Agricultural intensification and farmland birds

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Abstract

After the adoption of the Common Agricultural Policy by the European Economic Community in 1957, agricultural production practices have been intensified, as a result of which yields have tripled. The use of pesticides and artificial fertilizers has increased, fields and farms have been enlarged and landscapes have been homogenized. This has resulted in the loss and alteration of foraging and breeding habitats of farmland birds, causing population declines of many species throughout Europe.

The research project described in this thesis focused on the effects of various farming practices on species richness and the abundance of birds breeding and wintering on farmland. In addition, the effects of organic farming on farmland birds were investigated. Finally, habitat selection by farmland birds was studied with respect to food abundance, vegetation cover and landscape characteristics.

Effects of farm management on farmland birds were investigated simultaneously on arable farms in up to nine study areas in eight different European countries. Species richness and bird abundance proved to be low on high-yielding farms. Of the farming practices assessed, only the use of pesticides showed a consistent negative effect on the species richness as well as the abundance of breeding birds. Breeding farmland birds were more numerous on farms with a high crop diversity. Species richness and total abundance of breeding birds did not differ between the organic and conventional farms, although lapwings were more abundant and meadow pipits less abundant on organic farms than on conventional farms.

In winter, species richness and bird abundance were lower on organic farms where frequent mechanical weeding was used than on organic farms with less frequent mechanical weeding. Organic farms supported more species and higher numbers of birds than conventional farms, but only in simple landscapes, consisting of 80-99% agricultural land. Wintering farmland birds were more numerous on mixed farms, comprising arable crops as well as pastures.

In February, seed densities in the upper centimetre of arable soils were ten times higher in organic compared to conventional wheat fields in Flevoland, the Netherlands. Fields with higher seed densities attracted more species and higher numbers of birds. On organic farms, frequent mechanical weeding reduced soil seed densities. Preferences for fields with different vegetation cover proved species-specific.

Skylarks wintering in an agricultural region in the north of the Netherlands preferred to forage in large cereal stubble fields with soil seed densities above 860 seeds m^{-2}. They avoided former maize fields, grassland and fields surrounded by tall boundary vegetation. Skylark faeces collected on potato fields comprised a higher proportion of dicotyledonous seeds, whereas faeces found on cereal fields contained a higher proportion of cereal grains. However, the proportion of cereal grains in the skylark faeces dropped steeply at the beginning of winter. The proportion of invertebrates in the faeces was low throughout the winter.

These results suggest that if bird conservation on farmland is to be successful, the use of pesticides has to be drastically reduced. Breeding habitats may be improved by increasing the diversity of arable crops, and seed availability in winter may be increased by less frequent mechanical weeding and the retention of stubbles in winter. The effectiveness of agri-environment schemes, including organic farming, is likely to increase if conservation measures are customized for species and tailored to landscape type.

Contents

Chapter 1

General introduction

Biodiversity on farmland

Landscapes have been influenced by humans since the beginning of agricultural cultivation (Donald et al., 2002). Farmland management has gradually changed the composition of the landscape, creating a large diversity of habitats, inhabited by a wide range of wildlife (Pain & Dixon, 1997). In the past, many plant and animal species have benefited from and adapted to farmland and agricultural activities (Pain & Pienkowski, 1997; Potts, 1991). Agricultural intensification in the second half of the twentieth century, however, has resulted in an impoverishment of the diversity of flora and fauna on farmland (Baessler & Klotz, 2006; Benton et al., 2002; Krebs et al., 1999).

Nevertheless, there are still many species that rely on farmland for part or all of their life cycle (Bignal & McCracken, 1996; Lahr et al., 2007; Potter, 1997; Tucker, 1997), mainly as a result of the large areas of agricultural landscapes that are available. In 2007, 45% of the land surface of the European Union (EU 27) was used for agricultural production (FAOSTAT, 2010). In addition, agricultural practices influence many adjacent habitats, e.g. nature conservation areas, and the species that inhabit them. It is therefore important to adapt current farm management in such a way as to halt biodiversity loss on farmland and improve the remaining habitats.

Agricultural intensification

European agricultural policy and mechanization have been pointed out as the main causes of agricultural intensification in the second half of the twentieth century. The food shortages caused by World War II meant that there was a need for increased food production to meet the demand in Europe. Uncertainties regarding farmers' incomes due to unstable weather conditions, variable food prices and the aim of a raised food production resulted in the need for governmental intervention (Ackrill, 2000). In 1957, the Common Agricultural Policy (CAP) was adopted by member states of the European Economic Community (EEC) to safeguard farmers' incomes, stabilize markets, increase agricultural productivity and provide consumers with food at reasonable prices. Since then, financial incentives for farmers to use new technologies have led to increased mechanization (Pain & Dixon, 1997). By the early 1980s, the support of technical progress, price protection for various agricultural products and payments to farmers directly linked to production resulted in huge food surpluses (Donald et al., 2002). At the same time, the amount of labour required was reduced by the promotion of mechanization and farm enlargement (Pain & Dixon, 1997).

Since its introduction in 1957, the CAP has regularly been amended, and many reforms have been introduced. By 1973, environmental impacts of agricultural practices first became a subject of policy discussions, which resulted in the 'First Environmental

Action Programme' (Robson, 1997). Since then, production quotas have been introduced and product price supports have been reduced to decrease the huge food surpluses. In 1991, a new Council Directive was adopted to limit the use of pesticides posing high risks to the environment (Council Directive 91/414/EEC of 15 July 1991). Structural changes in agriculture and the need to comply with international agreements (e.g. the GATT[1]) led in 1992 to the MacSharry reform (Pain & Dixon, 1997). This reform resulted in the reduction of payments to farmers linked to production and in the introduction of direct payments to farmers to compensate for income losses. Additionally, measures to protect the environment, so called agri-environment schemes, such as obligatory set-asides, have been introduced (Berger et al., 2006). Thus, political pressure to intensify production had finally abated. After 1999 (Agenda 2000 reform), linkage of payment to the sustainable development of rural areas was made possible. Examples include the payments to farmers producing in areas with natural constraints to prevent land abandonment, investments to protect the environment, and payments to preserve rural heritage (Ackrill, 2000). By 2003, production and payment were partially decoupled. Payments have been linked to farm management that complies with national standards on public health and that maintains farmland in good agricultural condition (cross-compliance) (Coucil Regulation (EC) No 1782/2003 of 29 September 2003).

As a result of public pressure and international agreements (e.g. the agreement concluded at the UN World Summit on Sustainable Development in September 2002 to significantly reduce the current rate of biodiversity loss by 2010), the development of rural areas became an increasingly important issue. Farm management no longer includes only the production of food, but also the management of the countryside and its wildlife, i.e. farm management has become multifunctional. In 2005, the European Commission introduced a new Regulation (Coucil Regulation (EC) No 1698/2005 of 20 September 2005), with the aim of combining sustainable food production with agricultural landscapes of high environmental quality (Bos & Schröder, 2009).

At the same time, however, further increases in agricultural production, at least at a global scale, will be necessary to meet the demand for food of a growing world population (Wilson et al., 2010). These different perspectives on the use of agricultural land will ultimately determine the future of agricultural policy and environmental development on farmland.

Due to differences in environmental conditions, national policies and the moment when countries joined the EU, the rate and timing of agricultural intensification differs between European countries and regions (Stoate et al., 2009). The various components of agricultural intensification and their impacts on biodiversity described below apply

[1] General Agreement on Tariffs and Trade

mainly to arable farming in Northern and Western Europe.

Agricultural intensification affects farmland at different spatial scales, ranging from field to landscape scale. Field and landscape structures have changed due to technical progress and mechanization. Farming practices have become less labour-intensive and manpower has largely been replaced by agricultural machinery (Pain & Dixon, 1997). Fields have been cleared of trees and shrubs to allow access by large machinery and to increase cultivation efficiency. Moreover, land consolidation, drainage and the desire to cultivate larger areas in a shorter time have resulted in the removal of non-cultivated field margins and boundaries and the enlargement of fields (Pain & Dixon, 1997; Potter, 1997). The remaining semi-natural habitats have become fragmented by agricultural expansion (Tucker, 1997). As less labour force was needed per unit area, farm sizes have increased through farm amalgamation. Furthermore, farms have become more specialized, resulting in monocultures and the loss of mixed farming systems (Donald et al., 2002; Stoate et al., 2001). The separation of pastoral and arable farming has led to reduced habitat diversity in arable (Atkinson et al., 2002) and grassland landscapes (Robinson et al., 2001). Consequently, agricultural intensification has resulted in the structural simplification and homogenization of agricultural landscapes.

Agricultural policy has not only led to the intensification of agricultural production practices, but also to farmlands being abandoned. The decoupling of subsidies and production resulted in low-productive and often species-rich farmland being abandoned in Eastern and Southern and to a lesser extent also in Western and Northern Europe (Henle et al., 2008; Stoate et al., 2009).

In addition to spatial simplification of farmland, agricultural intensification has also resulted in a temporal homogenization. For example, crop rotation schemes have been simplified and farmers have specialized in the economically most profitable crop types, leading to reduced crop diversity not only in spatial but also in temporal terms (Benton et al., 2003; Stoate et al., 2001; Tucker, 1997). Variation in crop growing patterns and crop structure have become smaller by the earlier and simultaneous sowing of different crops and by improved crop management through the use of pesticides and fertilizers (Stoate et al., 2009; Stoate et al., 2001). The area under break crops and stubble has been reduced as autumn-sown crops replaced spring-sown crops (Benton et al., 2003). These changes in the timing of various agricultural activities and crop management have reduced the temporal diversity of habitats on farmland.

To raise production, the use of chemicals, such as artificial fertilizers and pesticides, applied to farmland has been increased since the 1960s (Potter, 1997). Between 1960 and 1988, total fertilizer consumption in Northern, Western and Southern Europe doubled from 11.8 to 23.5 mln tons, before decreasing again to 15.8 mln tons in 2002 (FAOSTAT, 2010). A similar increase and subsequent decrease was seen in the use of some pesticides, for example insecticides in the Netherlands (CBS, 2010). New national policies and more accurate application of fertilizer adjusted to crop needs (Stoate et al., 2001) led to a reduction of the consumption of fertilizers and pesticides after the 1990s (Robson, 1997). Energy consumption on farmland also increased rapidly in the second half of the twentieth century, due to the replacement of human labour by agricultural machinery (Potter, 1997). The intensification of farm management did result in the intended increase in food production. For example, wheat yield per ha in the Netherlands trebled between 1946 and 2009 (Fig. 1.1; CBS, 2010).

Biodiversity loss on farmland

Agricultural intensification was followed by the steep decline of biodiversity on farmland. The link between agricultural intensification, environmental degradation and the loss of species has been studied extensively and is now widely acknowledged (Benton et al., 2002; Donald et al., 2006; Krebs et al., 1999; Robinson & Sutherland, 2002; Stoate et al., 2009). There have been considerable declines in the populations of farmland species from various taxa, such as vascular plants (Andreasen et al., 1996; Baessler & Klotz, 2006; Rich & Woodruff, 1996), birds (Donald et al., 2006; Fuller et al., 1995; Herzon et al., 2008) and a wide range of arthropods (Attwood et al., 2008; Benton et al., 2002). In addition, important ecosystem functions in agro-ecosystems associated with biodiversity, such as biological control of agricultural pests, nutrient cycling and crop pollination, have become threatened by the loss of species (Altieri, 1999; Biesmeijer et al., 2006; Hooper et al., 2005; Matson et al., 1997).

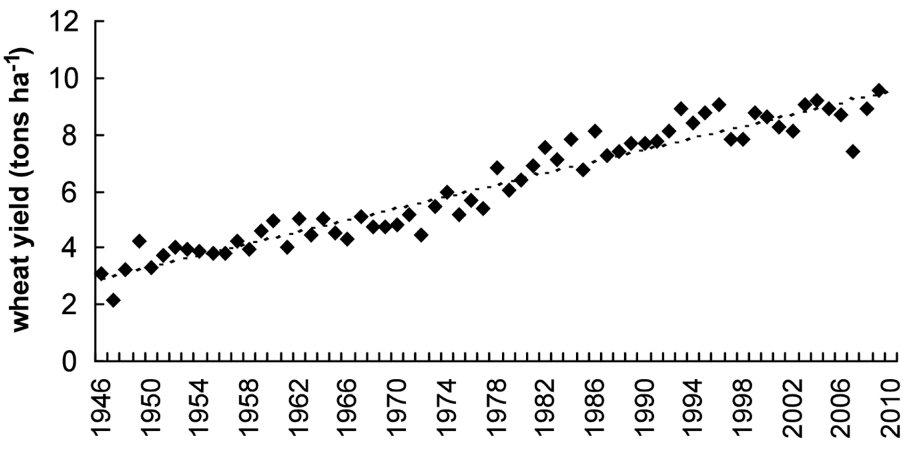

Figure 1.1 *Development of wheat yield in the Netherlands between 1946 and 2009.*

Intensified farming practices affect farmland species, directly or indirectly. Depending on their traits, such as dispersal ability and reproductive strategy, species may be influenced by different components of agricultural intensification, or their interactions. Birds are often used as biodiversity indicators and indicators of environmental quality. In 1966, a farmland bird indicator including the trends of 19 species was introduced in England, and used to evaluate government policy in terms of reversing the decline of farmland birds. A common farmland bird indicator for the European Union has been in use since the 1980s. Although birds are not the most sensitive species group and often respond to changes with a time lag, they are easily monitored, are among the best studied taxonomic groups, are long-lived and are located high up in the food-chain (Tucker, 1997). Birds are likely to react to changes in food-webs and are useful indicators of changes in biodiversity. The next section describes the effects of agricultural intensification on birds in more detail, focusing on species that breed or forage in winter mainly on arable farmland.

Agricultural intensification and farmland birds

Many direct and indirect effects of agricultural intensification on farmland birds have been reported by various studies, most of them carried out in the UK. Several studies have suggested that the two main proximate reasons for farmland bird declines are a low reproductive rate in summer and high mortality in winter (Gregory et al., 2004; Newton, 2004; Siriwardena et al., 2008). Reproductive rates and winter mortality have both been influenced by changes in breeding habitats and wintering grounds and thus indirectly by agricultural intensification.

In their habitat selection, breeding as well as wintering birds have to deal with a trade-off between energy intake and predation risk, i.e. food availability and shelter. Both habitat characteristics have been influenced by intensified farm management (see Fig. 1.2).

First of all, the area of suitable breeding and wintering habitats has decreased due to field enlargement and the associated removal of field margins, hedgerows and other semi-natural habitats (Baessler & Klotz, 2006). In addition, the loss of temporal and spatial diversity in cropping systems has reduced suitable nesting opportunities within arable crops, including those for consecutive breeding attempts (Benton et al., 2003).

This is compounded by the fact that the remaining breeding habitats often provide less food, such as invertebrates and weeds. Food abundance on farmland has been reduced by the use of pesticides, mechanical weed control and soil disrupting activities (Brickle et al., 2000; Potts, 1997; Stoate et al., 2001). Reduced food availability around nests not only affects the energy intake by chicks and adults, but may also increase the risk of predation due to greater foraging distances (Brickle et al., 2000; Morris & Gilroy, 2008).

Crop density and vegetation composition (of field margins) have been shown to be influenced by fertilizer use (Whittingham et al., 2006). The resulting denser crops and homogenized vegetation structures might hamper food accessibility. Moreover, they may be unsuitable for breeding birds, as they do not provide sufficient shelter against predators (Benton et al., 2003).

Reproductive success is also directly affected by farming practices such as disturbance due to frequent farming operations. The use of mechanical weeding on organic farms, for example, has been shown to destroy nests (Kragten & de Snoo, 2007).

Food availability in winter has been reduced by improved harvesting techniques that spill less grain (Wilson 2007), as well as by post-harvest herbicide applications (Moreby & Southway, 1999), tillage and the early ploughing of stubbles (Newton, 2004; Stoate et al., 2009). Moreover, tillage and the use of herbicides shortly after the crop harvest may decrease the vegetation cover on arable fields, and thus food and shelter opportunities for foraging birds in winter (Evans et al., 2004; Stoate et al., 2001).

In summary, by altering the vegetation structure (i.e. shelter) and food availability, the intensification of farming practices has directly and indirectly affected the suitability of breeding and foraging habitats for farmland birds.

Mitigation measures

The most widely introduced measures on farmland to reduce the negative impacts of intensified farming practices on the environment and biodiversity are organic farming and agri-environment schemes.

Agri-environment schemes were included in the CAP in 1992. Farmers have been stimulated to adopt agri-environment schemes by financial compensations. The schemes vary in their goals, ranging from the prevention of environmental pollution by creating field margins as buffer zones to the protection of individual species by means of specifically designed measures. Agri-environment schemes also differ in their spatial scale, ranging from field margins to whole farms (e.g. organic farming in some countries) or even to landscape scale (e.g. mosaic management covering several farms (Schekkerman et al., 2008)). However, severe doubts about the effectiveness of agri-environment schemes were raised at the beginning of the present century (Berendse et al., 2004; Kleijn & Sutherland, 2003). Their effectiveness might be reduced by their spatial arrangement and scale, by their implementation and by the composition of the surrounding landscape (Berendse et al., 2004; Tscharntke et al., 2005).

Organic farming, which covered about 4% of the farmland of the European Union (EU 25) in 2005 (Eurostat, 2007b), excludes the application of chemicals, such as artificial fertilizer and pesticides. The goals of organic farming are a more environment-friendly production, the preservation of natural resources and the conservation of a high level of biodiversity (Council Regulation (EC) No 834/2007 of 28 June 2007).

Whether birds breeding and wintering on farmland benefit from organic farming remains unclear (Bengtsson et al., 2005; Chamberlain et al., 2010; Fuller et al., 2005; Hole et al., 2005). For example, literature reviews by Bengtsson et al. (2005) and Hole et al. (2005) found positive effects of organic farming on species richness and abundance of birds, while Kragten et al. (2008) and Chamberlain et al. (2010) found only species-specific responses to organic farming. Some species were more abundant on organic farms, while densities of others did not differ or were even lower on organic farms. Furthermore, Kragten et al. (2007; 2008) found that although breeding skylarks (*Alauda arvensis*) preferred crop types that were grown over larger areas on organic farms, their reproductive success, as well as that of lapwings (*Vanellus vanellus*), was reduced by the more frequent farming operations on the same farms.

The effectiveness of agri-environment schemes and organic farming probably also depends on landscape composition. Mitigation measures have been shown to be most effective in homogeneous landscapes with low numbers of semi-natural habitats (Concepción et al., 2008; Dänhardt et al., 2010; Roschewitz et al., 2005; Smith et al., 2010). Thus, the effectiveness of an agri-environment scheme might not only depend on its design and the species it is designed for, but also on other variables, such as the spatial context and the characteristics of the surrounding landscape.

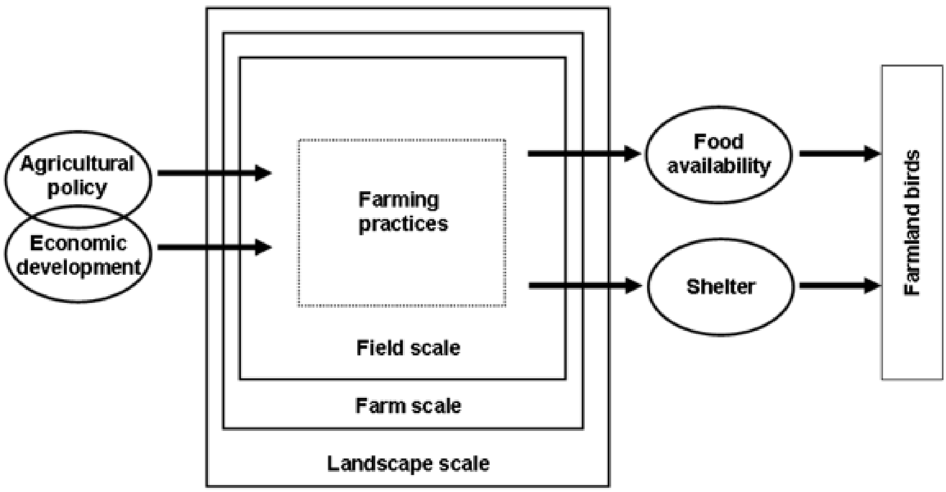

Figure 1.2 *Different scales of agricultural intensification and their indirect effects on farmland birds.*

Aim and outline of this thesis

The simultaneous intensification of various farming practices makes it difficult to disentangle their effects on biodiversity. Reduced abundance of food and suitable cover for birds on farmland is the result of intensive farm management at different spatial scales (Fig. 1.2; Benton et al., 2003; Robinson & Sutherland, 2002). A better understanding of the most important components of agricultural intensification affecting farmland biodiversity is needed to conserve biodiversity on farmland more efficiently (Newton, 2004), and may provide a tool to take decisive action to preserve biodiversity in agricultural landscapes.

The aim of the research reported on in this thesis was therefore to investigate indirect effects of different components of agricultural intensification on the abundance and species richness of farmland birds at various spatial scales (see Fig. 1.2). We also investigated the effectiveness of organic farming in counteracting the negative impacts of agricultural intensification on farmland birds. Finally, we studied the influence of the food abundance and vegetation characteristics of arable fields and their surrounding areas on habitat selection by wintering birds.

European agricultural policy is one of the main driving factors behind agricultural intensification in EU member states. Consequently, EU accession date has influenced the rate of agricultural intensification in various European countries and regions (Stoate et al., 2009). Additionally, differences in agricultural intensification between member states have been determined by national policies, as well as by climatic and environmental conditions (Henle et al., 2008; Stoate et al., 2009).

We therefore investigated the effects of agricultural intensity on biodiversity simultaneously in up to nine different agricultural regions across eight European countries, covering climatic and geographic gradients from Spain to Sweden and from Ireland to Poland (as part of the EuroDiversity AgriPopes programme, chapters 2-4). Chapter 2 describes the effects of different components of agricultural intensification on the species richness in terms of wild plants, carabids and ground-nesting farmland birds. The effects of farming practices on the biological control of insect pests by natural enemies, an important ecosystem service in agro-ecosystems, were studied experimentally. In addition, we investigated whether organic farming effectively reduces the negative impacts of agricultural intensification on biodiversity.

Chapter 3 elaborates on the effects of the components of agricultural intensification and organic farming on the abundance of farmland bird species.

Chapter 4 reports on our study of the effects of farm management and landscape characteristics on the diversity and abundance of farmland birds in winter, investigating the interaction between the effectiveness of organic farming and landscape composition.

The next two chapters (5 and 6) are based on research conducted in two different agricultural regions in the Netherlands. Chapter 5 deals with habitat selection by wintering farmland birds in relation to food abundance and vegetation cover, analysing the effects of farm management and farm type (organic vs. conventional) on food abundance and vegetation cover.

