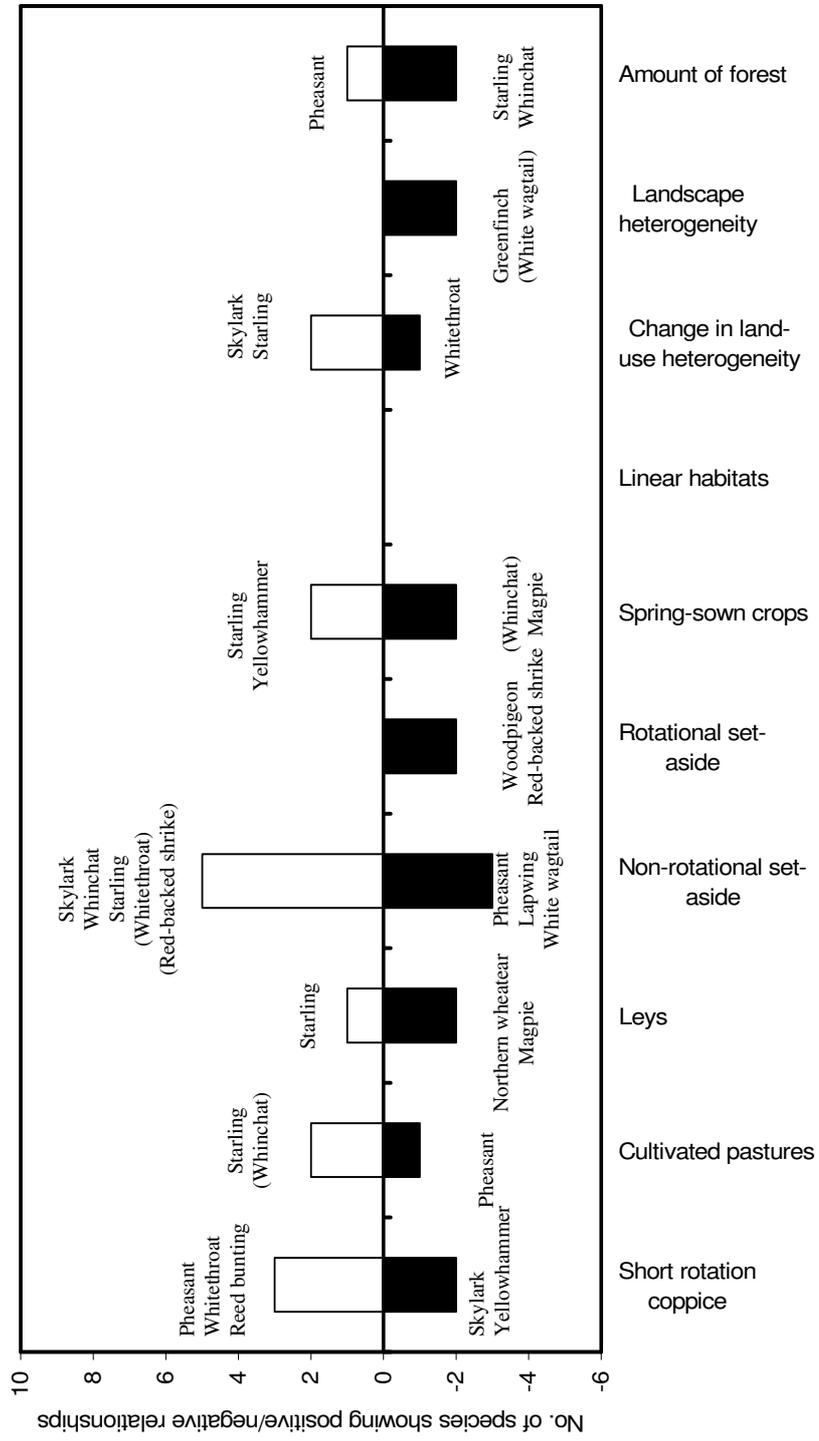


Fig. 9. Effects of change in area of different land-use types, total length of linear habitats, change in land-use heterogeneity, landscape heterogeneity and amount of forest on changes in abundance for 16 farmland bird species (repeated surveys in 1994 and 2004). Results are from ordinal logistic regression with backward stepwise selection of variables. $P < 0.10$ for species in brackets. All other species have $P < 0.05$.

Conclusions

Correlative results such as those presented in this thesis imply that alternative explanations for the observed patterns of population trends may exist. Below I will briefly discuss three of the most likely explanations: namely, climate change, predation and buffer effects.