To investigate habitat selection by skylarks in winter, we studied the influence of food abundance and vegetation characteristics of arable fields and field boundaries on skylark abundances (chapter 6). In addition, differences in skylark diet between seasons and habitat types were analysed based on the content of skylark faeces.

Finally, chapter 7 presents an overview of the most important results and discusses them in the context of foraging ecology and farmland bird conservation.

Chapter 2

Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland

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Abstract

During the last 50 years, agricultural intensification has caused many wild plant and animal species to go extinct regionally or nationally and has profoundly changed the functioning of agro-ecosystems. Agricultural intensification has many components, such as loss of landscape elements, enlarged farm and field sizes and larger inputs of fertilizer and pesticides. However, very little is known about the relative contribution of these variables to the large-scale negative effects on biodiversity. In this study, we disentangled the impacts of various components of agricultural intensification on species diversity of wild plants, carabids and ground-nesting farmland birds and on the biological control of aphids.

In a Europe-wide study in eight West and East European countries, we found important negative effects of agricultural intensification on wild plant, carabid and bird species diversity and on the potential for biological pest control, as estimated from the number of aphids taken by predators. Of the 13 components of intensification we measured, use of insecticides and fungicides had consistent negative effects on biodiversity. Insecticides also reduced the biological control potential. Organic farming and other agri-environment schemes aiming to mitigate the negative effects of intensive farming on biodiversity did increase the diversity of wild plant and carabid species, but - contrary to our expectations - not the diversity of breeding birds.

We conclude that despite decades of European policy to ban harmful pesticides, the negative effects of pesticides on wild plant and animal species persist, at the same time reducing the opportunities for biological pest control. If biodiversity is to be restored in Europe and opportunities are to be created for crop production utilizing biodiversity-based ecosystem services such as biological pest control, there must be a Europe-wide shift towards farming with minimal use of pesticides over large areas.

Introduction

Farmland is the most extensive habitat for wild plant and animal species in Europe, covering 43% of the EU members states' surface area (EU-27) and still harbouring a large share of European biodiversity, e.g., 50% of all European bird species (Pain & Pienkowski, 1997) and 20-30% of the British and German flora (Marshall et al., 2003). In recent decades, however, agricultural intensification has unquestionably contributed to the impoverishment of European farmland biodiversity (Donald et al., 2001c; Krebs et al., 1999; Robinson & Sutherland, 2002; Stoate et al., 2001). There is considerable concern that declines in biodiversity affect the delivery of ecosystem services (Hooper et al., 2005). In agricultural landscapes, the services considered most at risk from agricultural intensification are biological pest control (Tscharntke et al., 2005), crop pollination (Biesmeijer et al., 2006) and protection of soil fertility (Brussaard et al., 1997).

Agricultural intensification takes place at various spatial scales, from increased application of herbicides, insecticides, fungicides and chemical fertilizer on local fields to loss of natural and semi-natural habitats and decreased habitat heterogeneity at the farm and landscape levels (Attwood et al., 2008; Benton et al., 2003; Billeter et al., 2008; Hendrickx et al., 2007; Tscharntke et al., 2005; Weibull et al., 2000). So far it has been difficult to disentangle the impacts of intensified management of local fields from changes in land use at the landscape level, since both occur simultaneously in most agricultural landscapes (Robinson & Sutherland, 2002).

In addition, previous assessments have generally focused on a few taxa or countries and hardly any study has simultaneously addressed the effects of agricultural intensification on key ecosystem services such as the biological control of agricultural pests.

Since the early 1990s the EU has promoted initiatives to prevent and reduce the negative effects of intensive farming. In 1991, legislation limiting the use of pesticides with high risks to the environment came into force (Council Directive 91/414/EEC of 15 July 1991). The reform of the Common Agricultural Policy (CAP) in 1992 aimed to reduce the negative consequences of agricultural intensification by financially supporting agri-environment schemes and organic farming (Council Regulation 2078/92/EEC of 30 June 1992). However, several studies have shown that agri- environment schemes and organic farming do not always deliver the expected benefits (Bengtsson et al., 2005; Berendse et al., 2004; Kleijn et al., 2001). So, an important, but yet unanswered question is whether policies have significantly reduced the adverse effects of intensive farming on biodiversity and, closely linked to this, on the delivery of key ecosystem services such as biological pest control. In this study, we investigated in nine European areas the effects of agricultural intensification and its components on the species diversity of wild plants, carabids and ground-nesting farmland birds (thus considering three different trophic levels) and biological control potential. We measured eight landscape structure variables and 13 components of agricultural intensification at farm and field level and disentangled their different effects on biodiversity loss. Moreover, we tested the hypothesis that both organic farming and agri-environment schemes reduce the negative effects of intensive farming on biodiversity.

Material and methods

Study area

The nine areas studied were located in eight countries: Sweden, Estonia, Poland, the Netherlands, Germany (two areas: close to Göttingen, West-Germany and Jena, East-Germany, respectively), France, Spain and Ireland (see Appendix Fig. 2.3 for the locations of the nine study areas). Each area was between 30×30 and 50×50 km^2 in size to minimize differences in the regional species pools among farms within each area. In each area, 30 arable farms were selected along an intensification gradient using cereal yield as a proxy for agricultural intensification. The farms were selected so that the previous year's yield and landscape composition were uncorrelated within the study area in question.

Sampling protocol

On each farm, five points distributed over no more than five arable fields were selected for sampling wild plants and carabids and estimating the biological control potential. Most (80%) of the sampling points were in fields of winter wheat (the major cereal crop in much of Europe). The remainder was in winter barley (9%), spring wheat (5%), winter rye (5%) or triticale (<1%). To avoid field margin effects on observations, the sampling points were positioned 10 m from the centre of one side of the field. Whenever two sampling points were located in the same field, they were placed at opposite sides of the field. On each farm, one area of 500×500 m^2 was selected around one of the sampled fields, for the survey of breeding birds. All sampled fields from different farms were at least 1 km apart. Sampling was performed during spring and summer 2007 and was synchronized using the phenological stages of winter wheat in each study area as a time reference.

Wild plants

At each sampling point, vegetation relevées were made once during the flowering to the milk-ripening stage of winter wheat, using three plots of 2×2 m^2. The plots were placed 5 m apart on a line parallel to the field borders. All species with at least the first two leaves (after the cotyledon) were recorded per plot. To avoid phenological effects of sampling, the sequence of farm surveys was randomized over the intensification gradient within each study area.

Carabids

Carabids were caught with two pitfall traps per sampling point, which were opened during two periods of 7 days. The first sampling period occurred 1 week after the appearance of spikes of winter wheat (immediately after the biological control experiment, see below) and the second sampling period coincided with the milk-ripening stage of winter wheat. The two pitfall traps (90 mm diameter, filled with 50% ethylene glycol) were placed in the middle of the two outer vegetation plots. The invertebrates caught were fixed in the lab with 70% ethanol. We identified all the species caught in one trap randomly selected from each pair of traps.

Birds

The bird surveys were conducted according to a modified version of the British Trust for Ornithology's Common Bird Census (Bibby et al., 1992), starting according to local information on the phenology of breeding birds. They were conducted three times, at intervals of 3 weeks. Bird inventory quadrats of 500×500 m^2 were surveyed in such a way that each spot within the quadrat was no more than 100 m from the surveyor's route. The surveys took place between 1 h after dawn and noon, but only if it was not windy, cloudy, or raining. Breeding bird territories for ground-nesting farmland species were determined using the three survey rounds (see Appendix Table 2.2). Three different criteria were used to define breeding bird territories, depending on the species' detectability and breeding behaviour (see Appendix Table 2.2).

Biological control potential

Biological control potential was estimated experimentally during the emergence of the first inflorescence of winter wheat (Östman, 2004). The experiment lasted 2 days and was repeated once within 8 days. In the morning of the first day, live pea aphids (*Acyrthosiphon pisum*) of the third or fourth instar were glued to plastic labels (three per label) by at least two of their legs and part of their abdomen. Odourless superglue was used. At noon, the labels were placed in the three vegetation plots at three of the five sampling points per farm. The labels were bent over slightly, so the aphids were on the lower surface, protected from rain. Three labels were placed along the diagonal of each plot. Hence, at each farm there were 27 labels, with 81 aphids in total. Immediately after the aphids had been placed in the field, the numbers of aphids present were recorded. Thereafter, the labels were checked four more times during 30 h: around 6 p.m. of the first day, at 8 a.m., 1 p.m. and about 6 p.m. on the following day, the exact time varying depending on the study area. After the last check, the labels with the remaining aphids were taken to the lab and checked under stereo microscopes to check whether remaining aphids could not have been removed by predators because they were covered with glue. The data used for the analyses was from one or both of the rounds, depending on what was available from each study area.

Farmers' questionnaire

Information about yields and farming practices (pesticide and fertilizer use, ploughing and mechanical weed control regime) and farm layout (number of crops, percentage land covered by an agri-environment scheme, field size) was collected by means of a questionnaire sent out to all participating farmers. The response was 98%.

Landscape structure

On the landscape scale, eight landscape structure variables were estimated within circles around each sampling point (with radii of 500 and 1000 m) and additionally four variables around each bird quadrat (used for the analysis of the bird data; only 500 m radius): mean field size and its standard deviation, the percentage of land planted with arable crops within the area and the Shannon habitat diversity index. The following habitat classes were used to estimate the habitat diversity (according to the definitions from the European Topic Centre on Land Use and Spatial Information (Büttner et al., 2000)): continuous urban fabrics, discontinuous urban fabrics, cultivated arable lands, fallow lands under rotation systems, permanent crops, pastures, forests, transitional woodland-scrub and water.

Statistics

Generalized linear mixed models (GLMM) (Breslow & Clayton, 1993) were used to analyse the effects of agricultural intensification on biodiversity and the biological control potential in GenStat 11.1 (Payne et al., 2008). All explanatory variables were included as fixed effects. Because of the sampling structure of the data, fields nested within farms, farms within study area, and study area, were included as random effects. To identify the distribution of the species diversity data (see Appendix Table 2.6), the variance to mean relationship was explored at the lowest stratum. This revealed that a Poisson distribution was appropriate for the numbers of plant, carabid and bird species. The median survival time of aphids was heavily skewed and was therefore assumed to follow a lognormal distribution.

Heavily skewed explanatory variables were log-transformed and the percentage of land planted with arable crops was logit transformed (see Appendix Table 2.5). All variables were standardized according to $(x-\mu)/s$, with $x =$ measurement, $\mu =$ mean and $s =$ standard deviation to enable comparison of the magnitude of their effects.

To reduce the number of landscape variables, a principal component analysis (PCA) was done with Canoco for Windows 4.5 (Ter Braak, & Šmilauer, 2002). This revealed two distinct groups of variables (see Appendix Fig. 2.4): the first group was mean field size and its standard deviation, the second was the percentage of land planted with arable crops and the Shannon habitat diversity index. Because it had the highest correlation with the plane defined by the two axes (longest PCA arrow), mean field size within a radius of 500 m was selected from the first group to be included in the analyses. In the second group, the highest correlation with the plane was the percentage land planted with arable crops. We chose the variable with the same radius as mean field size (selected from the first group), i.e. 500 m.

Only a few intensification variables showed high correlations between each other (Pearson correlation coefficient > 0.7; see Appendix Tables 2.7 and 2.8). The number of insecticide applications correlated with the amount of fungicides applied ($r = 0.75$) and the number of fungicide applications ($r = 0.73$) at the farm level only. Number of fungicide applications and the amount of fungicides applied were correlated both at the farm level and at the sampling point level ($r = 0.87$ and $r = 0.83$, respectively), as were the amount of inorganic fertilizer applied and the amount of fungicides used (for both, $r = 0.72$). These correlations cannot be considered problematic under the present modelling approach (Brotons, et al., 2004).

The mean values and standard deviations of all response and explanatory variables included in the analyses are given in the Appendix, Table 2.9.

Three separate analyses were done using different sets of explanatory variables, but always including the two landscape variables (mean field size and percentage land planted with arable crops within 500 m) as covariates. The first analysis included yield (as a summary variable for agricultural intensification, see Tilman et al., 2002) and its interaction with study area. The second analysis included 13 components of agricultural intensification related to farming practices: amounts of chemical N fertilizer, amounts of organic fertilizer, number of applications of herbicides, insecticides and fungicides, applied amounts of the active ingredients of herbicides, insecticides and fungicides, number of crops per farm, field size, frequency of ploughing, frequency of mechanical weed control and the percentage of arable land under agri-environment schemes (Appendix Table 2.5). Models were derived using forward and backward selection. The forward selection started with an empty model (except for the two landscape variables) and at each step the variable with the most significant effect was included, on the basis of the results of Wald tests ($p < 0.05$). This procedure was reiterated until variables no longer added significant effects to the model. The backward selection started with a full model and at each step the most non-significant variable, i.e., the variable with the highest p-value, was removed. Forward, as well as backward selection, resulted in identical models in all cases. In a third analysis, we investigated the single effects of farm type (conventional or organic) and the percentage of land under agri-environment schemes. Organic farmers do not apply chemical fertilizers and use only a very limited set of pesticides. Agri-environment schemes include commitments to lower fertilizer and pesticides application, while in some countries, margins or entire fields are excluded from fertilizer or pesticide applications.

We emphasize that in the text the term 'effect' is used for statistical associations and relationships, and does not necessarily mean a causal relation between two variables.

Data availability

For the second analysis (13 variables of farming practices as explanatory variables), sampling points with one or more missing variables were removed. Bird data were not collected in France. There were no data on aphid survival for Spain and France.

Results

We first investigated the relationship between cereal yield, a variable closely related to many different intensification measures (Donald et al., 2001c; Tilman et al., 2002), and wild plant, carabid and breeding bird species diversity (Appendix Table 2.3) on arable fields. We found strong negative relationships between cereal yields and the species diversity of wild plants, carabids and ground-nesting farmland birds (Wald tests: $\chi^2_1 = 141.56$, $p < 0.001$; $\chi^2_1 = 23.72$, $p < 0.001$; $\chi^2_1 = 7.68$, $p = 0.006$; Appendix Table 2.3). On average, in the sampled area, an increase in cereal yield from 4 to 8 tons/ha results in the loss of five of the nine plant species, two of the seven carabid species and one of the three bird species (Fig. 2.1A-C).

Crop yield correlated positively with median aphid survival time ($\chi^2_1 = 6.86$; $p = 0.009$), suggesting a negative effect on the biological control potential (Fig. 2.1D).

The effects of wheat yield on wild plant and carabid species diversity and aphid survival time differed among study areas (yield x study area interaction: $\chi^2_8 = 36.94$, $p < 0.001$; $\chi^2_8 = 24.65$, $p = 0.002$; $\chi^2_6 = 17.77$, $p = 0.007$, respectively). Comparison of the yield effects among study areas revealed that in some countries, yield had negative effects on these variables, but in other countries there was no relationship (Fig. 2.2; Appendix Table 2.4). In two of the three study areas where we found no relationship, the variation in yield among fields and farms was much smaller than in the other countries, which probably explains the lack of significant effects. There were no consistent differences between West and East European countries.

As a second step, we investigated the relative importance of 13 variables we considered as relevant components of agricultural intensification (Appendix Table 2.5). The characteristics of the surrounding landscape had significant effects on wild plant species diversity only (Table 2.1). The number of plant species was inversely related to average size of fields within a radius of 500 m, emphasizing the importance of field margins for the establishment of wild plant species on arable land. The number of wild plant species declined as the frequency of herbicide and insecticide application and the amounts of active ingredients of fungicides increased (Table 2.1). The number of carabid species was negatively affected by the amounts of active ingredients of insecticide applied. Bird species diversity declined with increasing frequency of fungicide application, a variable closely correlated with the frequency of insecticide application (Pearson's correlation coefficient $r = 0.732$; $p < 0.001$). The predation on aphids declined as the applied

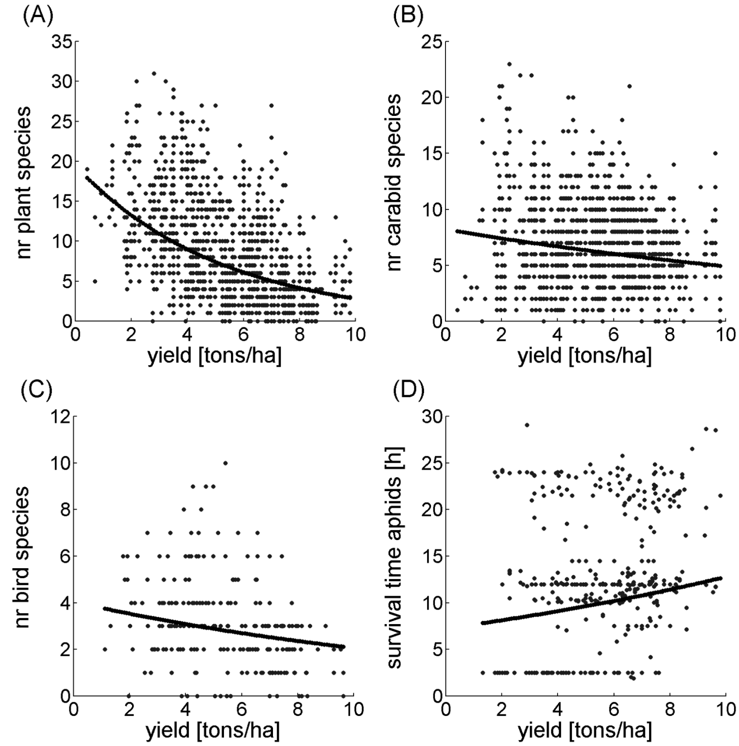

Figure 2.1 *Effects of cereal yield (tons/ha) on: (A) the number of wild plant species per sampling point (in 3 plots of 4 m^2), (B) the number of carabid species per sampling point (per trap during 2 sampling periods), (C) the number of ground-nesting bird species per farm (one survey plot of 500×500 m^2), and (D) the median survival time of aphids (h). Trend lines were calculated using GLMM including the two surrounding landscape variables as covariates and field, farm and study area as nested random effects.*

amounts of insecticides increased (Table 2.1).

Thirdly, we examined the effects of organic farming and the implementation of agri-environment schemes on biodiversity and the biological control potential. Organic farms

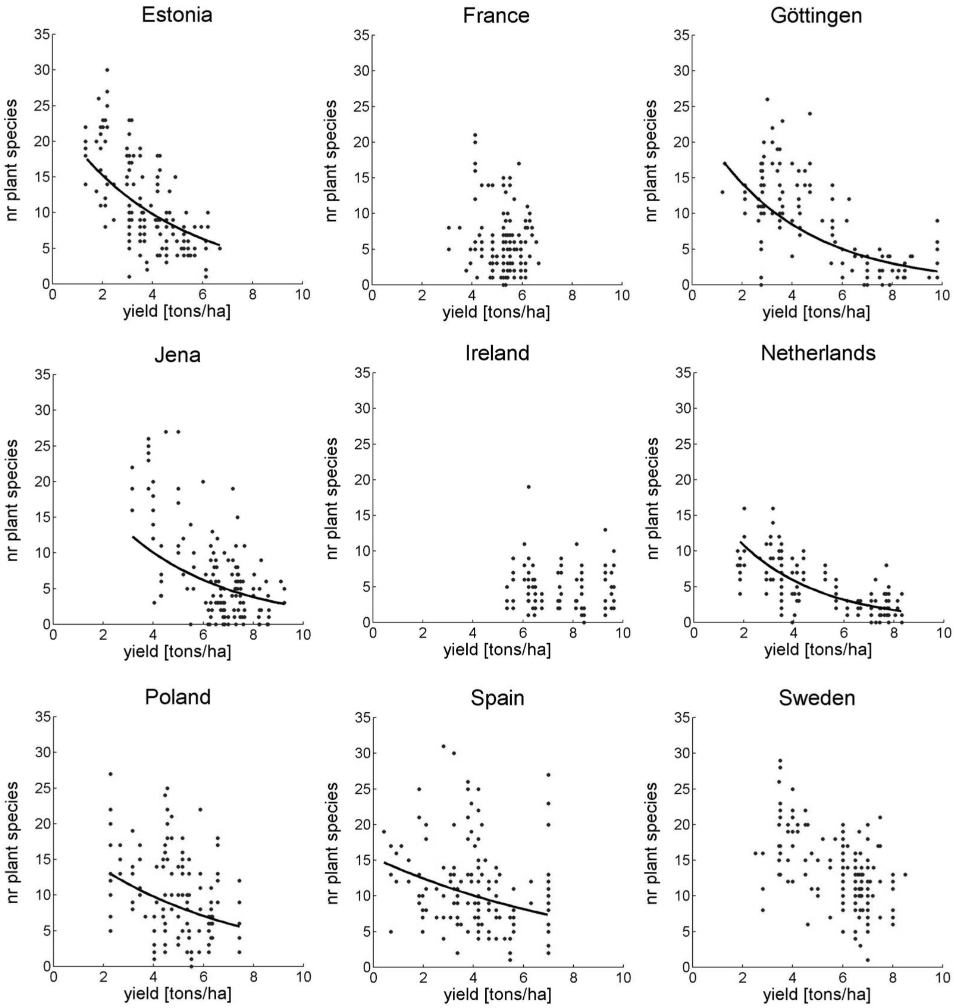

Figure 2.2 *Effects of cereal yield (tons/ha) on the number of wild plant species per sampling point (in 3 plots of 4 m^2) in each of the study areas. Trend lines were calculated using GLMM including the two surrounding landscape variables as covariates and field, farm and study area as nested random effects and are plotted, whenever the relationship was significant ($p < 0.05$).*

Table 2.1 *Effects of different components of agricultural intensification on the diversity of plants, carabids and birds and median aphid survival time. The models selected after considering all 13 intensification variables using forward selection (backward selection produced identical models) are presented. All models included the two landscape variables (mean field size and percentage of land planted with arable crops within a radius of 500 m, in italics), even if these had no significant effects (non-significant effects are not shown). Intensification variables were only included if they had significant effects using the Wald test (p < 0.05). AES = agri-environment scheme, amount of a.i. = amount of active ingredients.*

Response variable	**Explanatory variable**	**Standardized effect**	χ^2_1	**p-value**
Number of plant species	*Mean field size*	-0.096	6.30	0.012
	% of land under AES	0.150	12.28	<0.001
	Frequency of herbicide application	-0.106	8.90	0.003
	Frequency of insecticide application	-0.105	6.15	0.013
	Applied amounts of a.i. of fungicides	-0.263	31.46	<0.001
Number of carabid species	% of land under AES	0.065	6.80	0.009
	Applied amounts of a.i. of insecticides	-0.061	10.80	0.001
Number of breeding bird species	Frequency of fungicide application	-0.134	6.30	0.012
Median survival time of aphids	% of land under AES	-0.143	9.33	0.002
	Applied amounts of a.i. of insecticides	0.114	11.17	0.001

comprised 22% of the total number of selected farms in our study and occurred in five of the nine study areas. These farms harboured more wild plant and carabid species (single effects of farm type: $\chi^2_1 = 165.29$, $p < 0.001$; $\chi^2_1 = 4.20$, $p = 0.040$, respectively; Appendix Table 2.3), but not significantly more bird species ($\chi^2_1 = 1.27$, $p = 0.260$). Aphid survival was not significantly lower on organic farms as compared with conventional farms ($\chi^2_1 = 2.90$, $p = 0.088$). 45% of the selected farms had agri-environment schemes. These schemes had positive effects on the number of wild plant and carabid species and the predation of aphids (single effects of percentage of land with agri-environment scheme: $\chi^2_1 = 52.15$, $p < 0.001$; $\chi^2_1 = 7.24$, $p = 0.007$; $\chi^2_1 = 13.13$, $p < 0.001$, respectively; Appendix Table 2.3), but not on bird species diversity ($\chi^2_1 = 1.45$, $p = 0.228$).

Discussion

We studied the effects of agricultural intensification on biodiversity across three trophic levels and the potential for biological pest control in eight European countries. Out of the 13 studied components of agricultural intensification, use of pesticides, especially insecticides and fungicides, had the most consistent negative effects on the species diversity of plants, carabids and ground-nesting farmland birds, and on the potential for biological pest control. We conclude that despite several decades of implementing a Europe-wide policy intended to considerably reduce the amount of chemicals applied on arable land, pesticides are still having disastrous consequences for wild plant and animal species on European farmland. Importantly, this impact is also manifested as a reduction of the potential of natural enemies to control pest organisms.

It is noteworthy that both organic farms, which apply only those pesticides considered harmless to the environment, and agri-environment schemes had positive effects on plant and carabid diversity, but did not show the expected positive effects on bird species diversity. A possible explanation for the lack of such positive effects is the large spatial scale of the pollution associated with pesticide use across Europe, which inevitably leads to negative effects of pesticides - even in areas where the application of these substances has been reduced or terminated. Such large-scale effects will be especially relevant for taxa that utilize large areas, such as birds, mammals, butterflies (Rundlöf et al., 2008) and bees (Clough et al., 2007; Holzschuh et al., 2008).

We conclude that if biodiversity is to be restored in Europe and opportunities are to be created for crop production utilizing biodiversity-based ecosystem services such as biological pest control, a Europe-wide shift towards farming with minimal use of pesticides over large areas is urgently needed.

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Appendix

Table 2.2 *List of farmland bird species (species nesting on the ground of arable fields, pastures or field margins) and the corresponding requirements for assigning breeding territories. Categories: A: at least two observations of birds displaying territorial behaviour (foraging, calling, singing, conflicts indicating territory defence) at the same spot during different survey rounds; B: one observation of territorial behaviour (species unlikely to be present during all the three survey visits, for example because of long-distance migration, or species considered difficult to observe); C: direct evidence of breeding activities.*

English name	**Scientific name**	**Breeding category**
Black-tailed Godwit	*Limosa limosa*	A
Corn Bunting	*Miliaria calandra*	A
Corncrake	*Crex crex*	B
Crested Lark	*Galerida cristata*	A
Curlew	*Numenius arquata*	B
Fan-tailed Warbler	*Cisticola juncidis*	A
Great Bustard	*Otis tarda*	B
Lapwing	*Vanellus vanellus*	A
Little Bustard	*Tetrax tetrax*	B
Mallard	*Anas platyrhynchos*	C
Montagu's Harrier	*Circus pygargus*	C
Meadow Pipit	*Anthus pratensis*	A
Marsh Harrier	*Circus aeruginosus*	C
Marsh Warbler	*Acrocephalus palustris*	B
Ortolan Bunting	*Emberiza hortulana*	B
Oystercatcher	*Haematopus ostralegus*	A
Grey Partridge	*Perdix perdix*	B
Pheasant	*Phasianus colchicus*	A
Quail	*Coturnix coturnix*	B
Red-legged Partridge	*Alectoris rufa*	B
Short-toed Lark	*Calandrella brachydactyla*	A
Stonechat	*Saxicola torquata*	A
Snipe	*Gallinago gallinago*	A
Tawny Pipit	*Anthus campestris*	B
Wheatear	*Oenanthe oenanthe*	A
Whinchat	*Saxicola rubetra*	A
Woodlark	*Lullula arborea*	A
Yellowhammer	*Emberiza citrinella*	A
Yellow Wagtail	*Motacilla flava*	A

Table 2.3 *Results of the Generalized linear mixed models that we applied for the different response variables: a) relationship with yield and its interaction with country; b) selected models after forward selection considering 13 intensification variables (amount of a.i. = amount of active ingredients); c) single effects of farm type and percentage agri-environment schemes; d) relationships between biodiversity variables and the biodiversity at the lower trophic level and between aphid survival and diversity and density of carabids as possible predators (single effects). All analyses included the two surrounding landscape variables (mean field size and percentage of land planted with arable crops); they are only included in this table if the effect was significant. Note, that percentage agri-environment scheme is included as part of the selected model in b) and as single effect in c).*

Response variable		Explanatory variable	Standardized effect	χ^2	p-value
Number of plant species	a	Yield	-0.362	141.56	<0.001
		Yield*country		36.94	<0.001
	b	*Mean field size*	-0.096	6.30	0.012
		% of land under AES	0.150	12.28	<0.001
		Herbicide applications	-0.106	8.90	0.003
		Insecticide applications	-0.105	6.15	0.013
		Fungicides (amounts a.i.)	-0.263	31.46	<0.001
	c	Farm type	0.403	165.29	<0.001
		% of land under AES	0.327	52.15	<0.001
Number of carabid species	a	Yield	-0.097	23.72	<0.001
		Yield*country		24.65	0.002
	b	% of land under AES	0.065	6.80	0.009
		Insecticides (amounts a.i.)	-0.061	10.80	0.001
	c	Farm type	0.042	4.20	0.040
		% of land under AES	0.067	7.24	0.007
	d	Number of plant species	0.010	15.82	<0.001
Number of breeding bird species	a	Yield	-0.132	7.68	0.006
		Yield*country		7.33	0.395
	b	Fungicide applications	-0.134	6.30	0.012
	c	Farm type	0.050	1.27	0.260
		% of land under AES	0.065	1.45	0.228
	d	Number of carabid species	0.036	5.07	0.024
		Number of carabid individuals	0.097	3.58	0.058
		number of plant species	0.026	12.19	<0.001
Median survival time aphids	a	Yield	0.108	6.86	0.009
		Yield*country		17.77	0.007
	b	% of land under AES	-0.143	9.33	0.002
		Insecticides (amounts a.i.)	0.114	11.17	0.001
	c	Farm type	-0.156	2.90	0.088
		% of land under AES	-0.176	13.13	<0.001
	d	Number of carabid species	-0.020	6.44	0.011
		Number of carabid individuals	0.000	0.02	0.891

Table 2.4 *Differences between study areas of the effects of yield on wild plant species diversity, carabid species diversity and the median survival time of aphids. Estimates of the effects of yield on the number of plant and carabid species and the survival time of aphids are given for each study area. Different letters denote significant differences between countries.* [1]*and* [2]*are the two different study areas in Germany: Göttingen and Jena, respectively.*

	Number of plant species				**Number of carabid species**			**Median survival time aphids**			
	Estimate				Estimate			Estimate			
Estonia	-0.450	a	b		-0.107	a	b	0.446			c
France	-0.261		b	c	0.108		b				
Germany[1]	-0.511	a	b		-0.238	a		0.211		b	c
Germany[2]	-0.533	a	b		-0.095	a	b	0.051	a	b	
Ireland	-0.129			c	-0.045		b	0.201	a	b	c
Netherlands	-0.583	a			-0.023		b	-0.090	a		
Poland	-0.301	a	b	c	-0.247	a		-0.025	a	b	
Spain	-0.179			c	-0.051		b				
Sweden	-0.133			c	-0.002		b	0.105	a	b	

Table 2.5 *List of explanatory variables included in the analyses: explanatory variables, variable description, units and sampling level (landscape, farm or field);* [1]*variables were log-transformed* [2]*percentage of land planted with arable crops was logit transformed, i.e.* $\log(\textit{percentage arable crops}+5)/(105-\textit{percentage arable crops})$.

	Explanatory variable	**Description**	**Unit**	**Sampling level**
	Farm type	conventional or organic		farm
	Yield	standardized according to 14% moisture content of the grains	tons ha^{-1}	field
Farm layout and farming practices	Number of crops	number of crops cultivated in 2007	$farm^{-1}$	farm
	Agri-environment scheme	% area of farm with agri-environment scheme	%	farm
	Field size[1]	size of sampled field	ha	field
	Pesticides (herbicides, insecticides, fungicides)	number of applications	y^{-1}	field
	Pesticides (herbicides, insecticides, fungicides[1])	total amount of active ingredients	kg ha^{-1} y^{-1}	field
	Inorganic N fertilizer	total amount of inorganic nitrogen fertilizer	kg N ha^{-1} y^{-1}	field
	Organic fertilizer	total amount of organic fertilizer	kg ha^{-1} y^{-1}	field
	Ploughing	ploughing (yes or no)		field
	Mechanical weed control	frequency mechanical weed control	y^{-1}	field
Landscape	Mean field size[1]	mean field size within 500m radius of sampling points	ha	landscape
	Percentage arable crops[2]	% arable crop within 500m radius of sampling points	%	landscape

Table 2.6 *List of response variables included in the analyses: response variable, variable description, sampling level (farm or sampling point) and distribution of the variables.*

Response variable	**Description**	**Sampling level**	**Data distribution**
Number of plant species	total number in the 3 plots	sampling point	Poisson
Number of carabid species	total number collected during 2 rounds	sampling point	Poisson
Number of breeding bird species	only ground-nesting farmland species	farm	Poisson
Median survival time of aphids	time elapsed until half the aphids had been removed	sampling point	log-normal

Table 2.7 *Correlation matrix (Pearson correlation coefficients) including all intensification and landscape variables at sampling point level: farm type, no. crops (number of crops), % AES (percentage land of a farm under an agri-environment scheme), field size, herb appl (number of herbicide applications), herb ai (amounts of active ingredients of herbicides), insect appl (number of insecticide applications), insect ai (amounts of active ingredients of insecticides), fung appl (number of fungicide applications), fung ai (amounts of active ingredients of fungicides), inorg fert (amount of inorganic N fertilizer), org fert (amount of organic fertilizer), plough (ploughing), weed control (frequency of mechanical weed control), field size 500 (landscape structure variable: mean field size within radius 500m), % arable crop 500 (landscape structure variable: percentage land under arable crops within radius 500m). Pearson correlation coefficients higher than 0.7 are in bold (average n = 1398).* [1] *variables were log transformed* [2] *variable was logit transformed.*

	farm type	yield	no. crops	% AES	field size[1]	herb appl	herb ai	insect appl	insect ai	fung appl	fung ai[1]	inorg fert	org fert	plough	weed control	field size 500[1]	% arable crop 500[2]
farm type	1																
yield	-0.52	1															
no. crops	0.18	-0.03	1														
% AES	0.46	-0.40	0.19	1													
field size[1]	-0.03	0.12	0.13	0.18	1												
herb appl	-0.55	0.48	0.02	-0.27	0.15	1											
herb ai	-0.40	0.27	0.04	-0.13	0.07	0.51	1										
insect appl	-0.31	0.53	0.06	-0.18	0.10	0.38	0.29	1									
insect ai	-0.20	0.28	0.09	-0.02	0.13	0.08	0.22	0.60	1								
fung appl	-0.40	0.59	0.04	-0.23	0.15	0.54	0.35	0.69	0.46	1							
fung ai[1]	-0.52	0.59	0.13	-0.24	0.13	0.53	0.41	0.66	0.44	**0.83**	1						
inorg fert	-0.69	0.66	0.01	-0.40	0.13	0.53	0.35	0.51	0.25	0.61	**0.72**	1					
org fert	0.30	-0.07	0.11	0.03	0.05	-0.13	-0.10	-0.09	-0.11	-0.13	-0.10	-0.26	1				
plough	0.19	-0.11	0.10	-0.09	-0.21	-0.14	0.10	0.01	0.12	0.01	0.05	-0.08	0.10	1			
weed control	0.29	-0.39	-0.18	-0.01	-0.09	-0.36	-0.16	-0.29	-0.15	-0.38	-0.47	-0.44	0.12	-0.11	1		
field size 500[1]	0.23	0.00	0.33	0.21	0.57	0.05	-0.02	-0.10	-0.02	-0.05	0.03	-0.03	0.23	-0.11	-0.06	1	
% arable crop 500[2]	-0.02	0.00	0.26	-0.12	0.16	0.16	0.06	-0.12	-0.08	-0.05	0.04	0.00	0.08	0.00	-0.06	0.37	1

Table 2.8 *Correlation matrix (Pearson correlation coefficients) including all intensification and landscape variables at farm/bird plot level: farm type, no. crops (number of crops), % AES (percentage land of a farm under an agri-environment scheme), field size, herb appl (number of herbicide applications), herb ai (amounts of active ingredients of herbicides), insect appl (number of insecticide applications), insect ai (amounts of active ingredients of insecticides), fung appl (number of fungicide applications), fung ai (amounts of active ingredients of fungicides), inorg fert (amount of inorganic N fertilizer), org fert (amount of organic fertilizer), plough (ploughing), weed control (frequency of mechanical weed control), field size 500 (landscape structure variable: mean field size within radius 500m), % arable crop 500 (landscape structure variable: percentage land under arable crops within radius 500m). Pearson correlation coefficients higher than 0.7 are in bold (average n = 251).* [1] *variables were log transformed* [2] *variable was logit transformed.*

	farm type	yield	no. crops	% AES	field size[1]	herb appl	herb ai	insect appl	insect ai	fung appl	fung ai[1]	inorg fert	org fert	plough	weed control	field size 500[1]	% arable crop 500[2]
farm type	1																
yield	-0.52	1															
no. crops	0.19	-0.05	1														
% AES	0.46	-0.45	0.20	1													
field size[1]	-0.10	0.12	0.14	0.15	1												
herb appl	-0.60	0.48	0.02	-0.32	0.18	1											
herb ai	-0.45	0.28	0.04	-0.17	0.07	0.53	1										
insect appl	-0.35	0.55	0.07	-0.23	0.11	0.39	0.34	1									
insect ai	-0.24	0.29	0.10	-0.05	0.16	0.09	0.27	0.61	1								
fung appl	-0.43	0.59	0.04	-0.25	0.19	0.56	0.38	**0.73**	0.50	1							
fung ai[1]	-0.51	0.59	0.14	-0.21	0.23	0.58	0.48	**0.75**	0.53	**0.87**	1						
inorg fert	-0.70	0.70	-0.01	-0.39	0.23	0.60	0.42	0.58	0.31	0.66	**0.72**	1					
org fert	0.34	-0.08	0.11	0.06	0.00	-0.17	-0.12	-0.12	-0.15	-0.15	-0.11	-0.28	1				
plough	0.22	-0.09	0.15	-0.02	-0.19	-0.13	0.10	0.00	0.15	-0.03	-0.03	-0.15	0.13	1			
weed control	0.25	-0.41	-0.18	-0.04	-0.14	-0.39	-0.18	-0.33	-0.19	-0.40	-0.45	-0.42	0.08	-0.07	1		
field size 500[1]	0.22	0.00	0.37	0.21	0.66	0.06	-0.03	-0.06	-0.01	-0.02	0.09	0.01	0.22	-0.07	-0.12	1	
% arable crop 500[2]	-0.01	-0.02	0.34	-0.06	0.25	0.15	0.01	-0.18	-0.10	-0.06	0.03	0.01	0.04	-0.07	-0.05	0.47	1

Table 2.9 *Mean values and standard deviations (stdev) of all explanatory and all response variables are given at the sampling point and at the farm level, i.e. the data used for the bird analyses. Amount a.i. = amounts of active ingredients.* [1]*percentage conventional farms* [2]*percentage farms with a ploughing regime*

		Farm		**Sampling point**	
		mean	**(stdev)**	**mean**	**(stdev)**
	Farm type[1]	77.5			
	Yield [kg ha^{-1}]	5401.8	(1929.1)	5398.9	(1878.9)
Farm layout and farming practices	Number of crops [farm^{-1}]	5.0	(2.6)	5.0	(2.5)
	Agri-environment scheme [%]	26.9	(40.5)	23.9	(39.0)
	Field size [ha]	11.2	(12.1)	10.5	(13.4)
	Herbicide applications [y^{-1}]	1.3	(1.1)	1.2	(1.1)
	Insecticide applications [y^{-1}]	0.5	(0.8)	0.5	(0.8)
	Fungicide applications [y^{-1}]	1.1	(1.4)	1.1	(1.3)
	Herbicides amount a.i. [kg ha^{-1} y^{-1}]	0.8	(0.9)	0.7	(0.9)
	Insecticides amount a.i. [kg ha^{-1} y^{-1}]	0.1	(0.1)	0.0	(0.1)
	Fungicides amount a.i. [kg ha^{-1} y^{-1}]	0.5	(0.6)	0.5	(0.6)
	Inorganic N fertilizer [kg ha^{-1} y^{-1}]	103.1	(79.2)	110.1	(78.5)
	Organic fertilizer [kg ha^{-1} y^{-1}]	3585.5	(9332.2)	3076.1	(9110.6)
	Ploughing[2]	75.3			
	Mechanical weed control [y^{-1}]	0.8	(1.4)	0.7	(1.3)
Landscape	Mean field size [ha]	17.1	(29.7)	14.1	(19.1)
	Percentage arable crops [%]	76.4	(18.5)	74.4	(19.5)
Response variables	Number of plant species			8.7	(6.3)
	Number of carabid species			6.8	(3.9)
	Number of breeding bird species	3.1	(2.0)		
	Median survival time of aphids [h]			12.4	(7.2)

Figure 2.3 *Map of the study areas: The locations of the study areas are indicated by black dots: Sweden, Estonia, Ireland, Netherlands, Germany (Göttingen), Germany (Jena), Poland, France and Spain.*

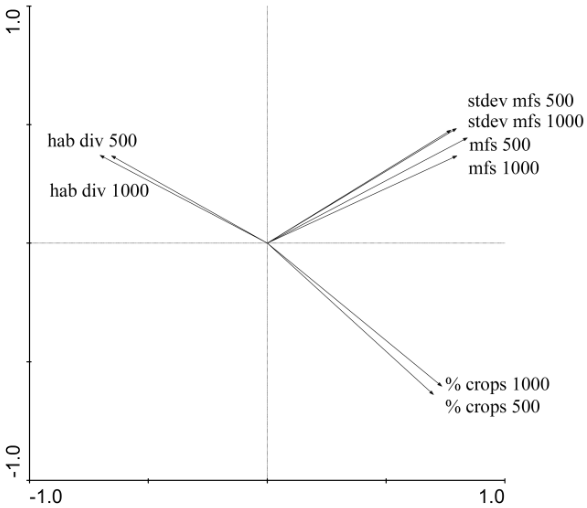

Figure 2.4 *Scatterplot of the principal component analysis (PCA) showing the 8 landscape variables estimated around the sampling points within circles with radius 500 and 1000m: Shannon habitat diversity (hab div), mean field size (mfs), standard deviation of mean field size (stdev mfs), percentage of land planted with arable crops (% crops). Mean field size (radius 500m) and percentage of land planted with arable crops had the highest correlation with the plane defined by the two axes (longest PCA arrow).*

Chapter 3

Mixed responses of farmland birds to agricultural intensification across Europe

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Abstract

In recent decades, many farmland birds have been affected by habitat loss and degradation due to agricultural intensification. The impacts of different farming practices are often species-specific, and disentangling their effects remains difficult. Although organic farming is a widespread management option that could potentially counteract species decline, its effectiveness varies between taxonomic groups and regions.
This large-scale study, including eight study areas in seven European countries, analysed the effects of various aspects of agricultural intensification, including yield, farming practices and farm type (organic vs. conventional), on the abundance of ground-nesting farmland birds.
Total breeding bird abundance, including 30 species breeding on farmland, was lower on high-yielding farms. Breeding bird abundances were affected by landscape characteristics, such as field size and percentage of land planted with arable crops, as well as by farm management. Crop diversity positively influenced total breeding bird abundances, but the increased use of pesticides and artificial fertilizer reduced total breeding bird abundance, as well as abundances of five of the nine individually investigated species. Abundances of yellow wagtails (Motacilla flava) and meadow pipits (Anthus pratensis) were positively related to intensive farm management. Compared to conventional farms, organic farms supported more lapwings (Vanellus vanellus) and fewer meadow pipits.
Based on our results, we emphasize the need to reduce pesticide and artificial fertilizer use as well as to enhance local habitat diversity for the benefit of farmland birds. In addition, the mixed results suggest that species-specific responses to intensification should be considered when implementing conservation measures.

Introduction

Farmland is one of Europe's most species-rich habitats, thanks to its wide diversity of habitat types (Bignal & McCracken, 1996; Tucker, 1997). In recent decades, however, populations of many bird species breeding on farmland have decreased to a worrying extent (Donald et al., 2001c; Donald et al., 2006; Wretenberg et al., 2006). In the second half of the last century, the decline of farmland bird populations was clearly steeper than that of species linked to other habitat types (de Heer et al., 2005; Thaxter et al., 2010). Numbers of skylarks (*Alauda arvensis*), for example, decreased by almost 30% in the Netherlands, Germany and Sweden between 1990 and 2000 (BirdLife International, 2004). Populations of yellow wagtails (*Motacilla flava*) were halved in Sweden and declined by 20-30% in Germany and Estonia between 1990 and 2000, and populations of corn buntings (*Miliaria calandra*) were reduced by almost 70% in the Netherlands and by 24% in France in the same period. These population declines have mainly been driven by agricultural intensification, and the steepest declines in Europe occurred in countries with high-yield farming (Donald et al., 2001c; Wilson et al., 1999).

The alterations and simplification of agricultural land, at field as well as landscape scale, influence the availability of suitable breeding and foraging habitats (Söderström & Pärt, 2000; Stoate et al., 2009). At landscape scale, the decrease in the habitat diversity provided by mixed farming systems, the disappearance of uncultivated field margins and the intensification of rotation schemes have resulted in a reduction of important food sources and of breeding and foraging habitats (Herzon & O'Hara, 2007; Stoate et al., 2001). At field scale, frequent tillage, improved seed-cleaning technologies, the use of pesticides and the cultivation of competitive crops have resulted in decreased availability of bird food plants and invertebrates (Wilson et al., 1999). More dense, faster growing crops and more uniform sward structures are unsuitable for nesting birds (Chamberlain et al., 1999; Kragten et al., 2008; Wilson et al., 1997) as the accessibility and detectability of prey items by foraging birds is hampered (Odderskaer et al., 1997; Wilson et al., 2005). Several agricultural production practices, such as the use of pesticides and fertilizers, mechanization and rotation schemes, have been simultaneously intensified, making it difficult to disentangle their effects on farmland birds (Donald et al., 2001c; Robinson & Sutherland, 2002).