The impact of weather on birds is well known (Newton 1998). During the last years an increasing amount of studies have focussed on the effects of global warming. The potential effects of global warming on bird populations are numerous and include e.g. changes in geographical range, changes in phenology and demographic factors, see review by Crick (2004). It is therefore possible that observed negative long-term population trends in Papers I and II have partly been caused by a corresponding long-term change in climate and not in agricultural practices. Although climate change may have affected population trends of some species, the rapid population trend switches shown in Paper II is not in line with climate changes scenarios. Thus I conclude that factors associated with agricultural changes have been a major driver behind most of the observed temporal patterns in population trends.

Reduction in habitats and/or food is thought to be the main underlying causes of the declines in most farmland bird species (Newton 2004). However, such habitat changes may also interact with predator numbers and predation risk. Thus, predation could potentially explain some of the observed population trend patterns (Whittingham & Evans 2004). For example, agricultural intensification has implied habitat loss and structurally more simple landscapes. This may result in higher nest densities in remaining habitats which in turn may cause higher nest predation rates (Chamberlain, Hatchwell & Perrins 1995; Roos 2004). A second example is when species with high nest predation risk are forced to occupy predator rich areas. For example semi-natural pastures located away from human settlements have lower densities of magpies, an important nest predator, than semi-natural pastures close to human settlements. Thus, if e.g. semi-natural pastures located far from villages are abandoned, farmland birds with preferences for this habitat may be forced to nest in areas with higher risk for nest predation (Roos 2004). Thus, predation processes have the potential of affecting local bird communities, and possibly also long-term population trends. However, there is still almost no evidence of that increased predation has caused large-scale population declines of farmland birds. For example, Thomson *et al.* (1998) found no evidence that an increase in number of magpies and sparrowhawks *Accipiter nisus* had caused the long-term declines in songbirds in Britain. Similarly, the most pronounced declines of ground-nesting species such as curlew, lapwing and skylark between the mid-1970s and the mid-1980s (Paper I and II) coincided with the collapse in population numbers of an important predator on ground nesting birds, the red fox *Vulpes vulpes* (Lindström *et al.* 1994). However, Roos (2004) showed that both spatial range and population numbers of red-backed shrikes were negatively related to increased range and numbers of magpies in an open Swedish farmland.

The hypothesis of buffer effect (Brown 1969a, 1969b) implies that when all good habitats are occupied, a proportion of a population have to occupy poorer habitats. However, as soon good habitats become available, individuals from poor habitats are expected to move into the good habitats. In that way individuals from the poorer habitats buffer the dynamics of population numbers in the good habitats. Two factors must interact to cause the buffer effect: (i) habitats must differ in quality and (ii) the population size is reduced by an external factor (e.g. climate). Theoretically, the regional differences in population trends of the migratory species in Paper II could potentially be explained by buffer effects caused by regional differences in habitat quality and a reduced winter survival at wintering grounds that reduces the numbers of the whole Swedish populations. For example assume that the mosaic farmlands have generally high quality habitats, whereas forest regions (marginal farmland with abandonment) and the open plains (intensively managed agriculture with a highly simplified landscape structure) mainly constitute poor farmland bird habitats. A reduced survival at wintering grounds outside Sweden would then induce movements of individuals from the forest regions and the open plains towards the mosaic farmlands when good habitats become vacant in the mosaic farmlands. The result would be highest population declines in the forest regions and the open plains, whereas the mosaic farmland population would be buffered and therefore decline less. However, two factors suggest that buffer effects are unlikely to have caused the population trend patterns observed in Paper II. First, individuals are unlikely to display an unconstrained dispersal between the three regions because of site-fidelity (Greenwood & Harvey 1982). Second, within each region the habitat quality varies considerably and we would therefore expect buffer effects to be more obvious at a smaller spatial scale, as e.g. the scale of Paper III and IV. The study design of these two studies was made in the same region and included several small marginal farmland sites surrounded by forest. For most farmland bird species such sites are likely to be sub-optimal and the decline in species richness and abundance of individual species would be expected to be most pronounced here. However, the fact that species richness increased even at marginal farmland sites when the proportion of low-intensity land-use decreased suggest that changes in land-use changes were a more important factor moulding landscape-specific population trends than buffer effects. On the other hand, this is not to say that buffer effects are unimportant and it is still possible that the results found in the studies are partly affected by buffer effects in local population dynamics.