Organic farming, currently covering about 4% of the farmland in the European Union (EU 25) in 2005, is a management strategy that could potentially counteract the loss of biodiversity on farmland (Eurostat, 2007b). It excludes the use of artificial fertilizers and pesticides and often supports higher bird abundance and species richness than conventional farming (Beecher et al., 2002; Belfrage et al., 2005; Bengtsson et al., 2005; Hole et al., 2005, but see Piha et al., 2007). However, findings regarding the effects of organic farming practices on individual bird species, their breeding success and chick survival have varied between studies (Bradbury et al., 2000; Hole et al., 2005; Kragten & de Snoo, 2008).

Although agricultural intensification and its effects on farmland birds are internationally recognized as a serious problem, these effects have mostly been investigated at local, regional or national scale. As the decline of farmland species does not stop at national borders, it is worthwhile to identify farming practices that influence several farmland species across regions and countries. Moreover, many studies are based on intensification data that are extracted from regional or even national statistics, due to a lack of locally collected data, resulting in analyses at rather coarse scales.

In this study, we investigated the impacts of agricultural intensification at local and landscape scales on ground-nesting farmland birds in eight study areas in seven European countries, covering a north-south, as well as an east-west gradient. This was done by focusing on three questions: (a) Does yield, as a summary measure of farm management intensity, affect the abundance of ground-nesting farmland birds? (b) Which components of agricultural intensification - landscape characteristics or local farm management - affect the abundance of ground-nesting farmland birds? (c) Is there a positive effect of organic farming on the abundance of ground-nesting farmland birds?

We counted birds nesting on arable farms situated in agricultural landscapes. The effects of various aspects of agricultural intensification were analysed on the total abundance of ground-nesting farmland birds, to detect possible general patterns, as well as on the abundances of the nine most abundant species.

Materials and methods

Study area

Bird observations were done in eight study areas situated in seven European countries: Sweden, Estonia, Poland, the Netherlands, western Germany, eastern Germany, Spain and Ireland (Fig. 3.1). The study areas ranged from 30×30 km to 50×50 km, to minimize differences in the regional species pools among farms. Thirty to 32 arable farms per study area were selected along a local intensity gradient, using cereal yield in the previous year as a proxy measure of agricultural intensity. Because information on farm management was missing for about 5% of the selected farms, 22 to 32 farms per study area were finally included in the analyses (see Table 3.1). Farms were defined as one or more fields located no more than 1 km apart and cultivated by the same farmer.

Organically managed farms (52 of the 232 farms) were selected in Estonia, the two German study areas, the Netherlands and Sweden. Farms were selected in such a way that cereal yield and landscape composition were uncorrelated within a study area (see *Statistical analyses*).

Bird surveys

To ensure that bird counts were comparable, one 500 × 500 m survey plot was selected per farm. Although most of the survey plot consisted of fields belonging to one farm, it could also include fields managed by another farmer. This was unavoidable in some countries, such as Spain and the Netherlands, due to farm property structures or farm sizes. Depending on the farm layout, each survey plot comprised one or more arable field types and permanent grasslands, but it always included at least one cereal field. Most cereal fields were sown with winter wheat (79%), the major crop in Europe (Eurostat, 2007a). The remainder was winter barley (9%), spring wheat (6%), winter rye (5%) or triticale (< 1%). All survey plots were at least 1 km apart.

Surveys were performed during the spring and summer of 2007, starting on dates determined from local information on the phenology of breeding birds and repeated two more times at three-week intervals. Survey plots were walked in such a way that the whole plot was covered within 100 m from the surveyor's route. For each species, its

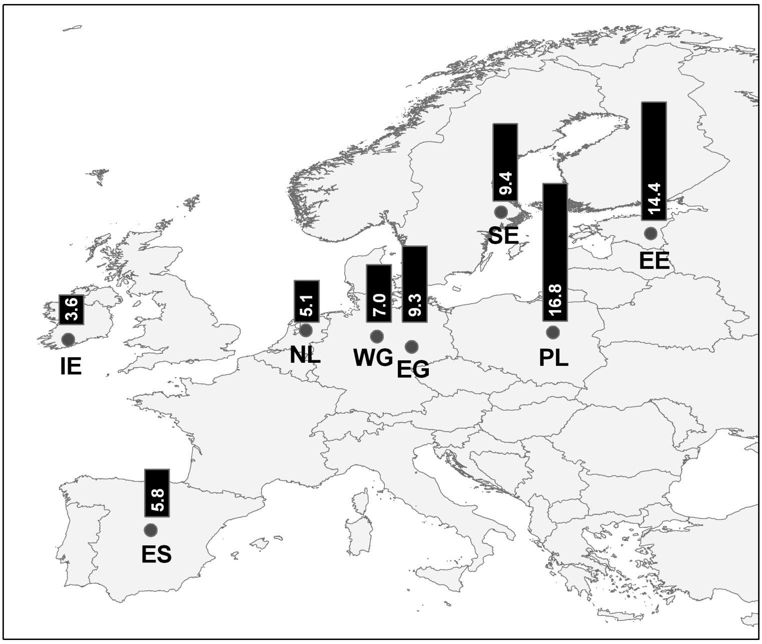

Figure 3.1 *Locations of the eight study areas and abundances of all ground-nesting farmland birds. Bars represent the mean abundance of breeding birds per survey plot in the study area. Densities are shown on the bars. Study areas: EE = Estonia, WG = western Germany, EG = eastern Germany, IE = Ireland, NL = Netherlands, PL = Poland, ES = Spain, SE = Sweden.*

position and type of activity (e.g. singing, foraging, calling) was recorded on a detailed map. Surveys took place between one hour after dawn and noon, avoiding excessively windy, cloudy or rainy weather.

Breeding territories of ground-nesting farmland birds were determined using the three survey rounds. Three different criteria, one for each of three categories, were used to define breeding bird territories. The criteria were based on the detection probability of a species in relation to its migratory and breeding behaviour (see also Geiger et al., 2010). To meet the criteria for being recorded as having a breeding territory, species of category A (see Table 3.1) had to be observed at least twice displaying territorial behaviour (foraging, calling, singing, conflicts indicating territory defence) at the same spot during different survey rounds. Category B comprised species unlikely to be present during all three survey visits, because of their migratory behaviour (e.g. long-distance migrants arriving relatively late), and species considered difficult to observe. This category required only one observation of territorial behaviour. Category C species required direct evidence of breeding activities. These categories were used in a similar way for all survey plots, and thus did not affect the analyses, which were based on relative abundance estimates.

Farm management data

Information about yield and farm management (farm type, number of crops per farm, pesticide and fertilizer use, ploughing and mechanical weed control regime) was collected by means of a questionnaire sent out to all participating farmers (Table 3.2). The information on farm-level variables (i.e. number of crops and farm type) was based on the total area belonging to that farm, thus always including land outside the survey plot (see also Geiger et al., 2010). Information about yield and farming practices (i.e. pesticide and fertilizer use, mechanical weed control regime and ploughing) was based either only on the cereal field within the survey plot (see *Bird surveys*) or on the average of up to five cereal fields, depending on the availability of cereal fields on the farm. These fields could be situated outside the survey plot. The perimeter-to-area ratio of the cereal field situated within the survey plot was estimated using GPS or geospatial data and was assumed to indicate the spatial arrangement of fields within a survey plot.

Table 3.1 *Abundances of farmland bird species observed in the study areas: English and scientific species name, category for assigning a breeding territory (cat), the average number of all breeding pairs per survey plot (500 × 500 m) for all study areas (total), the average number of breeding pairs per survey plot in each study area. EE: Estonia, WG: West Germany, EG: East Germany, IE: Ireland, NL: Netherlands, PL: Poland, ES: Spain, SE: Sweden. The number of survey plots per study area are given in brackets below the country codes. Breeding category A: at least two observations of birds displaying territorial behaviour (foraging, calling, singing, conflicts indicating territory defence) at the same spot during different survey rounds; B: one observation of territorial behaviour (species unlikely to be present during all the three survey visits, for example because of long-distance migration, or species considered difficult to observe); C: direct evidence of breeding activities.*

English name	**Scientific name**	**Cat**	**Total**	**EE**	**WG**	**EG**	**IE**	**NL**	**PL**	**ES**	**SE**
				(29)	(22)	(30)	(30)	(30)	(29)	(30)	(32)
Skylark	*Alauda arvensis*	A	4.42	9.34	3.91	7.47	0.03	1.13	6.48		6.94
Yellowhammer	*Emberiza citrinella*	A	0.88	0.90	1.95	0.60	2.37		0.31		1.16
Yellow Wagtail	*Motacilla flava*	A	0.80		0.05	0.27		1.37	4.66		
Whinchat	*Saxicola rubetra*	A	0.40	1.83		0.03			0.97		0.34
Corn Bunting	*Miliaria calandra*	A	0.32			0.10			0.93	1.50	
Marsh Warbler	*Acrocephalus palustris*	B	0.29	0.69	0.95	0.27			0.66		
Lapwing	*Vanellus vanellus*	A	0.25	0.38				1.13	0.10	0.17	0.19
Quail	*Coturnix coturnix*	B	0.24	0.24	0.09	0.50		0.30	0.48	0.23	0.03
Meadow Pipit	*Anthus pratensis*	A	0.20	0.31				0.87	0.28		0.13
Pheasant	*Phasianus colchicus*	A	0.17				0.40	0.03	0.76		0.13
Red-legged Partridge	*Alectoris rufa*	B	0.16				0.07			1.13	
Crested Lark	*Galerida cristata*	A	0.13							1.03	
Fan-tailed Warbler	*Cisticola juncidis*	A	0.13							0.97	
Wheatear	*Oenanthe oenanthe*	A	0.11	0.24			0.03		0.21		0.38
Stonechat	*Saxicola torquata*	A	0.08				0.60				
Ortolan Bunting	*Emberiza hortulana*	B	0.07						0.48		0.06
Corncrake	*Crex crex*	B	0.04	0.24					0.10		
Grey Partridge	*Perdix perdix*	B	0.04	0.14		0.07			0.14		
Little Bustard	*Tetrax tetrax*	B	0.04							0.30	
Great Bustard	*Otis tarda*	B	0.03							0.27	
Oystercatcher	*Haematopus ostralegus*	A	0.03					0.20			
Tawny Pipit	*Anthus campestris*	B	0.03						0.17	0.03	
Black-tailed Godwit	*Limosa limosa*	A	0.01				0.03	0.07			
Curlew	*Numenius arquata*	B	0.01	0.10							
Mallard	*Anas platyrhynchos*	C	0.01				0.03			0.03	
Montagu's Harrier	*Circus pygargus*	C	0.01							0.07	
Marsh Harrier	*Circus aeruginosus*	C	0.01						0.03	0.03	
Woodlark	*Lullula arborea*	A	0.01								0.06
Snipe	*Gallinago gallinago*	A	<0.01						0.03		
Short-toed Lark	*Calandrella brachydactyla*	A	<0.01							0.03	
Total			**8.9**	**14.4**	**7.0**	**9.3**	**3.6**	**5.1**	**16.8**	**5.8**	**9.4**

Table 3.2 *Information about response and explanatory variables that were included in the analyses. Response variables: species name; species observations (number of study areas where the species was observed and between brackets number of survey plots included in the analyses); data distribution; mean numbers of breeding pairs per survey plot (mean) and its standard deviation (stdev). Explanatory variables: variable name; description; unit or if the variable is a factor, the percentage of farms with a positive response; mean value (mean) and standard deviation (stdev) based on all study areas.* [1]*Variables were log-transformed.* [2]*Percentage of land planted with arable crops was logit transformed, i.e.* $\log(\textit{percentage arable crops}+5)/(105-\textit{percentage arable crops})$. [3]*Average value of 1 - 5 cereal fields per farm.* [4]*Average value of conventional farms.*

Response variable	**# Study areas (# survey plots)**	**Data distribution**	**Mean**	**(stdev)**
Total breeding bird abundance	8 (232)	Negative binomial	8.9	(6.0)
Skylark	7 (201)	Poisson	5.0	(4.3)
Yellowhammer	6 (171)	Poisson	1.2	(1.5)
Yellow Wagtail	4 (111)	Poisson	1.7	(2.2)
Whinchat	4 (119)	Poisson	0.8	(1.3)
Corn Bunting	3 (89)	Poisson	0.8	(1.5)
Marsh Warbler	4 (110)	Poisson	0.6	(1.1)
Lapwing	5 (149)	Poisson	0.4	(1.0)
Quail	6 (201)	Poisson	0.3	(0.6)
Meadow Pipit	4 (119)	Poisson	0.4	(0.8)
Explanatory variable	**Description**	**Units**	**Mean**	**(stdev)**
Yield	average (wheat) yield per farm, standardized according to 14% moisture content of the grains	$kg\ ha^{-1}$	5393.2	(1916.6)

Table 3.2 *continued*

	Explanatory variable	Description	Units	Mean	(stdev)
Farm management	Farm type	conventional or organic	22% organic farms		
	Number of crops	number of crops cultivated in 2007	$farm^{-1}$	5.0	(2.6)
	Perimeter-area ratio[1]	perimeter to area ratio of cereal fields	m^{-1}	0.0	(0.0)
	Herbicide[3,4]	number of applications	y^{-1}	1.6	(1.0)
	Herbicide a.i.[3,4]	total amount of active ingredients	$kg\ ha^{-1}\ y^{-1}$	1.0	(0.9)
	Insecticide[3,4]	number of applications	y^{-1}	0.7	(0.8)
	Insecticide a.i.[3,4]	total amount of active ingredients	$kg\ ha^{-1}\ y^{-1}$	0.1	(0.1)
	Fungicide[3,4]	number of applications	y^{-1}	1.4	(1.4)
	Fungicide a.i.[1,3,4]	total amount of active ingredients	$kg\ ha^{-1}\ y^{-1}$	0.6	(0.7)
	Artificial fertilizer[3,4]	total amount of inorganic nitrogen fertilizer	$kg\ N\ ha^{-1}\ y^{-1}$	131.6	(64.5)
	Organic fertilizer[3]	total amount of organic fertilizer	$kg\ ha^{-1}\ y^{-1}$	3672.1	(9455.8)
	Ploughing	ploughing (yes or no)	77% of fields are ploughed		
	Mechanical weed control[3]	frequency mechanical weed control	y^{-1}	0.8	(1.4)
Landscape characteristics	Mean field size[1]	mean field size within a circle (500 m radius) around the survey plot	ha	17.4	(30.1)
	Percentage land with crops[2]	% land planted with arable crop within a circle (500 m radius) around the survey plot	%	77.2	(17.8)

Landscape characteristics

The character of the landscape was defined on the basis of a 500-m radius circle around the centre of each survey plot. At this scale, landscape composition was described by means of four variables, which were estimated using geospatial data: the mean field size and its standard deviation, the percentage of land planted with arable crops and the Shannon habitat diversity index. The Shannon habitat diversity index was calculated as the proportions of the following habitat classes within the 500-m radius circle as proposed by the European Topic Centre on Land Use and Spatial Information (Büttner et al., 2000): continuous urban fabrics, discontinuous urban fabrics, cultivated arable lands, fallow lands under rotation systems, permanent crops, pastures, forests, transitional woodland-scrub and water.

Statistical analyses

Effects of various aspects of agricultural intensification on ground-nesting farmland bird species were analysed, considering both total breeding bird abundance and the abundance of individual species occurring in at least three of the study areas, i.e. skylarks (*Alauda arvensis*), yellowhammers (*Emberiza citrinella*), yellow wagtails (*Motacilla flava*), whinchats (*Saxicola rubetra*), marsh warblers (*Acrocephalus palustris*), corn buntings (*Miliaria calandra*), lapwings (*Vanellus vanellus*), quails (*Coturnix coturnix*) and meadow pipits (*Anthus pratensis*). Since pheasants (*Phasianus colchicus*) are often introduced for hunting reasons (BirdLife International, 2004), this species was not included in the analyses, even though it occurred in four of the study areas. Generalized linear mixed models (GLMM) in GenStat 12.1 (Payne et al., 2008) were used to analyse the effects of different aspects of agricultural intensification on the number of breeding bird pairs. Study areas were included as random effects in the GLMM. Depending on the presence of the species in the study areas, not all study areas were included in the analyses (Table 3.1, Appendix Fig. 3.2).

In calculating the abundances of individual species, residuals were assumed to follow a Poisson distribution (Table 3.2). Residuals of total breeding bird abundance were overdispersed relative to the Poisson distribution, and graphical examination revealed that a negative binomial distribution was more appropriate.

Heavily skewed explanatory variables were log-transformed, and the percentage of land planted with arable crops was logit-transformed (Table 3.2). All variables were standardized according to $(x-\mu)/s$, with $x =$ measurement, $\mu =$ mean and $s =$ standard deviation, to enable comparison of the magnitude of their effects.

To disentangle the effects of landscape composition and local farm management on breeding birds, landscape variables were forced as fixed effects into all models. Landscape variables were checked for correlations to reduce the number of covariables in the model. Mean field size and its standard deviation were strongly correlated (Pearson correlation coefficient = 0.75), as were the percentage of land planted with arable crops and habitat diversity (Pearson correlation coefficient = -0.93). Mean field size and the percentage of land planted with arable crops were selected for inclusion in the models as fixed effects.

Yield was not significantly correlated ($p > 0.05$) with the two landscape variables within study areas. Depending on the study area, Pearson correlation coefficients for correlations between yield and the percentage of land planted with arable crops and between yield and mean field size ranged from -0.15 to 0.30 and from -0.25 to 0.24, respectively.

Explanatory variables were also checked for correlations. In most analyses, there were strong correlations (Pearson correlation coefficient > 0.7) between the use of fungicides and other pesticides, fertilizer use or yield (Appendix Table 3.5). Where relevant, correlations are discussed in the Results and Discussion sections.

Three separate analyses were performed using different sets of explanatory variables, but always including the two landscape variables (mean field size and percentage of land planted with arable crops) as fixed effects. Firstly, we analysed the effect of yield, as a summary measure of farm management intensity, and its interaction with study area, on the abundance of ground-nesting farmland birds.

Next, to disentangle the effects of individual components of agricultural intensification on breeding birds, 12 variables related to farm management were included in the model selection: number of crops per farm; perimeter-to-area ratio; use of pesticides, artificial fertilizer and organic fertilizer; ploughing and mechanical weed control regime (Table 3.2). Models were derived using forward selection, starting with an empty model, except for the two landscape variables mean field size and percentage of land planted with arable crops. At each subsequent step, the variable with the most significant effect ($p < 0.05$) was included and the procedure was reiterated until variables no longer added significant effects to the model.

Thirdly, we investigated the single effect of farm type (organic vs. conventional) on the abundance of breeding birds.

All explanatory variables were compared between organic and conventional farms using GLMM, including study area as random effect and farm type as fixed effect. As a farm type is usually associated with particular farming practices (e.g. use of pesticides and artificial fertilizer), all analyses were repeated, including farm type as a fixed effect. Yield was additionally included in single-effect analyses of farm type to reveal underlying relations. We emphasize that the term ‘effect’ is used in this text for statistical associations and relationships, and does not necessarily imply a causal relation between two variables.

Results

On average, 8.9 breeding territories of ground-nesting farmland birds were mapped per 500×500 m survey plot (Table 3.1, Fig. 3.1). The largest numbers of breeding territories were found in Poland (16.8 per survey plot) and the lowest numbers in Ireland (3.6 per survey plot). Skylarks were most abundant, with 4.4 territories per survey plot, accounting for almost half of the total number of breeding pairs.

Effects of yield on ground-nesting farmland birds

We investigated the effect of cereal yield on the abundance of ground-nesting farmland birds. As yield differed significantly between conventional and organic farms (Appendix Table 3.6), relations between yield and bird abundances and those between farm type and bird abundances were partly interlinked (see *Results: Effects of farm type on ground-nesting farmland birds*).

Total breeding bird abundance and the abundances of whinchats, corn buntings and marsh warblers were negatively affected by yield (Table 3.3). Yield had an almost significant negative effect on abundances of skylarks, quails and yellowhammers and an almost significant positive effect on abundances of meadow pipits (Table 3.3). The abundance of lapwings was negatively affected by yield. However, the relation was no longer significant when farm type was first included in the model (Table 3.3, Appendix Table 3.7).

The interaction between yield and study area had no significant effect on breeding bird abundances (results not shown).

Effects of landscape characteristics and farm management

Both aspects of agricultural intensification, i.e. landscape characteristics and farm management, were found to affect ground-nesting farmland birds. The final models include all variables that were significantly related to bird abundances (Table 3.4).

As expected, total breeding bird abundance and the abundances of most of the individual bird species were related to at least one of the two landscape variables. Total breeding bird abundances and the abundances of skylarks and meadow pipits were positively related to the percentage of land planted with arable crops, while the same variable negatively affected the abundance of yellowhammers. Abundances of breeding skylarks, yellowhammers, whinchats and marsh warblers were negatively related to field size, but the abundance of lapwings was positively related to the same variable.

In addition to landscape characteristics, farm management, particularly the use of pesticides and artificial fertilizers, affected most species (Table 3.4). No artificial fertilizers or pesticides were used on organic farms, and many of the farming practices differed

Table 3.3 *Results of Generalized linear mixed models including study area as random effect: effects of cereal yields and farm type on the total breeding bird abundance (total) and single species. The two landscape variables (mean field size and % land planted with arable crops) were forced into the model as fixed effects. Standardized effects (of organic farms), F statistics (F stat.), significance (p-value) and significance level (*** for p < 0.001; ** for p < 0.01;* for p < 0.05; ns for p > 0.05) are given.* [1] *The effect of yield was not significant anymore, when farm type was included in the model as fixed effect (see text and Appendix Table 3.7).* [2] *The effect of farm type was significant when yield was added to the model as fixed effect (see text and Appendix Table 3.7).*

	Cereal yield				Farm type			
Response variable	**Std effect**	**F stat.**	*p*	**Sign**	**Std effect**	**F stat.**	*p*	**Sign**
Total	-0.15	11.08	<**0.001**	***	0.10	1.05	0.306	ns
Skylark	-0.08	3.20	0.073	ns	0.06	0.60	0.439	ns
Yellowhammer[1]	-0.16	3.52	0.061	ns	0.29	2.52	0.112	ns
Yellow Wagtail	0.07	0.60	0.438	ns	-0.53	3.08	0.079	ns
Whinchat[2]	-0.68	19.21	<**0.001**	***	0.25	0.86	0.353	ns
Corn Bunting	-0.36	7.10	**0.008**	**	0.32	0.07	0.785	ns
Marsh Warbler	-0.40	7.86	**0.006**	**	0.55	3.65	0.061	ns
Lapwing[1]	-0.37	8.15	**0.004**	**	1.01	12.04	<**0.001**	***
Quail	-0.30	3.72	0.054	ns	0.48	1.94	0.164	ns
Meadow Pipit	0.26	3.20	0.074	ns	-0.76	4.07	**0.044**	*

significantly between the two farm types (Appendix Table 3.6). Therefore, model selections were repeated including farm type as a fixed effect (Table 3.4, Appendix Table 3.8). Total breeding bird abundances, as well as abundances of breeding whinchats, yellow wagtails and corn buntings were negatively affected by the use of fungicides (frequency or amounts of active ingredients, see Table 3.4). Abundances of quails were negatively related to the amounts of active ingredients of fungicides applied, but positively to the frequency of fungicide applications, two highly correlated variables (Appendix Table 3.5). The abundance of yellow wagtails was positively related to the amounts of active ingredients of herbicides. This relationship, however, was no longer significant when farm type was added to the model or within conventional farms alone (Table 3.4, F statistics = 2.01, $p = 0.15$, respectively). Lapwing abundance was positively related to the frequency of mechanical weed control and negatively to the amount of artificial fertilizer applied. Both relations were no longer significant when farm type was added to the model. Yet, lapwing abundance was marginally negatively affected by the amount of artificial fertilizer applied within conventional farms (F statistics = 2.84 and $p = 0.092$), as well as almost significantly positively affected by the frequency of mechanical weed control within organic farms (F statistics = 3.05, $p = 0.081$). The abundance of marsh warblers was negatively related to the amount of artificial fertilizer applied. The abundance of meadow pipits was only positively related to the amount of artificial fertilizer applied when farm type was excluded from the model. Yellowhammer abundance was only negatively affected by ploughing regime if farm type was included in the model.

Total breeding bird abundance, as well as the abundance of quails, were positively influenced by the number of different crops per farm (Table 3.4). Whinchat abundance was positively related to the perimeter-to-area ratio of the cereal field within the survey plot.

In all analyses, the amounts of active ingredients of fungicides applied were strongly correlated with the frequency of fungicide applications (Appendix Table 3.5). Moreover, regarding the marsh warbler data, the amounts of artificial fertilizer applied were strongly correlated with the amounts of active ingredients of fungicides. Regarding the numbers of breeding quails, the amounts of active ingredients of fungicides were also correlated with the number of insecticide applications. Finally, the perimeter-to-area ratio was strongly correlated with the landscape variable mean field size.

Effects of farm type on ground-nesting farmland birds

The total breeding bird abundance and the abundances of skylarks, yellowhammers, corn buntings and quails did not differ between organic and conventional farms (Table 3.3). Lapwing abundance was significantly higher on organic farms, and marsh warbler abundance was almost significantly higher on organic farms. By contrast, meadow pipits were more abundant and yellow wagtails marginally more abundant on conventional farms. Whinchats were less abundant on organic farms, when yield was included in the model first (Table 3.3, Appendix Table 3.7).

Table 3.4 *Effects of landscape characteristics and farm management on total breeding bird abundances (total) and single species. Model selections (forward selection: Generalized linear mixed models including study area as random effect) are given for (a) variable selection without and (b) with farm type as fixed effect only if models change significantly. An overview of all models including farm type as fixed effect is given in Appendix Table 3.8. Information about response and explanatory variables is given in Table 3.2. Significant explanatory variables (structured according to their spatial scale), F statistics (F stat), standardized effects (std effect), significance (p-value) and significance level (*** for $p < 0.001$; ** for $p < 0.01$;* for $p < 0.05$; ns for $p >$ 0.05) are given. Standardized effects of farm type refer to organic farms.*

Response variables		**Explanatory variables**		**Std effect**	**F stat**	*p*	**Sign**
		Landscape characteristics	**Farm management**				
Total	**a**	% arable crops		0.19	15.92	<0.001	***
			fungicide (a.i.)	-0.11	6.08	0.014	*
			number of crops	0.09	4.77	0.029	*
Skylark	**a**	mean field size		-0.13	4.78	0.029	*
		% arable crops		0.35	57.61	<0.001	***
Yellowhammer	**a**	mean field size		-0.02	8.26	0.004	**
		% arable crops		-0.60	31.81	<0.001	***
	b	mean field size		-0.06	7.76	0.005	**
		% arable crops		-0.54	30.73	<0.001	***
			farm type	0.47	2.13	0.145	ns
			ploughing	-0.52	5.66	0.017	*
Yellow Wagtail	**a**		herbicide (a.i.)	0.20	5.92	0.015	*
	b		farm type	-0.95	3.11	0.078	ns
			fungicide (a.i.)	-0.22	5.04	0.025	*
Whinchat	**a**	mean field size		-0.40	8.80	0.003	**
			fungicide	-0.51	5.95	0.015	*
			perimeter-area ratio	0.36	4.09	0.043	*
Corn Bunting	**a**		fungicide	-1.07	9.45	0.002	**

Table 3.4 *continued*

Response variables		Explanatory variables: Landscape characteristics	Explanatory variables: Farm management	Std effect	F stat	*p*	Sign
Marsh Warbler	**a**	mean field size		-0.26	4.60	0.034	*
			artificial fertilizer	-0.62	14.30	<0.001	***
	b	mean field size		-0.18	4.61	0.034	*
			farm type	-0.65	1.95	0.166	ns
			artificial fertilizer	-0.91	13.34	<0.001	***
Lapwing	**a**	mean field size		0.63	5.68	0.017	*
			mechanical weed control	0.20	8.32	0.004	**
			artificial fertilizer	-0.41	6.79	0.009	**
	a	mean field size		0.50	4.57	0.033	*
			artificial fertilizer	-0.49	11.91	<0.001	***
	b	mean field size		0.60	5.74	0.017	*
			farm type	0.15	11.11	<0.001	***
			mechanical weed control	0.19	2.63	0.105	ns
			artificial fertilizer	-0.35	1.61	0.205	ns
Quail	**a**		fungicide (a.i.)	-0.79	5.72	0.017	*
			fungicide	0.41	4.53	0.033	*
	b		farm type	-0.45	1.56	0.211	ns
			fungicide (a.i.)	-0.91	4.86	0.027	*
			fungicide	0.46	4.96	0.026	*
			number of crops	0.25	4.05	0.044	*
Meadow Pipit	**a**	% arable crops		0.47	9.69	0.002	**
			artificial fertilizer	0.34	6.83	0.009	**
	b	% arable crops		0.48	9.46	0.002	**
			farm type	-0.18	4.29	0.038	*
			artificial fertilizer	0.29	2.41	0.121	ns

Discussion

General considerations

We examined how different aspects of agricultural intensification affected birds nesting on arable farms located in eight study areas across seven European countries. We found negative as well as positive effects of various components of agricultural intensification on the abundance of ground-nesting farmland birds. Bird abundances were affected by landscape characteristics, such as the percentage of land planted with arable crops and the field size, as well as by local farming practices, such as the use of artificial fertilizers and pesticides, and crop diversity. The effects of organic farming on the abundance of ground-nesting farmland birds were found to be species-specific.

Imperfect detection of species has been identified as a problem in many studies (Kéry et al., 2009; MacKenzie et al., 2009). Our results are based on a survey method with three visits, and do not fully account for species-specific differences in detection probabilities. We used three criteria to assign territories to species, to partly adjust for differences in detection probability between species due to different arrival times and cryptic behaviour. The main consequence of our inventory method in comparison to a full territory mapping is a reduced precision of the abundance estimates, i.e. increased error variation. However, species-specific variation in detection probability is less of a problem when analysing relationships between relative abundance estimates and various environmental variables.

Effects of yield on ground-nesting farmland birds

This research confirms the findings of several studies showing that a majority of farmland bird species have been affected by agricultural intensification (Billeter et al., 2008; Donald et al., 2006). In contrast to most previous research, which used regional or national agricultural statistics (e.g. Benton et al., 2002; Chamberlain et al., 2000; Donald et al., 2001c), our study was based on information collected at field, farm and landscape scale.

We found that farms with higher cereal yields - a result of many farming practices and associated with agricultural intensity (Bas et al., 2009; Donald et al., 2001c; Geiger et al., 2010; Tilman et al., 2002) - supported fewer pairs of 30 species of breeding farmland birds. Moreover, four of the nine species studied individually (whinchats, corn buntings, marsh warblers and lapwings) were less abundant on higher yielding farms. These results suggest that not only bird species richness is decreased as a consequence of agricultural intensification (Geiger et al., 2010), but that most of the more wide-spread farmland species also suffer, and that less intensive farm management can support a greater overall abundance of ground-nesting farmland birds.

Effects of landscape characteristics and farm management

The majority of the investigated farmland species were influenced by landscape composition. Since our species selection was limited to ground-nesting farmland birds, it is not surprising that more breeding pairs were observed in landscapes with a high percentage of arable land. Characteristic species of open, arable landscapes, such as skylarks and meadow pipits, profit from a high percentage of land with arable crops (Atkinson et al., 2002; Benton et al., 2002; Herzon et al., 2008; Robinson et al., 2001; Sheldon et al., 2007; SOVON, 2002). However, the enlargement of fields, resulting in reduced availability of boundary structures (Baessler & Klotz, 2006), might decrease the availability of foraging and breeding habitats for species that prefer mixed and small-scale landscapes, such as whinchats, yellowhammers and marsh warblers (Morris et al., 2001; Perkins et al., 2002; Whittingham & Evans, 2004). Our study demonstrated that landscape characteristics, which are greatly affected by agricultural practices and intensification (Herzon & O'Hara, 2007; Söderström & Pärt, 2000; Stoate et al., 2009), influence many farmland bird species at European scale (Smith et al., 2010; Whittingham et al., 2009).

However, we found that not only landscape structure, but also farm management played an important role in determining the species distribution on farmland. Though our survey plots did not correspond entirely with farms, we found positive effects of crop diversity on total breeding bird abundances. A high crop diversity offers spatial heterogeneity and hence provides not only breeding and foraging habitats for many different bird species, but also temporal heterogeneity, enabling birds to switch to other breeding habitats during the breeding season (Benton et al., 2003; Chamberlain & Gregory, 1999; Chamberlain et al., 1999; Pepin et al., 2008; Siriwardena et al., 2000; Tucker, 1997).

The use of pesticides and artificial fertilizers affects the food availability and habitat composition for farmland birds (Stoate et al., 2009). Fewer breeding birds were observed in areas where higher amounts of fungicides were applied. However, the use of fungicides showed a strong positive correlation with the use of insecticides and artificial fertilizer, and disentangling the effects of these variables would only be possible by studying their effects on farmland birds experimentally. Nevertheless, insecticides and some fungicides have been shown to negatively affect invertebrate abundance through direct toxic effects and through negative effects on fungi included in the diet of saprophytic species (Holland, 2004; Morris et al., 2005; Sotherton & Moreby, 1988). Moreover, the pesticides and fertilizers often do not end up only on the targeted crop fields, but drift into margins, affecting flora and fauna (de Snoo, 1999; Stoate et al., 2009) and consequently also altering the food availability for bird species foraging in such margins. Not only pesticide use, but also soil disrupting activities, such as ploughing, have negative impacts on invertebrate abundances on arable fields (Thorbek & Bilde, 2004). This reduction in food availability can have consequences for the reproductive success of farmland birds (Boatman et al., 2004; Brickle et al., 2000).

The use of artificial fertilizers has been shown to influence the vegetation structure and composition of fields, as well as of field margins (Kleijn & van der Voort, 1997; Stoate et al., 2009; Wilson et al., 2005). Fertilization results in more dense and homogeneous crops and not only influences vegetation structures within fields, but might also change the vegetation of field margins (from perennials to annuals) and the associated invertebrate community, affecting species that forage in field margins, like marsh warblers (Boatman, 1994; Kleijn & Snoeijing, 1997; Stoate et al., 2001).

Effects of farm type

Some studies have shown that the diversity and abundance of birds are higher on organic than on conventional farms (Bengtsson et al., 2005; Hole et al., 2005). Compared to conventional farms, which generally have a lower percentage of non-crop habitats and where pesticides and artificial fertilizers are used, higher food availability and habitat heterogeneity on organic farms might increase bird abundances (Freemark & Kirk, 2001; Kragten et al., 2010; Morris et al., 2005). The present study, however, did not find that organic farms supported a higher total breeding bird abundance than conventional farms. Responses of individual species to organic farming, however, differed. While abundances of meadow pipits were lower on organic farms than on conventional farms, lapwings were more numerous on organic farms. These results underline the species-specific reactions to farm management and the importance of species-specific investigations of the effects of agricultural intensification.

Surprisingly, species that were negatively affected by the use of pesticides, such as whinchats and corn buntings, were not more abundant on organic farms. One possible explanation might be that some of the survey plots included not only organic fields, but possibly also conventional fields. Another explanation could be that breeding birds may have been influenced by neighbouring conventional farming practices, and therefore the influence of organic farming may be underestimated. The effects of pesticides are often not limited to the arable fields themselves, but also influence adjacent habitats or even larger spatial scales (de Jong et al., 2008). Therefore, organic farming may not always be successful in counteracting the negative effects of intensified farming practices. Not only farmland birds, but also species of other taxa with high dispersal abilities, such as butterflies (Rundlöf et al., 2008), syrphids (Schweiger et al., 2007) and bees (Steffan-Dewenter & Westphal, 2008), might profit from low-intensity farming practices and habitat diversification at local and landscape scales (Schweiger et al., 2005; Tscharntke et al., 2005).

While higher abundances of a number of individual bird species on organic farms compared to conventional farms were also found by other studies (yellowhammers: Bradbury et al., 2000, skylarks: Piha et al., 2007, and Kragten & de Snoo, 2008, lapwings: Kragten & de Snoo, 2007), breeding success is often not enhanced on organic farms. Reasons might be changes in crop structure making nesting habitats unsuitable (Kragten et al., 2008) or nest losses by mechanical weed control (Kragten & de Snoo, 2007; Lokemoen & Beiser, 1997). Our research confirms the findings of other studies, which found varying effects of organic farming on breeding farmland birds (Fuller et al., 2005).

Different responses of yellow wagtails and meadow pipits

While our results indicate that intensified farming practices negatively affect breeding bird abundances of most species, two species - yellow wagtail and meadow pipit - seem to be able to adapt at least partly to the changes in farming practices that have taken place over the past decades. More meadow pipits were observed on conventional farms. Yellow wagtails were slightly, but not significantly, more numerous on conventional farms. One explanation for the response of these species is altered breeding and foraging habitats, leading to changes in preferences for crops that are grown on larger areas at conventional farms (Kragten & de Snoo, 2008). The fact that these species share their original habitat preferences (i.e. damp grassland (Cramp et al., 1988)) and thus are likely to be affected by agricultural intensification in a similar way, suggests that these results are not just spurious correlations. Both species are known to suffer from intensified management on grassland (Batary et al., 2007; Chamberlain & Fuller, 2001; Wilson & Vickery, 2005) and populations are declining steeply in grassland-dominated areas (Bradbury & Bradter, 2004; Henderson et al., 2004a; Mason & Macdonald, 2000; SOVON, 2002). In open, arable landscapes, however, yellow wagtails have expanded their range in England as well as the Netherlands in recent decades (Mason & Macdonald, 2000; SOVON, 2002). A similar development has been found for meadow pipits in the Netherlands, whose populations in open grassland dominated landscapes are declining, whereas those in areas dominated by arable crops are stable (van Dijk et al., 2009).

Conclusions

We have shown that various components of agricultural intensification negatively affect the majority of farmland bird species, although two species, yellow wagtails and meadow pipits, seem to be able to adapt to intensified farming practices on arable land and changes in their breeding habitat. We found that farmland birds were influenced not only by differences in landscape composition, but also by farming practices. While crop diversity supported higher total breeding bird abundance, the use of pesticides and artificial fertilizers had negative impacts on most species. Only one species, the lapwing, was more abundant on organic farms, whereas the total breeding bird abundance was not affected by farm type.

These findings imply that there is an urgent need for further reduction of the use of pesticides and artificial fertilizers in European agriculture, for the benefit of farmland birds. In addition, we suggest that conservation measures should be taken to enhance habitat heterogeneity in agriculture-dominated landscapes, by increasing non-crop and margin habitats and diversifying crop types to support a greater number of ground-nesting farmland bird species. Species-specific responses of farmland birds should be taken into consideration when implementing conservation measures at local scale.

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Appendix

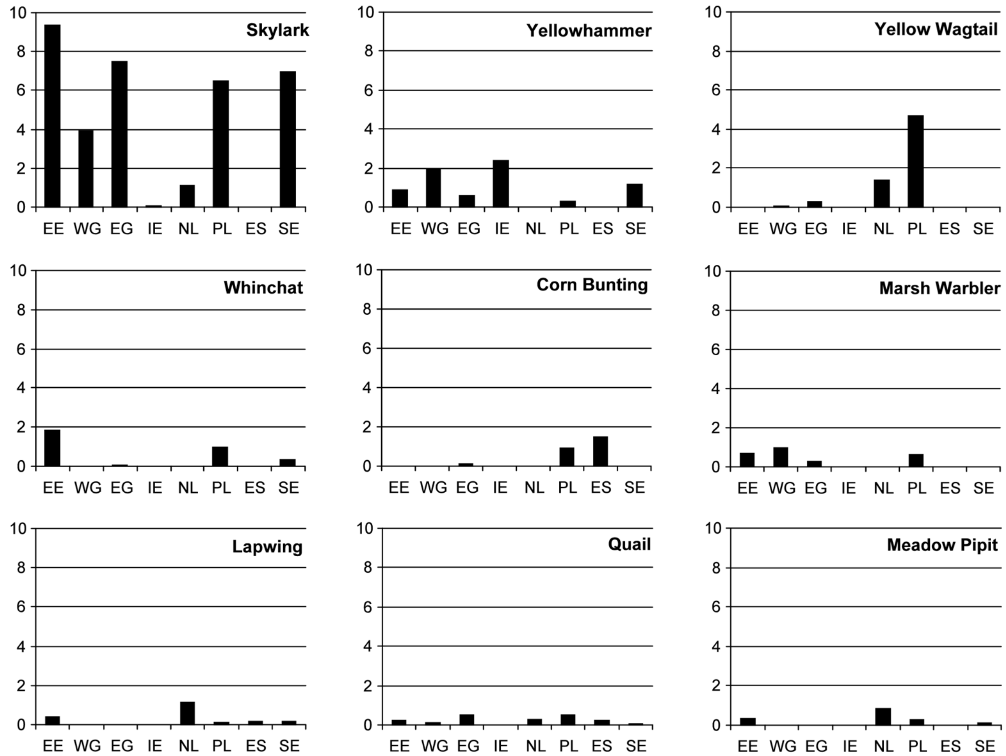

Figure 3.2 *Breeding bird abundances per species. Bars represent average abundance of breeding birds per survey plot (y-axes) within a study area (x-axes). Study areas: EE = Estonia, WG = western Germany, EG = eastern Germany, IE = Ireland, NL = Netherlands, PL = Poland, ES = Spain, SE = Sweden.*

Table 3.5 *Correlations between explanatory variables that are higher than 0.7 (Pearson Correlation coefficient) are indicated for each response variable: Total = total breeding bird abundance, S = Skylark, Y = Yellowhammer, YW = Yellow Wagtail, WC = Whinchat, MW = Marsh Warbler, CB = Corn Bunting, L = Lapwing, Q = Quail, MP = Meadow Pipit. The number of survey plots included in the analyses is given in brackets. Explanatory variables: frequency of fungicide applications (= fung), frequency of insecticides applications (= ins), amount of active ingredients (=a.i.), perimeter to area ratio (pa ratio).*

	Total (232)	**S (201)**	**Y (171)**	**YW (111)**	**WC (119)**	**CB (89)**	**MW (110)**	**L (149)**	**Q (201)**	**MP (119)**
fung * fung (a.i.)	0.87	0.85	0.86	0.80	0.80	0.83	0.79	0.94	0.83	0.93
fung (a.i) * artificial fertilizer	0.71	0.71		0.80		0.71	0.73			
fung * ins	0.74	0.72	0.72							
fung (a.i.) * ins	0.75	0.73	0.74						0.70	
fung (a.i.) * cereal yield				0.78						
ins * ins (a.i.)								0.72		0.71
artificial fertilizer * cereal yield	0.71	0.72								
pa ratio * mean field size	-0.70		-0.72	-0.72	-0.76	-0.79	-0.78		-0.74	

Table 3.6 *Effects of farm type on each explanatory variable (generalized linear mixed models including study area as random effect): standardized effects of organic farms (std effect), F statistics (F stat) and significance (p). For variable explanations see Table 3.2.*

	Std effect	**F stat**	*p*
Fungicide	-1.01	31.53	<0.001
Fungicide a.i.	-1.36	57.16	<0.001
Herbicide	-1.64	85.0	<0.001
Herbicide a.i.	-1.11	39.9	<0.001
Insecticide	-0.86	22.6	<0.001
Insecticide a.i.	-0.57	10.38	0.001
Mechanical weed control	0.85	22.29	<0.001
Number of crops	0.33	3.33	0.068
Artificial fertilizer	-1.78	99.79	<0.001
Organic fertilizer	0.67	15.04	<0.001
Cereal yield	-1.52	71.71	<0.001
pa ratio	0.07	0.14	0.711
Mean field size	-0.02	0.02	0.896
% arable crops	-0.25	1.95	0.162

Table 3.7 *Additional effects of farm type (after yield, A) and yield (after farm type, B) on total breeding bird abundances (total) and single species. Standardized effects (of organic farms, std effect), F statistics (F stat.), significance (p-value) and significance level (*** for $p < 0.001$; ** for $p < 0.01$;* for $p < 0.05$; ns for $p > 0.05$) are given.*

	Farm type effects after yield					Yield effects after farm type				
Response variable	**A**	**Std effect**	**F stat**	***p***	**Sign**	**B**	**Std effect**	**F stat**	***p***	**Sign**
Total	Yield	-0.22	11.20	<0.001	***	Farm type	-0.22	1.13	0.289	ns
	Farm type	-0.22	2.82	0.093	ns	Yield	-0.22	12.90	<0.001	***
Skylark	Yield	-0.13	3.19	0.074	ns	Farm type	-0.11	0.59	0.441	ns
	Farm type	-0.11	0.80	0.371	ns	Yield	-0.13	3.39	0.065	ns
Yellowhammer	Yield	-0.13	3.45	0.063	ns	Farm type	0.11	2.40	0.121	ns
	Farm type	0.11	0.19	0.665	ns	Yield	-0.13	1.24	0.226	ns
Yellow Wagtail	Yield	-0.10	0.52	0.472	ns	Farm type	-0.74	3.08	0.079	ns
	Farm type	-0.74	3.06	0.080	ns	Yield	-0.10	0.50	0.480	ns
Whinchat	Yield	-0.95	21.21	<0.001	***	Farm type	-0.70	0.76	0.383	ns
	Farm type	-0.70	4.70	0.030	*	Yield	-0.95	25.15	<0.001	***
Corn Bunting	Yield	-0.38	7.23	0.007	**	Farm type	-0.46	0.01	0.926	ns
	Farm type	-0.46	0.16	0.691	ns	Yield	-0.38	7.38	0.007	**
Marsh Warbler	Yield	-0.36	7.91	0.006	**	Farm type	0.15	3.22	0.076	ns
	Farm type	0.15	0.22	0.641	ns	Yield	-0.36	4.91	0.029	*
Lapwing	Yield	-0.06	7.96	0.005	**	Farm type	0.91	11.79	<0.001	***
	Farm type	0.91	3.91	0.048	*	Yield	-0.06	0.07	0.785	ns
Quail	Yield	-0.29	3.75	0.053	ns	Farm type	0.05	1.83	0.176	ns
	Farm type	0.05	0.01	0.912	ns	Yield	-0.29	1.93	0.164	ns
Meadow Pipit	Yield	0.02	3.00	0.083	ns	Farm type	-0.73	4.10	0.043	*
	Farm type	-0.73	1.10	0.294	ns	Yield	0.02	0.00	0.956	ns