To conclude, it has been claimed that we know the causes to why most species of farmland birds decline (Newton 2004). However, the results from my thesis show on strong landscape effects on population declines. Therefore such statements should be taken cautiously. First, even if food abundance or availability is the driving casual factor of population declines (Newton 2004), the relative relationships between food and land-use may differ, e.g. depending of alternative habitats and climate. Therefore, detailed local demographic studies suggesting strong causal links between land-use and population growth may be of high value locally but less so at larger spatial scales or in other regions. Second, inter-specific interactions are likely to change when landscapes and habitats change. Therefore, we need to always keep an open mind to the possibility that e.g. predation may be

an additional driving force in the declines in some species in other geographical regions. Third, even if we know the cause of the decline at the local scale, dispersal and buffer effects may complicate predictions of population trends between regions. Furthermore, these predictions are even more complicated by complex relationships between wintering and breeding conditions. I therefore suggest that more effort should be put on the validation of suggested causal mechanisms of some well-studied species in other regions and landscape types. Studies of local dynamics, the framework of source-sink dynamics and buffer effects would also be invaluable when we interpreting regional differences and suggesting conservation strategies.

Conservation implications

The effects of agri-environment schemes are being put under critical scrutiny at present (Kleijn *et al.* 2001; Kleijn & Sutherland 2003; Kleijn *et al.* 2006). However, since conservation of farmland biodiversity implies conservation measures at the scale of whole countries, large-scale agri-environmental schemes will probably be the only practicable way (Vickery *et al.* 2004a). Furthermore, as discussed in Paper I, the declines of farmland birds in Sweden may also be caused by reduced survival at wintering grounds outside Sweden. This highlights the important fact that the conservation of farmland birds is an issue without country borders, and that many farmland bird species in Sweden may be dependent on well-designed agri-environmental schemes at wintering grounds in south-western Europe. However, as shown in Paper II, broad scale changes in agricultural policy that result in a large-scale reduction in agricultural intensity can also be highly effective in reversing negative farmland bird population trends, especially for those species that depend exclusively on farmland habitats. Clearly, the effects of changed agricultural policies give hope for future conservation of farmland biodiversity.

However, in the long run, a broad scale reduction in intensity may not be positive for farmland birds in all types of regions since Papers I, II and III suggest that increasing the amount of low-intensity crops may negatively affect several farmland bird species in the forest regions of Sweden. The ongoing polarisation of agriculture in Sweden since the early 1970s, towards intensive production in the open farmlands and extensively managed grasslands in the less productive forest regions (Statistic Sweden 1970-2004) has created more homogenous landscapes. Today, only 25% of arable land is used for cereals in the forest regions of Sweden (Statistics Sweden 2006). It is therefore possible that in some regions cereal habitats has become so rare that some species are unable to persist (see also Kyrkos, Wilson & Fuller 1998; Robinson, Wilson & Crick 2001). This idea was also supported by Paper III.

The latest reformation of the Common Agricultural Policy has decoupled payments from production and has thus encouraged especially small-scale farmers in Sweden to use their land in an extensive way since 2005 (EU Commission 2003; Statistics Sweden 2006). As a consequence, between 2004 and 2005 the

area of set-aside increased by 20%, and the area of leys and cultivated pastures by 10% (Statistics Sweden 2006), and this increase was most pronounced in the forest regions. In 2006, the smallest area of cereal production ever in Sweden was recorded (Swedish Board of Agriculture 2006b). This most recent trend, after the decoupling of payments in 2005, clearly indicates that extensification continues in forest-dominated regions, whereas in the farmland-dominated landscapes agricultural intensification is likely to continue.

This suggests that agri-environment schemes must consider landscape structure and relative frequency of different land-use types. For land-use on arable land, it implies increased area of low-intensity crops such as set-aside, leys, cultivated pastures and short-rotation coppice in areas where intensive cereal production dominates. This will not only increase habitat heterogeneity, but also reduce farming intensity. On the other hand, in already extensively managed regions, reduced farming intensity is unlikely to benefit farmland biodiversity (see Paper III). Instead, in these regions an increased cereal production would have the most positive effect.

To conclude, my thesis suggests that the highest agricultural intensification does not necessarily always imply the most severe population declines in farmland birds. Thus, to use degree of intensification (or intensity) as a tool to identify the areas where farmland biodiversity are most threatened may be misleading. Therefore, conservation actions aiming to reverse impoverishment of farmland biodiversity should not automatically focus on regions with the highest intensity. In general, however, there is a need to increase our knowledge about the specific effects of intensification, extensification and abandonment on species population numbers in different landscape types or regions. Such knowledge will facilitate the development of effective conservation measures.

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