Table 3.8 *Effects of landscape characteristics and farm management on farmland birds. Model selections (forward selection: Generalized linear mixed models including study area as random effect) are given for variable selection including farm type as fixed effect on total breeding bird abundances (total) and single species. For information about response and explanatory variables, see Table 3.2. Significant explanatory variables (structured according to their spatial scale), F statistics (F stat), standardized effects (std effect), significance (p-value) and significance level (*** for $p < 0.001$; ** for $p < 0.01$;* for $p < 0.05$; ns for $p > 0.05$) are given. Standardized effects of farm type refer to organic farms.*

Response variables	**Explanatory variables**		**Std effect**	**F stat**	*p*	**Sign**
	Landscape characteristics					
		Farm management				
Total	% arable crops		0.19	16.00	<0.001	***
		farm type	-0.12	1.18	0.277	ns
		fungicide (a.i.)	-0.15	5.40	0.020	*
		number of crops	0.09	5.23	0.022	*
Skylark	mean field size		-0.13	4.80	0.028	*
	% arable crops		0.36	57.75	<0.001	***
		farm type	0.06	0.60	0.439	ns
Yellowhammer	mean field size		-0.06	7.76	0.005	**
	% arable crops		-0.54	30.73	<0.001	***
		farm type	0.47	2.13	0.145	ns
		ploughing	-0.52	5.66	0.017	*
Yellow Wagtail		farm type	-0.95	3.11	0.078	ns
		fungicide (a.i.)	-0.22	5.04	0.025	*
Whinchat	mean field size		-0.38	8.78	0.003	**
		farm type	-0.15	0.69	0.407	ns
		fungicide	-0.54	5.27	0.022	*
		perimeter-area ratio	0.38	4.29	0.038	*

Table 3.8 *continued*

Response variables	Explanatory variables		Std effect	F stat	p	Sign
	Landscape characteristics					
		Farm management				
Corn Bunting		farm type	-1.43	0.22	0.642	ns
		fungicide	-1.25	11.27	<0.001	***
Marsh Warbler	mean field size		-0.18	4.61	0.034	*
		farm type	-0.65	1.95	0.166	ns
		artificial fertilizer	-0.91	13.34	<0.001	***
Lapwing	mean field size		0.60	5.74	0.017	*
		farm type	0.15	11.11	<0.001	***
		mechanical weed control	0.19	2.63	0.105	ns
		artificial fertilizer	-0.35	1.61	0.205	ns
Quail		farm type	-0.45	1.56	0.211	ns
		fungicide (a.i.)	-0.91	4.86	0.027	*
		fungicide	0.46	4.96	0.026	*
		number of crops	0.25	4.05	0.044	*
Meadow Pipit	% arable crops		0.48	9.46	0.002	**
		farm type	-0.18	4.29	0.038	*
		artificial fertilizer	0.29	2.41	0.121	ns

Chapter 4

Landscape composition influences farm management effects on farmland birds in winter: a pan-European approach

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Abstract

This study examined the effects of agricultural intensity, various farming practices, landscape composition and vegetation cover on the abundance and species richness of wintering farmland birds, assessed simultaneously across seven European regions.

The abundance and species richness of wintering farmland birds were negatively affected by agricultural intensity. The effects of yield and farm type were interlinked. Of the 10 farming practices assessed, mechanical weeding and the amount of organic fertilizer applied negatively affected farmland birds, presumably due to reduced food availability on arable fields. Positive effects of organic farming on farmland birds proved to be limited to simplified landscapes. More farmland birds were observed in areas with more stubble, pasture and green manure crops. Species richness was higher in areas with more pasture.

The results of this study show that farm management, vegetation cover and landscape composition all influence wintering farmland birds. Heterogeneous landscapes comprising arable crops as well as grasslands support most species of farmland birds in winter. The effectiveness of organic farming and agri-environment schemes depends on landscape composition. Therefore, different agri-environment schemes should be designed for different landscape types.

Introduction

Many farmland bird populations in Europe have declined dramatically in recent decades (BirdLife International, 2004). The causes of these declines include reduced reproductive success in summer and low adult survival in winter, caused by decreased abundance and accessibility of food on farmland (Kragten & de Snoo, 2007; Siriwardena et al., 2008; Stoate et al., 2009). Effects of farm management on breeding birds are well documented, and intensified practices as well as the simplification of agricultural landscapes have been identified as the main causes of the decline of farmland bird populations (Benton et al., 2002; Chamberlain et al., 2000; Donald et al., 2006). In addition to good breeding conditions, wintering habitats providing sufficient food and shelter are important to sustain population levels of many bird species (Robinson & Sutherland, 2002; Siriwardena et al., 1998, 1999).

Food abundance in winter has been reduced by improved harvesting techniques that spill less grain (Wilson et al., 1999), post-harvest herbicides (Moreby & Southway, 1999), tillage and the early ploughing of stubble (Newton, 2004; Stoate et al., 2009). However, little is known about the effects on winter food supplies of farming activities conducted during the growing season, such as the use of pesticides, artificial fertilizers, ploughing and mechanical weed control. Moreover, most of the studies about farmland birds in winter have been limited to the UK.

In addition to food abundance, the suitability of arable fields as foraging habitats for birds is also determined by vegetation cover (Moorcroft et al., 2002). Vegetation cover influences the accessibility of food, affects predator avoidance behaviour and provides shelter against harsh weather conditions (Butler et al., 2005a; Moorcroft et al., 2002; Wakeham-Dawson & Aebischer, 1998; Whittingham et al., 2006; Wilson et al., 1996). By influencing food abundance and vegetation cover, farm management determines the suitability of fields as foraging habitats for birds in winter.

Organically managed farms covered about 4% of the total area of agriculturally used land and accounted for 1.6% of the farms within in the European Union (EU 25) in 2005 (Eurostat, 2007b). Although organic farming does not use chemicals such as artificial fertilizers and pesticides, studies have differed in their findings regarding its effects on farmland birds. Species richness and overall bird abundance is often higher on organic compared with conventional farms (Bengtsson et al., 2005; Chamberlain et al., 2010; Hole et al., 2005), but see Geiger et al. (2010). However, single species respond differently to organic farming (Chamberlain et al., 2010; Fuller et al., 2005; Kragten & de Snoo, 2008). In general, food availability for farmland birds during the breeding season is higher on organic farms than conventional farms (Kragten et al., 2010; Moreby & Sotherton, 1997), but it is as yet unclear whether organic farms also provide more food in winter. Not only farm management, but also landscape composition influences bird communities on farmland (Dormann et al., 2007; Herzon & O'Hara, 2007; Söderström & Pärt, 2000; Wretenberg et al., 2010), with landscape heterogeneity generally associated with increased biodiversity (Benton et al., 2003). Tscharntke et al. (2005) hypothesized that conservation measures might be most effective in simple landscapes consisting of less than 20% non-crop habitats. Based on literature review, Andrén (1994) suggested that in landscapes with less than 20% of a species' original habitat, habitat isolation and extinction rates increase considerably for mammals and birds. Therefore, an increased area of suitable habitats in simple landscapes might support higher levels of biodiversity. As colonization of arable fields in complex landscapes (> 20% non-crop habitats) may be facilitated by large species pools present in these landscapes, differences in biodiversity between arable fields with and without conservation measures might be small (Tscharntke et al., 2005). Moreover, in cleared landscapes, which are dominated by arable fields and lack semi-natural habitats (< 1%), species diversity might be very low and additional conservation measures might be not effective due to the absence of immigration sources.

Studies comparing organic and conventional farming have shown that organic farming has positive effects on breeding and migrating birds in homogeneous but not in heterogeneous landscapes (Concepción et al., 2008; Dänhardt et al., 2010; Roschewitz et al., 2005; Smith et al., 2010). Whether landscape composition influences the effects of farm type on wintering birds, and whether these effects differ between simple and cleared landscapes, has not been studied previously.

In a comparison between Sweden and England, Wretenberg et al. (2006) found similar declines of breeding birds despite major differences in the degree and nature of agricultural intensification and distinct agricultural landscapes. One suggested cause of the similarity of population trends could be that populations from both countries are affected by the same intensified farming practices at common wintering grounds, i.e. a decreased area of cereal stubble. Winter conditions on farmlands in Western and Southern Europe are not only important for local bird populations, but also for migrating farmland birds from Northern countries. Considering the spatial scale of the potential causes of farmland bird declines, large-scale studies about farmland birds might identify the far-ranging effects of agricultural intensification and might improve the effectiveness of conservation measures. Therefore, this study investigated the effects of farm management on the species richness and abundance of birds foraging on farmland in winter, assessing them simultaneously in seven study areas distributed across six European countries. In a first step, the effects of local agricultural intensity on species richness and abundance of wintering farmland birds were investigated, using yield as a proxy for agricultural intensity and a summary variable of different farming practices (Tilman et al., 2002). Secondly, specific farming practices, conducted during the growing season, affecting species richness and bird abundance in winter were identified. Next, the effects of within-field vegetation cover on species richness and abundance of wintering birds were analysed.

Finally, this study investigated whether organic farming enhanced species richness and bird abundance, and whether its effectiveness depended on landscape complexity.

Materials and methods

This study included seven areas, referred to below as study areas, situated in six European countries: Sweden (SE), Poland (PO), the Netherlands (NL), western Germany (WG), eastern Germany (EG), France (FR) and Spain (ES). The study areas ranged in size from 30×30 to 50×50 km, to minimize differences between farms in the regional species pools. In each study area, 30 to 32 arable farms were selected so as to represent an intensity gradient, using the cereal yield of the preceding year as a proxy for agricultural intensity (Donald et al., 2001c; Tilman et al., 2002). Organic farms were selected in both of the German study areas, as well as in the Netherlands and Sweden.

Bird surveys

To ensure that bird counts were comparable, one bird survey plot with a size of 500×500 m was selected at each farm. Most of the survey plots included fields belonging to one farm. The survey plots comprised one or more arable fields or pastures, and at least one field where cereals had been grown in the preceding year. Most of these cereal fields (84%) had been used to grow winter wheat, while winter barley (8%) or spring wheat (7%) had been grown on the remaining cereal fields. All survey plots were at least 1 km apart. Birds were surveyed twice, in December 2007 and in January 2008, except in Spain, where only one survey was done, between late December and late January. Survey plots were walked in such a way that none of the spots within the plot was more than 100 m from the surveyor's route. A maximum of 2 h was spent per survey plot. The surveys took place between 1 h after dawn and 1 h before sunset. No surveys were done when it was too windy, cloudy or rainy. All foraging and resting birds were mapped.

Farm management

Information about yield, farm type (organic or conventional) and farming practices (pesticide and fertilizer use, ploughing and mechanical weed control regime) was collected by means of a questionnaire sent to the farmers (Table 4.1). 98% of the farmers replied. The information was based on the cultivation of cereal fields during the preceding growing season, lasting from the harvest of the preceding crop (autumn of 2006) to the harvest of the current crop (summer of 2007). Depending on the number of cereal fields per farm, data about farming practices was based either only on the cereal field within the survey plot or on the average of up to five cereal fields that belonged to the same farm, but were possibly situated outside the survey plot.

Table 4.1 *List of explanatory variables used for the statistical analyses, their descriptions, units and mean values with standard deviations. [a] Average value based on the cultivation of one to five cereal fields per farm; [b] Variables were averaged for conventional farms only; [c] Variables were log-transformed; [d] See text for the different habitat types; [e] Variables were logit transformed.*

	Variable	Description	Units	Mean (stdev)
	Yield	average cereal yield, standardized according to 14% moisture content of the grains	kg ha^{-1}	5403.4 (1664.5)
Farming practices	Farm type	conventional or organic	22% organic farms	
	Herbicides[a,b]	number of applications	y^{-1}	1.6 (1.0)
	Herbicide a.i.[a,b]	total amount of active ingredients	kg ha^{-1} y^{-1}	0.8 (0.8)
	Insecticides[a,b]	number of applications	y^{-1}	0.4 (0.6)
	Insecticide a.i.[a,b]	total amount of active ingredients	kg ha^{-1} y^{-1}	0.0 (0.1)
	Fungicides[a,b]	number of applications	y^{-1}	1.1 (1.2)
	Fungicide a.i.[a,b,c]	total amount of active ingredients	kg ha^{-1} y^{-1}	0.4 (0.4)
	Artificial fertilizer[a,b]	total amount of inorganic nitrogen fertilizer	kg N ha^{-1} y^{-1}	131.4 (62.7)
	Organic fertilizer[a]	total amount of organic fertilizer	kg ha^{-1} y^{-1}	3659.6 (9221.1)
	Ploghing	yes or no	78% of fields are ploughed	
	Mechanical weed control[a]	frequency of mechanical weed control	y^{-1}	0.8 (1.5)
Landscape characteristics	Mean field size[c]	area	ha	16.5 (30.7)
	Habitat diversity[d]	Shannon diversity index based on 8 different habitat types		0.6 (0.4)
Field types	Cereal stubble	area	%	14.8 (25.4)
	Bare soil[e]	area	%	44.5 (35.4)
	Pasture[e]	area	%	4.1 (10.2)
	Green manure	area	%	2.2 (7.7)
	Winter cereals or grass seed[e]	area	%	22.9 (29.0)

In some of the study areas, viz. those in eastern Germany, the Netherlands, Spain and Sweden, the vegetation cover of the fields within the survey plots was mapped during the bird surveys and later classified into five different vegetation cover types, viz. green manure crops, cereal stubble, winter cereals or grass seed crops, pastures and bare soil. The area covered by each cover type was averaged over the survey rounds.

Landscape characteristics

To be able to account for landscape effects on wintering birds, four different landscape variables were estimate: habitat diversity, % of land planted with arable crops, mean field size and the standard deviation of the mean field size. The area covered by eight different habitat types was derived from digital maps in a circle with a 500 m radius around the centre of each survey plot. Using definitions from the European Topic Centre on Land Use and Spatial Information (Büttner et al., 2000), the following habitat types were distinguished: urban fabrics, cultivated arable lands, fallow lands under rotation systems, permanent crops, pastures, forests, transitional woodland scrub, and water. The mean field size and the Shannon habitat diversity index using the above habitat types were calculated at the landscape scale (Table 4.1). Furthermore, the mean field size and its standard deviation were derived from digital maps. Variables measured within the 500 m radius circle were correlated with variables measured at a larger scale, i.e., within a circle with a 1000 m radius (Geiger et al., 2010).

To reduce the number of covariables included in the statistical analysis, only two of the four landscape variables were selected. Mean field size and its standard deviation, as well as habitat diversity and the % of land planted with arable crops were correlated (Pearson correlation coefficient = 0.6 and −0.9, respectively). Mean field size and habitat diversity were chosen for further use in the analysis.

Statistical analyses

The effects of farm management on the species richness and abundance of birds foraging mainly on agricultural land (referred to below as farmland birds) were analysed. Only species present in at least three study areas and represented by five or more individuals were included in the analyses (Table 4.2). Species richness and bird abundances were averaged over the two survey rounds, except for Spain, where only one round was available. Additional analyses were done for those species with an average of more than 300 observed individuals per survey round. To make the analyses consistent, farms with one or more missing variables were removed from the analysis (see Table 4.2 for the number of farms, i.e. survey plots per study area).

Generalized Linear Mixed Models (GLMM) in GenStat 12.1 (Payne et al., 2008) were used to analyse the effects of farm management on farmland birds. The response variables, i.e., species richness and bird abundance, were log-transformed to achieve normal distributions. Due to the heavily skewed data for individual species, GLMM with binomial distribution (presence-absence data) was used for single-species analyses. The factor study area was included as random effect and the two landscape variables of mean field size and habitat diversity were forced into all models as explanatory variables to account for the variation between study areas and landscapes.

Table 4.2 *List of bird species included in the analyses. Numbers represent mean numbers of birds observed per survey plot per survey round. See text for the areas included in the study. The numbers of survey plots per study area are given between brackets.*

English name	**Scientific name**	**FR** (29)	**WG** (26)	**EG** (30)	**NL** (30)	**PO** (29)	**ES** (28)	**SE** (32)	**Mean**
Carrion Crow	*Corvus corone corone*	0.7	3.1	1.8	1.6			1.1	1.7
Corn Bunting	*Miliaria calandra*	0.2	0.0			2.8	24.4		6.9
Chaffinch	*Fringilla coelebs*	2.0	1.8	0.1	0.6	0.0	3.1		1.3
Fieldfare	*Turdus pilaris*		0.2	0.1	0.2	0.7		1.4	0.5
Goldfinch	*Carduelis carduelis*	0.0	0.4	0.7	0.0	0.7	7.2		1.5
Greenfinch	*Carduelis chloris*	0.1	4.7	0.3	0.1	2.4	4.9	2.7	2.2
Jackdaw	*Corvus monedula*				0.7	0.1	0.4	2.4	0.9
Magpie	*Pica pica*	0.1	0.7	0.2	0.1	0.8	3.8	0.7	0.9
Meadow Pipit	*Anthus pratensis*	1.8			4.1		4.9		3.6
Skylark	*Alauda arvensis*	21.6	0.0	0.1	7.9	0.0	68.6		16.4
Starling	*Sturnus vulgaris*		0.3		6.4	0.0			2.2
Tree Sparrow	*Passer montanus*		0.3		0.2	1.7	0.5	1.0	0.7
Yellowhammer	*Emberiza citrinella*	0.9	5.6	1.4		4.6		8.5	4.2

First, the effects of agricultural intensity on farmland birds were analysed using yield as a measure of local intensity and as a summary variable of different farming practices (Donald et al., 2001c; Geiger et al., 2010; Tilman et al., 2002). This analysis was done with and without farm type as an additional explanatory variable, to unravel possible interlinked effects of yield and farm type.

Secondly, the effects of different farming practices on farmland birds were analysed by forward selection, starting with a model including only study area (random effect), habitat diversity and mean field size. In subsequent steps, the most significant variables (Wald tests, F statistics; $p < 0.05$) were added to the model. As farming practices are often linked to one of the two farm types, as for example pesticide use to conventional farming, farm type was added as an explanatory variable to consider these farm type differences between farming practices.

Thirdly, the effect of field cover type on farmland birds was tested using the same forward selection procedure as described above.

Finally, differences in species richness and bird abundance between organic and conventional farms were analysed using two different approaches. In a first approach, the

Table 4.3 *Number of farms per farm type (O = organic, C = conventional), study area and landscape type included in the analyses. See text for the areas included in the study and classification of landscape complexity.*

	Landscape complexity					
	Cleared		**Simple**		**Complex**	
	O	C	O	C	O	C
FR				18		11
WG	2	1	8	9	4	2
EG	2	15	4	9		
NL	3	3	12	11		1
PO		7		18		4
ES		1		13		14
SE		1	4	12	6	9
Total	7	28	28	90	10	41

effect of farm type on farmland birds was analysed with GLMM including habitat diversity and mean field size to account for variations in landscape composition between bird survey plots. In the second approach, the effect of the interaction between landscape complexity and farm type on farmland birds was analysed. Furthermore, the data was divided into three groups: cleared landscapes, consisting of more than 99% agricultural land (i.e., land under arable crops, permanent crops and pastures); simple landscapes, consisting of 80 to 99% agricultural land; and complex landscapes, consisting of less than 80% agricultural land (see Tscharntke et al. (2005) for a similar classification of landscape complexity). Subsequently, the effects of farm type were analysed in more detail within each landscape complexity type. Since study area was included as random effect, differences in numbers of bird survey plots per landscape and farm type within study areas were not expected to influence the results (see Table 4.3).

All explanatory variables were compared between organic and conventional farms by means of GLMM including study area as a random effect and farm type as an explanatory variable.

Explanatory variables were standardized according to to $(x-\mu)/s$, with $x =$ measurement, $\mu =$ mean and $s =$ standard deviation, to enable the magnitude of their effects to be compared, and heavily skewed variables were log- or logit-transformed (Table 4.1). Explanatory variables were checked for correlations. Strong, relevant correlations, i.e. those with a correlation coefficient > 0.7, are discussed in the results section (Appendix Tables 4.6 and 4.7).

Results

The surveys yielded a total of 13 different bird species foraging mainly on farmland and represented by at least five individuals in three or more study areas (Table 4.2). Skylarks were the most numerous species, with an average of 16.4 individuals per survey plot per round, followed by corn buntings and yellowhammers with 6.9 and 4.2 individuals, respectively.

As expected, all farming practices differed between the two farm types ($p < 0.05$; Appendix Table 4.2). Conventional farms applied larger amounts of artificial fertilizers and pesticides and had a higher cereal yield than organic farms. The frequency of mechanical weed control and the amount of organic fertilizer applied was higher on organic farms. Organic farms comprised more green manure crops within the survey plots than conventional farms.

When farm type was not included as an explanatory variable in the model, farmland bird abundance and species richness (the latter with marginal significance) were negatively related to yield (Table 4.4). However, yield no longer had a significant effect on bird abundance or species richness when farm type was included in the model. Neither of the single species was related to yield (Table 4.5).

Of the assessed farming practices, only mechanical weeding and the amount of organic fertilizer applied, affected wintering farmland birds. Species richness was negatively and farmland bird abundance was marginally negatively affected by the frequency of mechanical weeding (Table 4.4). These relations are probably restricted to differences within organic farms, as farm type was included in these analyses and as the significance of both relations increased when only organic farms were included in the analyses (F statistics = 10.07, $p = 0.003$ and F statistics = 7.62, $p = 0.009$ for species richness and bird abundance, respectively). Furthermore, greenfinches were negatively related to the amount of organic fertilizer applied (Table 4.5).

Bird abundance was positively related to the area covered by stubble, pasture and green manure crops within the bird survey plots (Table 4.4). Species richness was positively related to the area of pastures within the survey plots.

In general, organic farms supported more farmland bird species, as well as higher abundances of all farmland bird species and of greenfinches (Tables 4.4 and 4.5). The interaction between farm type and landscape complexity was significantly related to bird abundance, as well as species richness (F statistics = 4.64, $p = 0.011$ and F statistics = 3.38, $p = 0.036$, respectively). Farmland bird abundance and species richness were higher on organic than on conventional farms in simple landscapes (F statistics = 10.0, $p = 0.002$ and F statistics = 12.3, $p < 0.001$, respectively; Fig. 4.1). Species richness did not differ between the two farm types in cleared or complex landscapes (F statistics = 0.0, $p = 0.852$ and F statistics = 0.5, $p = 0.492$, respectively). Bird abundance was

Table 4.4 *Effects on farmland birds of (a) yield; (b) yield, including farm type as covariable; (c) different farming practices; (d) vegetation cover; and (e) farm type on farmland birds. See text for details about the statistics. The effects of mean field size and habitat diversity are only shown for analysis (c). Response variables are total bird abundance (Abundance) and the number of farmland bird species (Richness). F statistics (F), significance levels (p) and standardized effects (β) are given for explanatory variables. Effects regarding farm type are given for organic farms.*

		Variable	*F*	*p*	*β*
Abundance	**a**	Yield	4.8	**0.030**	-0.08
	b	Farm type	4.3	**0.040**	0.10
		Yield	1.0	0.323	-0.05
	c	Habitat diversity	2.4	0.122	0.00
		Mean field size	14.9	**<0.001**	-0.28
		Farm type	4.5	**0.035**	0.31
		Weed control	3.5	0.062	-0.10
	d	Cereal stubble	10.6	**0.002**	0.26
		Pasture	5.5	**0.021**	0.12
		Green manure	4.9	**0.028**	0.10
	e	Farm type	4.3	**0.039**	0.20
Richness	**a**	Yield	3.9	0.051	-0.03
	b	Farm type	6.1	**0.014**	0.08
		Yield	0.1	0.790	-0.01
	c	Habitat diversity	7.8	**0.006**	0.01
		Mean field size	16.9	**<0.001**	-0.11
		Farm type	6.6	**0.011**	0.14
		Weed control	7.9	**0.005**	-0.05
	d	Pasture	5.7	**0.019**	0.05
	e	Farm type	6.2	**0.014**	0.09

also equal for both farm types in cleared landscapes (F statistics = 0.4, $p = 0.530$), but was lower on organic farms situated in complex landscapes (F statistics = 7.5, $p = 0.009$; Fig. 4.1).

Variation in landscapes surrounding the survey plots was taken into account by forcing the variables mean field size and habitat diversity into all models, except for the analysis of the interaction between farm type and landscape complexity. Abundances of farmland birds, species richness and the presence of yellowhammers were negatively related to mean field size (Tables 4.4 and 4.5), while species richness, greenfinch and yellowhammer presence were positively related to habitat diversity.

Table 4.5 *Effects of (a) yield; (b) yield, including farm type as covariable; (c) different farming practices; and (d) farm type on the occurrence of individual species of farmland birds. See text for details about the statistics. Significant effects of mean field size and habitat diversity are only shown for analysis (c). Response variables are presence-absence data of individual species, including corn bunting (CB), greenfinch (GR), meadow pipit (MP), skylark (S) and yellowhammer (Y). No organic farms were surveyed in study areas where corn buntings were observed. F statistics (F), significance levels (p) and standardized effects (β) are given for explanatory variables. Effects regarding farm type are given for organic farms.*

		Variable	***F***	***p***	***β***
CB	**a**	Yield	0.3	0.607	0.24
	b	-	-	-	-
	c	-	-	-	-
	d	Farm type	-	-	-
GR	**a**	Yield	0.0	0.972	-0.01
	b	Farm type	5.7	**0.019**	1.90
		Yield	3.2	0.075	0.44
	c	Habitat diversity	6.1	**0.014**	0.42
		Mean field size	3.5	0.071	-0.66
		Farm type	6.2	**0.014**	1.59
		Organic fertilizer	3.9	**0.049**	-0.55
	d	Farm type	5.7	**0.019**	1.17
MP	**a**	Yield	1.3	0.263	0.28
	b	Farm type	0.1	0.711	1.70
		Yield	3.7	0.055	0.69
	c	-	-	-	-
	d	Farm type	0.2	0.649	0.33
S	**a**	Yield	1.4	0.244	-0.29
	b	Farm type	0.2	0.633	-0.93
		Yield	1.8	0.186	-0.58
	c	-	-	**-**	**-**
	d	Farm type	0.2	0.631	0.32
Y	**a**	Yield	1.8	0.179	-0.29
	b	Farm type	1.2	0.287	0.10
		Yield	0.7	0.405	-0.27
	c	Habitat diversity	7.1	**0.009**	0.37
		Mean field size	5.4	**0.022**	-0.55
	d	Farm type	1.3	0.266	0.55

Discussion

Wheat yields were higher on conventional than on organic farms. Both conventional farming and increased yields were associated with higher agricultural intensity and were negatively related to species richness and bird abundance. Due to their similar and interlinked effects, disentangling the influence of farm type and yield on farmland birds was not possible.

While organic farms supported more birds compared with conventional farms (see below), fewer farmland birds and species were observed on organic farms that had frequently used mechanical weed control during the preceding growing season. In most countries, this method was used only on organic farms, except for Spain, where mechanical weed control was also used on most conventional farms. In addition to reducing weed cover, mechanical weeding can also reduce invertebrate abundance, leading to decreased food abundance for birds in summer (Andreasen & Stryhn, 2008; Thorbek & Bilde, 2004), with possible consequences for food abundance in winter too. Less greenfinches were present on farms that had used more organic fertilizer, possibly due to its negative impact on food supply in crops (McKenzie & Whittingham, 2009).

Overall, more bird species and higher bird abundances were found on organic than on conventional farms. Chamberlain et al. (2010) suggested that the differences in bird numbers in winter are caused by variations in structural habitat between the two farm types. The only difference between the two farm types that could explain the

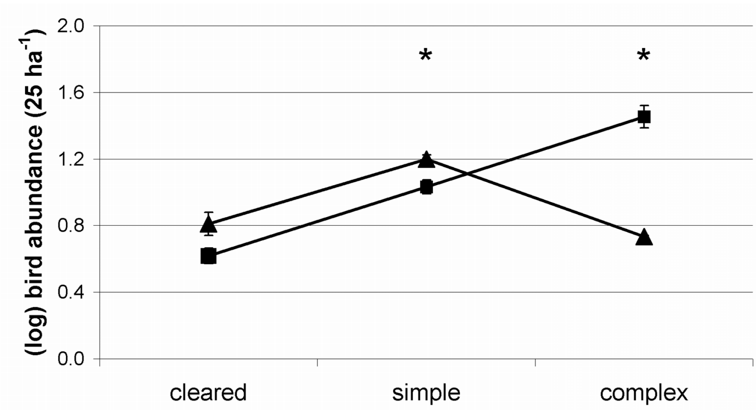

Figure 4.1 *Interaction effects of farm type and landscape composition on farmland birds (fitted values of bird abundances/survey/plot) on organic (▲) vs. conventional farms (■) in cleared, simple and complex landscapes (∗ statistically significant difference at 5% level (with S.E.)).*

higher abundances on organic farms in this study, was the larger area covered by green manure crops on organic farms. Moreover, farming activities after harvest, which were not included in this study, have been shown to strongly influence food abundance and vegetation cover (Moreby & Southway, 1999; Newton, 2004) and might be the reason for the difference in bird abundance and species richness between the two farm types.

When landscape complexity was taken into account, organic farming only had a positive effect on birds in simple and not in cleared or complex landscapes. Various empirical studies have shown that the effectiveness of agri-environment schemes and organic farming, depends on landscape complexity (plants: Roschewitz et al. (2005); bees and bumblebees: Holzschuh et al. (2006) and Heard et al. (2007); grasshoppers and birds: Concepción et al. (2008), Wretenberg et al. (2010), Smith et al. (2010) and Dänhardt et al. (2010)).

Landscape heterogeneity generally increases biodiversity (Benton et al., 2003; Wretenberg et al., 2010) and the differences between organic and conventional farms might be small in complex landscapes because fields are continuously recolonized (Concepción et al., 2008; Schmidt et al., 2005). Why bird abundances were lower on organic than on conventional farms in complex landscapes is not clear. A possible explanation is the difference in landscape characteristics between organic and conventional farms in the two study areas where both farm types were studied in complex landscapes (West-Germany and Sweden). At the landscape scale, the percentage forest was marginally higher and the mean field size was marginally smaller at conventional compared to organic farms (both $p = 0.071$, results not shown). Yellowhammers, the species that was most abundant in both study areas and negatively related to field size, were more numerous at conventional farms. This is probably the reason for the lower total bird abundance on organic farms in complex landscapes. Furthermore, no difference in bird abundance and species richness was found between conventional and organic farms in cleared landscapes, possibly due to a low species pool. Moreover, the sample size of organic farms within cleared landscapes was rather low and might have influenced the results.

Studies of the effectiveness of other agri-environment schemes applied in winter, such as food provision by overwinter stubble fields, non-harvested cereal margins or even whole cereal fields, have shown inconsistent results (Bradbury et al., 2004; Perkins et al., 2008; Siriwardena et al., 2007; Stoate et al., 2004; Suárez et al., 2004). However, most of these studies did not take landscape composition into account. The effectiveness of agri-environment schemes might be improved by designing different schemes for landscapes differing in the amount of non-crop habitats. In cleared landscapes, for example, a substantial extension of non-crop habitats might be necessary to increase species pools first. In simple landscapes, birds might profit from adaptations of farming practices that increase food abundance on farmland, for example less frequent mechanical weeding or conservation tillage. In heterogeneous landscapes, agri-environment schemes specifically designed for species associated with this landscape type, for example seed supply for yellowhammers, might be most effective.

Landscape complexity as classified in this study, i.e. the area of non-crop habitats, is continuous. Therefore the effectiveness of organic farming and agri-environment schemes is likely to gradually increase and decrease along this complexity gradient. Nonetheless, this classification based on empirical studies (Andrén, 1994; Tscharntke et al., 2005) may be useful in the design of landscape-dependent agri-environment schemes.

Acknowledgements

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Appendix

Table 4.6 *Correlation matrix of farming practices (n = 204) used in the analyses.*

	Fungicide	Fungicide a.i.	Herbicide	Herbicide a.i.	Insecticide	Insecticide a.i.	Weed control	Artificial fertilizer	Organic fertilizer
Wheat yield	0.52	0.55	0.53	0.21	0.50	0.22	-0.42	0.61	-0.10
Organic fertilizer	-0.41	-0.14	-0.17	-0.09	-0.01	-0.06	0.09	-0.33	
Artificial fertilizer	0.52	0.68	0.58	0.31	0.39	0.12	-0.44		
Weed control	-0.37	-0.48	-0.41	-0.13	-0.27	-0.13			
Insecticide a.i.	0.40	0.29	0.12	0.06	0.45				
Insecticide	0.65	0.59	0.49	0.15					
Herbicide a.i.	0.24	0.35	0.52						
Herbicide	0.63	0.58							
Fungicide a.i.	0.81								

Table 4.7 *Correlation matrix of field cover types (n = 120) used in the analyses.*

	Cereal stubble	Green manure	Bare soil	Pasture
Winter cereals	-0.11	-0.04	-0.61	-0.16
Pasture	0.05	-0.08	-0.22	
Bare soil	-0.46	-0.02		
Green manure	-0.13			

Table 4.8 *Differences in explanatory variables between organic and conventional farms, analysed using generalized linear mixed models including study area as random and farm type as fixed effect. See Table 4.1 and 4.3 for explanation of variables and sample sizes. Effects (β) refer to organic farms.*

		Conventional		Organic			
Variable	**Units**	**mean**	**stdev**	**mean**	**stdev**	***p***	**β**
Yield	kg ha^{-1}	5866.7	1490.6	3766.4	1134.9	**<0.001**	-1.926
Herbicides	y^{-1}	1.6	1.0	0.0	0.0	**<0.001**	-1.810
Herbicide a.i.	kg ha^{-1} y^{-1}	0.8	0.8	0.0	0.0	**<0.001**	-1.144
Insecticides	y^{-1}	0.4	0.6	0.0	0.0	**<0.001**	-1.296
Insecticide a.i.	kg ha^{-1} y^{-1}	0.0	0.1	0.0	0.0	**0.017**	-0.430
Fungicides	y^{-1}	1.1	1.2	0.0	0.0	**<0.001**	-1.346
Fungicide a.i.	kg ha^{-1} y^{-1}	0.4	0.4	0.0	0.0	**<0.001**	-1.526
Artificial fertilizer	kg N ha^{-1} y^{-1}	131.4	62.7	0.0	0.0	**<0.001**	-1.983
Organic fertilizer	kg ha^{-1} y^{-1}	1610.0	5743.1	11238.4	14426.8	**<0.001**	0.778
Mechanical weed control	y^{-1}	0.5	1.2	1.6	1.9	**<0.001**	1.020
Mean field size	ha	15.7	33.5	18.9	17.7	0.850	-0.019
Habitat diversity		0.6	0.4	0.6	0.4	0.108	0.255
Cereal stubble	%	17.7	27.6	6.4	15.2	0.135	0.196
Bare soil	%	40.6	35.3	55.7	33.7	0.621	-0.097
Pasture	%	4.1	10.4	4.1	9.7	0.888	-0.030
Green manure	%	0.7	3.1	6.4	13.5	**<0.001**	0.708
Winter cereals or grass seed	%	25.6	31.2	14.9	19.8	0.269	-0.238

Chapter 5

Higher food abundance on organic farmland attracts wintering birds

Flavia Geiger, Frank Berendse, Geert R. de Snoo, Maurits Gleichman

Abstract

In recent decades, many farmland bird populations have declined due to agricultural intensification. Intensified farming practices have altered breeding and foraging habitats, resulting in less food being available for birds in summer. It is not clear, however, whether farm type (conventional vs. organic) and farming practices, such as the use of pesticides and artificial fertilizers, also affect food availability in winter. The present study investigated the influence of vegetation cover and food abundance on birds wintering on farmland in the Netherlands. We also analysed the effects of farm type and several farming practices on food abundance in winter. Preferences for fields with different vegetation cover proved species-specific. Soil seed density was positively related to bird abundance and species richness. Food abundance, i.e. soil seed density, was higher on organic fields than on conventional fields. Soil seed density on organic fields was negatively affected by the frequency of mechanical weeding. We conclude that food shortage in winter might be a bottleneck for birds wintering on farmland. Farm management that increases food abundance, such as organic farming with reduced pesticide use and non-inversion tillage, should be encouraged, to support farmland birds in winter.

Introduction

Since the intensification of agriculture in the second half of the last century, populations of many farmland birds have declined, and they are still suffering from its ongoing ecological impacts on Dutch farmland (SOVON, 2002, 2008). In the last 20 years, populations of meadow pipits (*Anthus pratensis*) and starlings (*Sturnus vulgaris*) have decreased by 20% and 30%, respectively, and numbers of skylarks (*Alauda arvensis*) even declined by more than 60% (van Dijk et al., 2009). Previous studies suggested that the main proximate reasons for these population declines are reduced reproductive success and low adult survival in winter (Gregory et al., 2004; Newton, 2004; Siriwardena et al., 2008). Possible causes of low reproduction success include an increased predation rate and decreased food availability on farmland (Aebischer & Ewald, 2004; Kragten et al., 2010; Morris & Gilroy, 2008; Wilson et al., 2005). Mortality in winter is likely to be influenced by food availability and possibly also by predation (Newton, 2004; Siriwardena et al., 2007; Wilson et al., 1999).

The intensification of agricultural practices and the resulting uniformity of agricultural landscapes have altered foraging and breeding habitats of farmland birds (Bos & Schröder, 2009; Donald et al., 2006; Stoate et al., 2009). In summer, the use of pesticides and fertilizers reduces the availability of invertebrates and weeds (Boatman et al., 2004; Newton, 2004; Taylor et al., 2006). Harvesting techniques that spill less grain (Wilson et al., 1999), the use of post-harvest herbicides (Moreby & Southway, 1999), tillage and the early ploughing of stubble (Robinson & Sutherland, 2002; Stoate et al., 2009) reduce the availability of cereal grains, as well as the abundance of weed seeds and weed cover in winter. However, it is still unclear whether farming operations, such as the use of pesticides and artificial fertilizer during the growing season, also influence food availability in winter.

Weeds and crop residues not only provide food for birds, but may also offer shelter against predators and harsh weather conditions (Butler et al., 2005a; Whittingham et al., 2006). Whether a particular vegetation structure or cover type appears obstructive or protective to a foraging bird depends on its predator avoidance strategy (Lazarus & Symonds, 1992; Lima & Dill, 1990; Whittingham, 2004). Hence, wintering birds select fields not only for food availability but also for vegetation cover and structure.

Organic farming is a farm management strategy aiming to work in a more environment-friendly way and which offers the potential of increasing biodiversity on farmland. The main difference between conventional and organic farming is that the latter does not use synthetic pesticides or artificial fertilizers. Studies to determine whether organic farming increases biodiversity have mainly focused on summer situations, and have yielded different results for different taxa (Bengtsson et al., 2005; Hole et al., 2005). Plants, earthworms and spiders have been shown to benefit from organic farming, whereas varying effects have been reported for butterflies, arthropods, soil organisms and birds (Bengtsson et al., 2005; Geiger et al., 2010; Hole et al., 2005; Kragten & de Snoo, 2008). Generally, breeding birds find more abundant food on organic than on conventionally managed fields (Kragten et al., 2010; Vickery et al., 2009). Some studies have shown that farmland birds may benefit from organic farming in winter (Chamberlain et al., 2010; Wilson et al., 1996) or during migration (Dänhardt et al., 2010). It remains unclear whether food abundance in winter is also higher on organic than on conventional fields (Moorcroft et al., 2002) and whether wintering birds prefer habitats with certain characteristics associated with organic farming, in terms of boundary characteristics, crop diversity or crop type (Chamberlain et al., 2010; Dänhardt et al., 2010).

We investigated whether farm management affected vegetation cover and food abundance in winter, and how this in turn influenced foraging birds, by testing the following hypotheses: (a) Vegetation cover (i.e. the cover of weeds, green manure crops, cereal stubbles, winter cereals or grassland) increases the species richness and abundance of birds wintering on farmland. (b) Higher food abundance (i.e. seed density) increases the species richness and abundance of birds wintering on farmland. (c) Organic farming leads to greater food abundance on arable fields in winter.

Methods

Study area

Bird inventories were conducted on 30 arable farms in the province of Flevoland, the Netherlands. This province includes three polders reclaimed from the sea at different times: Northeastern Flevoland (1942), Eastern Flevoland (1957), and Southern Flevoland (1968). In each polder, five organic and five conventional farms were selected. These 30 farms represented a gradient of farming intensity, using the cereal yield of the previous year as a proxy for intensity. Wheat yields of the study year ranged from 2.3 to 6 tons ha^{-1} at organic and from 6.5 to 9.5 tons ha^{-1} at conventional farms.

On each farm, one 500 $\times$ 500 m bird survey plot was chosen so as to include at least one arable field where wheat had been cultivated in the preceding growing season. The sizes of the wheat fields selected within the survey plots ranged from 3 to 25 ha (total survey area). The remaining area in the plots comprised other arable crops, permanent pasture, and sometimes other infrastructure, such as paths, farmyards and water courses. Some survey plots also included fields belonging to neighbouring farms. In eight survey plots, 50 to 75% of the land they included belonged to the farm that owned the selected wheat field, while in half of the plots, 75 to 99% of the land belonged to that farm. There were seven survey plots in which the whole plot area belonged to the selected farm.

Farming practices

Data about farming practices were based on the cultivation of all, i.e. one or two, wheat fields within the bird survey plot. The data were collected by means of a questionnaire survey among farmers, with questions relating to the farming operations during the preceding growing season. The previous growing season lasted from the harvest of the preceding crop (autumn 2006) to the harvest of the most recent crop (summer 2007). The organic farms usually grew spring wheat, while the conventional farms grew winter wheat, with one exception for each farm type.

Bird surveys

Birds were surveyed three times: in December 2007; between mid-January and early February 2008; and in March 2008. Bird survey plots were walked in such a way that each spot within the plot was no more than 100 m from the surveyor's route. The surveys took place between one hour after dawn and one hour before sunset. No surveys were done when it was too windy, cloudy or rainy. All birds foraging or resting within the survey plot were counted and included in the analyses, except for individuals foraging on farmyards, in water courses or on ditch banks along wide canals (Table 5.1).

Field cover types (survey plot)

The vegetation cover of all fields within the survey plots was mapped during the bird surveys. Fields were classified into seven categories in terms of their field cover type: bare ground; cereal stubble; permanent grassland; winter cereals or grass seed; green manure crops, including clover, lucerne, fodder radish (standing crop or mown); grassy field margins; and other, including tree nurseries and tulip fields.

Soil seed density and vegetation cover within wheat fields

Within each survey plot, food availability was sampled once on one of the wheat fields included in the plot, in February. At the time of sampling, most (93%) of the sampled wheat fields had been ploughed. Only two fields were unploughed and were under green manure crops, both belonging to organic farms. Winter cereals had been sown on three of the ploughed fields. Food abundance was sampled and vegetation cover was estimated on the wheat field by selecting five 1×2 m sampling plots, evenly spaced out at a distance of 10 m from one of the field borders. Within these five sampling plots, we estimated the percentages covered by the following five vegetation cover types: total weed cover; dicotyledonous weeds; monocotyledonous weeds and winter cereals; green manure crops; and bare ground. In most sampling plots, all vegetation present within the plot, i.e. weeds and green manure crops, was harvested, dried (48 h, 70°C) and

Table 5.1 *Bird abundances (per survey round and ha) observed in the survey plot as a whole and in the wheat field included in the plot.*

English name	Scientific name	Survey plot	Wheat field
Golden Plover	*Pluvialis apricaria*	0.304	0.587
Skylark	*Alauda arvensis*	0.235	0.219
Starling	*Sturnus vulgaris*	0.188	
Meadow Pipit	*Anthus pratensis*	0.140	0.055
Stock Dove	*Columba oenas*	0.078	0.008
Egyptian Goose	*Alopochen aegyptiacus*	0.058	
Lapwing	*Vanellus vanellus*	0.053	0.065
Carrion Crow	*Corvus corone corone*	0.049	0.016
Blackheaded Gull	*Larus ridibundus*	0.041	0.006
Wood Pigeon	*Columba palumbus*	0.029	0.031
Fieldfare	*Turdus pilaris*	0.026	
Common Gull	*Larus canus*	0.024	
White Wagtail	*Motacilla alba*	0.020	0.010
Buzzard	*Buteo buteo*	0.018	0.016
Jackdaw	*Corvus monedula*	0.018	
Kestrel	*Falco tinnunculus*	0.008	0.004
Snipe	*Gallinago gallinago*	0.007	0.002
Whooper Swan	*Cygnus cygnus*	0.005	
Grey Heron	*Ardea cinerea*	0.004	0.004
Hen Harrier	*Circus cyaneus*	0.004	0.004
Great White Heron	*Egretta alba*	0.003	0.002
Mute Swan	*Cygnus olor*	0.002	
Reed Bunting	*Emberiza schoeniclus*	0.002	0.002
Robin	*Erithacus rubecula*	0.001	0.001
Wheatear	*Oenanthe oenanthe*	0.001	
Blackbird	*Turdus merula*	0.001	0.001
Mallard	*Anas platyrhynchos*	0.001	
Mistle Thrush	*Turdus viscivorus*	0.001	0.002
Wren	*Troglodytes troglodytes*	<0.001	
Blue Tit	*Parus caeruleus*	<0.001	
Goshawk	*Accipiter gentilis*	<0.001	
Jay	*Garrulus glandarius*	<0.001	
Sparrowhawk	*Accipiter nisus*	<0.001	

weighed. In plots with a high biomass, the vegetation sampling was limited to a 25×25 cm subplot. The height of the tallest plant within the plots was measured.

Soil samples were taken within each 1×2 m sampling plot to estimate seed densities. This was done by taking 10 randomly distributed sub-samples, using a bulb planter (6 cm diameter), to a depth of 10 mm. The sub-samples were mixed to form a composite sample. Before processing, the soil samples were stored at 4°C to prevent seed germination. The soil was sieved through two sieves with mesh sizes of 1.0 and 0.5 mm, respectively, which ensured that most of the seeds taken by birds like the skylark were collected (Green, 1978). The residue from sieving (including seeds, seashells, pebbles, vegetation remains) was dried (48 h, 70°C) and sorted by hand. Weed seeds were counted and identified to species level whenever possible. Seed biomass was estimated by averaging the weight of all or a maximum of 100 seeds per species. Since seed number and total seed weight were highly correlated (Pearson correlation coefficient = 0.99), only seed densities were used in subsequent analyses.

Landscape composition

To test whether the three polders differed in terms of landscape characteristics, mean field size and habitat diversity were estimated for circles with a 500 m radius around the centre of each survey plot. The Shannon diversity index was used to calculate habitat diversity, based on the area within the circle covered by six different habitat types. Areas covered by the different habitat types were derived from digital maps using ArcGis (ESRI, 2009). Using definitions from the European Topic Centre on Land Use and Spatial Information (Büttner et al., 2000), the following habitat types were distinguished: urban fabrics, cultivated arable lands, permanent crops, pastures, forests and water.

Statistics

The first two hypotheses were tested at two different scales. At the survey plot scale, we first investigated whether field cover type (i.e. bare ground, cereal stubble, permanent grassland, winter cereals, green manure crops and grassy field margins) affected bird abundance (hypothesis a), using χ^2 tests. Each bird record, i.e. single individuals or flocks, was log-transformed. Bird numbers (log) averaged over the three survey rounds per field cover type were used as observed values. Expected values were estimated based on the average proportion of a particular field cover type. We analysed the effects of field cover type on the abundances of individual species represented by at least 100 individuals observed within the survey plots during the three bird surveys.

Next, we analysed whether food abundance influenced the abundance of wintering farmland birds at the survey plot scale (hypothesis b). The effect of seed density on total bird abundance and species richness was analysed using generalized linear mixed models (GLMM) with repeated measures analysis, applying the method of residual maximum likelihood in GenStat 12.1 (Payne et al., 2008). The polder was included as a fixed effect to account for differences between the three polders in terms of landscape characteristics and the time available for colonisation by weed species. Analyses were repeated for abundances of individual species.

At the field scale, i.e. including only the wheat fields, hypotheses a and b were tested simultaneously. We analysed the effects of food abundance and vegetation cover (soil seed density, vegetation biomass, cover and height averaged over the five sampling plots) on bird abundance and species richness, applying GLMM with repeated measures analysis using the method of residual maximum likelihood and forward selection. Forward selection was started with a model including only field size and polder as fixed effects. In each subsequent step, the food or vegetation cover variable with the most significant effect was included, on the basis of the results of F statistics ($p < 0.05$). This procedure was reiterated until variables no longer added significant effects to the model.

Finally, we tested the effects of farming practices applied during the preceding growing season on food abundance (hypothesis c). Only those variables that were significantly related to the abundance and species richness of wintering birds were investigated. Effects of farming practices were analysed using generalized linear models (GLM) and forward selection. Again, polder was included as a fixed effect. As pesticides and artificial fertilizers are only used on conventionally managed fields, farm type (organic vs. conventional) was additionally included as a fixed effect to identify relations associated with farm type. Analyses were repeated including only one of the two farm types.

All explanatory variables were tested for differences between the two farm types using nonparametric Mann-Whitney U tests. Differences in field cover types (at the survey plot scale) between the two farm types were tested using GLMM with repeated measures analysis, with farm type as a fixed effect. Differences between the polders in terms of landscape characteristics, i.e. mean field size and habitat diversity, were analyzed with Mann-Whitney U tests.

If necessary, response and explanatory variables were transformed to meet normal distributions (see Table 5.2). Total bird abundance and species richness were log-transformed, while abundances of individual species were arcsinh transformed to meet normal distributions. Explanatory variables were standardized according to $(x-\mu)/s$, with x = measurement, μ = mean and s = standard deviation, to enable the magnitude of their effects to be compared. We emphasize that the term ‘effect’ is used in the text to indicate statistical associations and relationships, and does not necessarily imply a causal relation between two variables.

Table 5.2 *Descriptions and units of the explanatory variables used in the statistical analyses.* [1]*Average value based on the cultivation of one or two wheat fields per farm.* [2]*Variables are log-transformed.* [3]*The following habitat types were distinguished: urban fabrics, cultivated arable lands, permanent crops, pastures, forests, and water.*

	Explanatory variable	Description	Units
	Field size	size of wheat field	ha
	Farm type	conventional or organic	
	Polder	Southern, Eastern and Northeastern Flevoland	
Farming practices (previous growing season)	Herbicide[1]	number of applications	y^{-1}
	Herbicide a.i.[1]	total amount of active ingredients	kg ha^{-1} y^{-1}
	Insecticide[1]	number of applications	y^{-1}
	Insecticide a.i.[1]	total amount of active ingredients	kg ha^{-1} y^{-1}
	Fungicide[1]	number of applications	y^{-1}
	Fungicide a.i[1]	total amount of active ingredients	kg ha^{-1} y^{-1}
	Artificial fertilizer[1]	total amount of inorganic nitrogen fertilizer	kg N ha^{-1} y^{-1}
	Organic fertilizer[1]	total amount of organic fertilizer	kg ha^{-1} y^{-1}
	Ploughing[1]	ploughing depth	m
	Mechanical weed control[1]	frequency of mechanical weed control	y^{-1}
Landscape characteristics	Mean field size[2]		ha
	Habitat diversity[3]	Shannon diversity index based on 6 different habitat types	

Table 5.2 *continued*

	Explanatory variable	Description	Units
Food abundance and vegetation cover (field scale)	Seed density[2]	number of seeds	m^{-2}
	Total weed biomass	dry weight of weeds	$g\ m^{-2}$
	Grass biomass	dry weight of grassy weeds	$g\ m^{-2}$
	Dicotyledonous biomass[2]	dry weight of dicotyledonous weeds	$g\ m^{-2}$
	Green manure biomass	dry weight of green manure	$g\ m^{-2}$
	Vegetation height	height of tallest plant	cm
	Total weed cover[2]	cover	%
	Grass cover	cover	%
	Dicotyledonous cover	cover	%
	Green manure cover	cover	%
	Bare ground	cover	%
Field cover type (survey plot scale)	Bare ground	cover	%
	Cereal stubble	cover	%
	Winter cereals	cover	%
	Green manure crops	cover	%
	Permanent grassland	cover	%
	Grassy field margin	cover	%

Results

A total of 33 bird species were observed during the three survey rounds (Table 5.1). Across all three survey rounds, the following species were represented by more than 100 individuals: golden plover (*Pluvialis apricaria*), skylark (*Alauda arvensis*), starling (*Sturnus vulgaris*), meadow pipit (*Anthus pratensis*), stock dove (*Columba oenas*), Egyptian goose (*Alopochen aegyptiacus*), lapwing (*Vanellus vanellus*) and carrion crow (*Corvus corone corone*).

Effects of field cover type, vegetation cover and food abundance on wintering farmland birds

At the survey plot scale, we investigated whether abundances of wintering birds were related to different field cover types. Proportions of different cover types within survey plots did not change markedly between the survey rounds (Fig. 5.1). The numbers of meadow pipits and skylarks observed per field cover type differed significantly from expected values (Fig. 5.2). Meadow pipits were most abundant in field margins. Highest skylark densities were observed on cereal stubble, but none of the field types were completely avoided. Lapwings were most abundant during the final survey and were present on all field cover types except for cereal stubble (Fig. 5.3). Bird densities on bare ground were generally low, except for stock doves, starlings, golden plovers and carrion crows.

At the survey plot scale, bird abundance and species richness were positively related to soil seed density (Table 5.3, Fig. 5.4), whereas at the species level, only the abundance

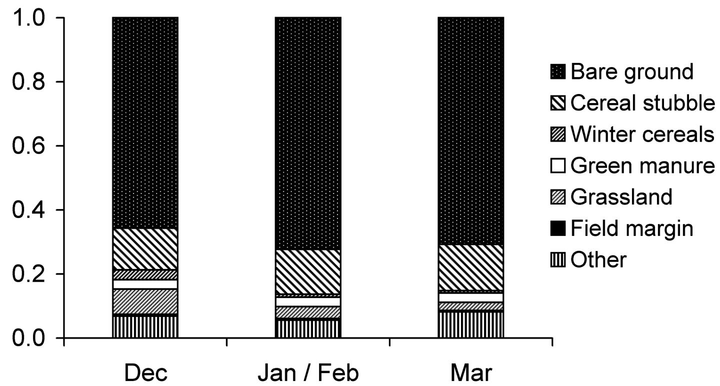

Figure 5.1 *Proportion of each field cover type within the survey plots per survey round: bare ground, cereal stubble, winter cereals, green manure crops, permanent grasslands, grassy field margins, other.*

of starlings was positively related to soil seed density.

In the course of the three survey rounds, most of the wheat fields were bare ground (Fig. 5.5: 63%, 80% and 73%, respectively). During the first survey round, 9% and 14% of the 30 fields was under green manure crops and cereal stubble, respectively. During the second and third survey rounds, winter cereals represented the second highest coverage of the field area (10% and 9%). Despite the large area of bare ground, 19 different bird species were observed on wheat fields (Table 5.1). Most numerous were golden plovers, skylarks, lapwings and meadow pipits, with 0.59, 0.22, 0.07 and 0.06 individuals per ha, respectively.

Seed densities in the soils of the wheat fields sampled in February ranged from 7 to 9472 seeds m^{-2}. The conventional and organic wheat fields contained an average of 200 and 2527 seeds m^{-2}, respectively. Seed density was highest in the two unploughed fields (both organic), with 9471.5 and 5524.4 seeds m^{-2}, and lowest (7 seeds m^{-2}) in an

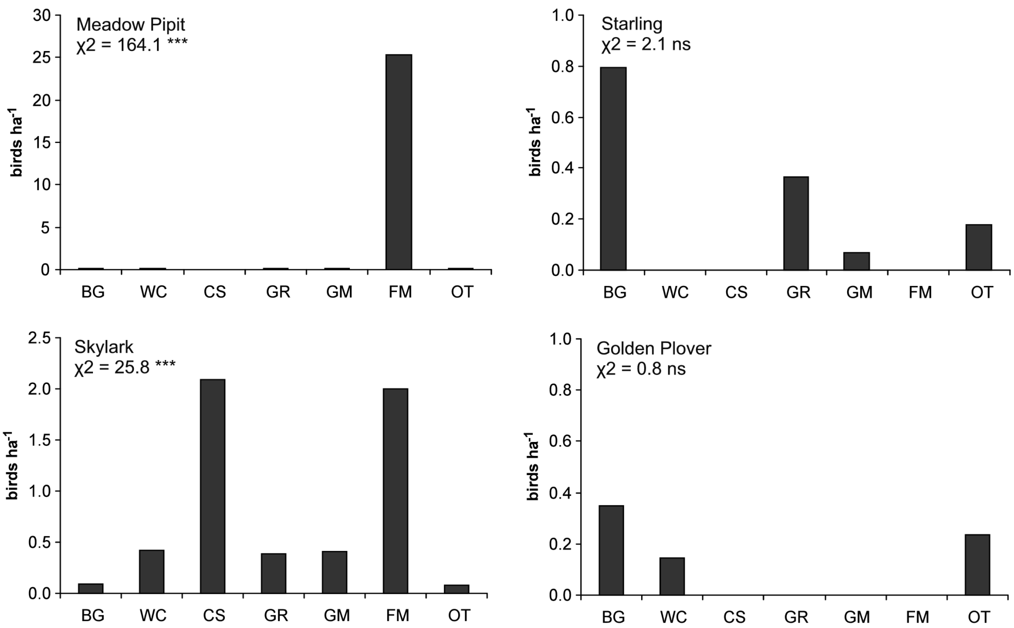

Figure 5.2 *Numbers of individual species (ha^{-1}) per survey round on different field cover types: BG = bare ground, WC = winter cereals, CS = cereal stubble, GR = permanent grassland, GM = green manure crops, FM = field margin, OT = other. Results of the χ^2 tests and significance levels are shown: ns for $p > 0.05$, * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$.*

Table 5.3 *Generalized linear mixed models with repeated measures were used to analyse the effects of seed density on total bird abundance, species richness and abundance of individual species at the survey plot scale. Models always included the polder as a fixed effect. F stat: F statistics, p: p-value, Std effect: standardized effect. Effects of Eastern Flevoland (EF) and Southern Flevoland (SF) are relative to the effects of Northeastern Flevoland.*

	Polder				Seed density		
	F stat	*p*	Effect EF	Effect SF	F stat	*p*	Std effect
Bird abundance	2.74	0.083	0.163	-0.127	16.26	**<0.001**	0.262
Species richness	0.71	0.501	0.051	-0.024	6.83	**0.015**	0.091
Carrion Crow	0.28	0.761	0.114	0.293	0.77	0.387	0.117
Egyptian Goose	0.33	0.723	-0.001	-0.136	0.02	0.896	0.011
Golden Plover	0.57	0.570	0.396	-0.051	2.47	0.128	0.285
Lapwing	0.45	0.643	-0.092	0.000	2.21	0.150	0.126
Meadow pipit	0.52	0.600	0.113	-0.205	1.21	0.281	0.176
Skylark	4.86	**0.016**	0.324	-0.804	1.16	0.291	0.182
Stock dove	0.77	0.475	0.135	0.532	2.09	0.160	0.227
Starling	1.36	0.273	-0.210	-0.187	8.78	**0.006**	0.523

organic field that had been ploughed to a depth of 1.2 m. Most abundant were seeds of *Stellaria media*, *Chenopodium sp.*, *Polygonum sp.* and *Solanum nigrum*. No weed seeds were found in the standing vegetation and no cereal grains were present in or on the soil.

At the field scale, bird abundance was positively related to seed density (Fig. 5.6), while species richness was negatively related to the percentage of bare ground (Table 5.4).

Differences between the three polders were only found for skylark abundance at the survey plot scale (Table 5.3): the highest abundances were observed in Eastern Flevoland, while the lowest abundances were found in Southern Flevoland.

Effects of farm management on food abundance

Next, we investigated the effects of farm type (conventional vs. organic) and different farming practices on seed density. Soil seed density was higher on organic than on conventional wheat fields (Table 5.5), and was negatively affected by the frequency of mechanical weeding when farm type was included as a fixed effect in the model selection (F statistics = 8.3, $p = 0.008$, standardized effect = -0.492).

In single-effect analyses, not including farm type as a fixed effect, soil seed density was negatively related to the use of artificial fertilizer, fungicides, herbicides and insecticides (generalized linear models, results not shown). However, when farm type was included as a fixed effect, none of these farming practices were significantly related to soil seed densities. Moreover, when analyses were repeated for conventional farms alone, the variables no longer significantly affected seed density (results not shown). These results indicate that farming practices and farm type were interlinked.

All farming practices we assessed differed between the two farm types (Table 5.5). Seed density, weed biomass and total weed cover were higher on organic fields than on conventional fields. The cover of permanent grassland was higher in organic survey plots. The two landscape variables (mean field size and habitat diversity) differed significantly between the three polders (Table 5.6). Mean field sizes were largest and habitat diversity was highest in Southern Flevoland. Mean field sizes were smallest in Northern Flevoland and intermediate in Eastern Flevoland.

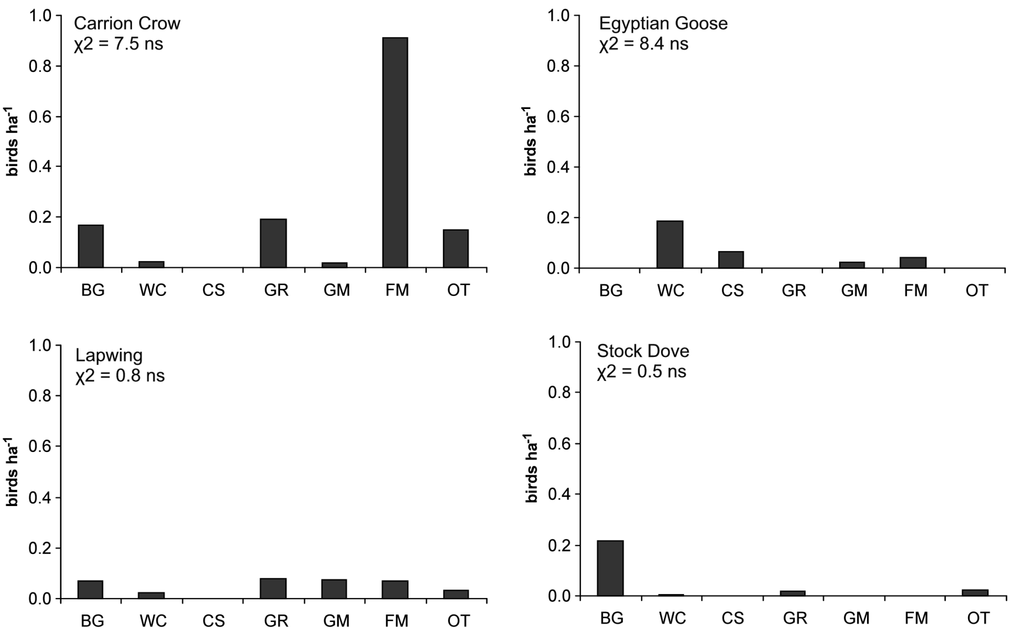

Figure 5.3 *Numbers of individual species (ha^{-1}) per survey round on different field cover types: BG = bare ground, WC = winter cereals, CS = cereal stubble, GR = permanent grassland, GM = green manure crops, FM = field margin, OT = other. Results of the* χ^2 *tests and significance levels are shown: ns for* $p > 0.05$, ** for* $p < 0.05$, *** for* $p < 0.01$, **** for* $p < 0.001$.

Discussion

We investigated the influence of vegetation cover and food abundance on wintering farmland birds, and analysed the effects of farming practices and farm type (conventional vs. organic) on food abundance.

Effects of vegetation cover and food abundance on wintering farmland birds

Species richness on wheat fields was lowest on bare ground, which confirms our first hypothesis. Similar avoidance of bare ground by many farmland species was found by Tucker (1992) and Wilson et al. (1996). Except for a short period after ploughing,

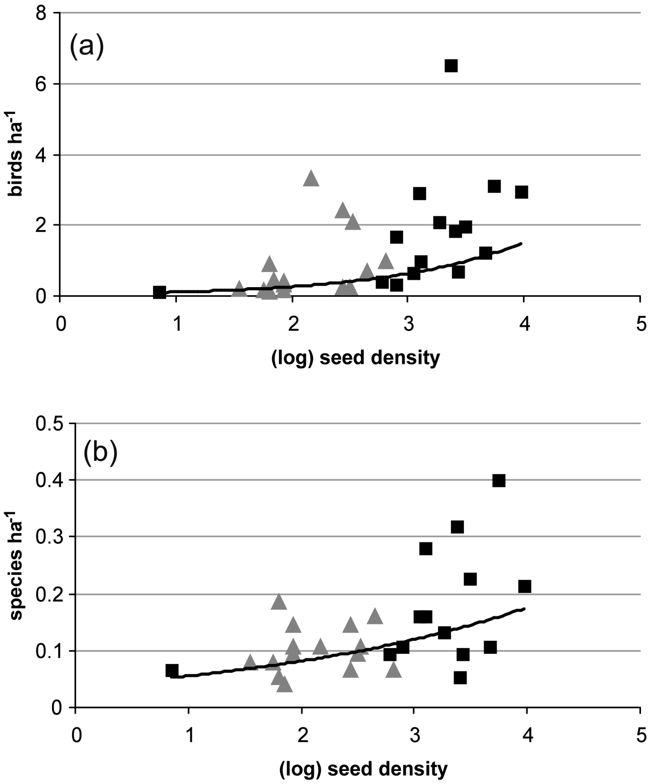

Figure 5.4 *(a) Number of birds (ha^{-1}) and (b) species richness (ha^{-1}) at survey plot scale (averaged over the three survey rounds) in relation to (log of) soil seed density (m^{-2}) on organic (black squares) and conventional (grey triangles) farms. Trend lines have been plotted for fitted values and significant relations.*

when seeds and invertebrates are exposed to the soil surface, food availability is probably lower on bare ground compared to other field cover types, making bare ground less attractive to foraging birds (Tucker, 1992; Wilson et al., 1996). At a larger scale, which includes several fields with different vegetation cover, we found that the abundances of wintering farmland birds varied between field cover types. Vegetation cover preferences and thus field preferences were species-specific and probably related to diet and predator avoidance strategy. Stock doves, starlings and resting golden plovers were most abundant on ploughed fields. These larger-bodied species have often been observed to forage in flocks and to fly away from approaching predators (Thompson & Barnard, 1983; Zoratto et al., 2009). In contrast, more cryptic species, such as skylarks and meadow pipits, depend on vegetation cover to hide (Lima & Dill, 1990; Whittingham et al., 2006). Field margins, i.e. margins with mainly grasses and some herbs, were important foraging habitats for meadow pipits, skylarks and carrion crows. Foraging skylarks and meadow pipits have both been shown to prefer tall over short vegetation, as the latter probably offers insufficient shelter (Butler et al., 2005a; Whittingham et al., 2006). Field margins offer not only shelter, but also various food sources, such as weeds, weed seeds and invertebrates (Vickery et al., 2002).

Egyptian geese and golden plovers, both of which eat grass, were fairly abundant in fields with winter cereals. Other studies have found similar habitat preferences for these species (Gillings et al., 2008). Foraging carrion crows and starlings were observed in relatively high densities on permanent grassland in January and February. These species, which are both invertebrate-feeders, were possibly attracted by high invertebrate densities in grassland (Tucker, 1992; Wilson et al., 1996).

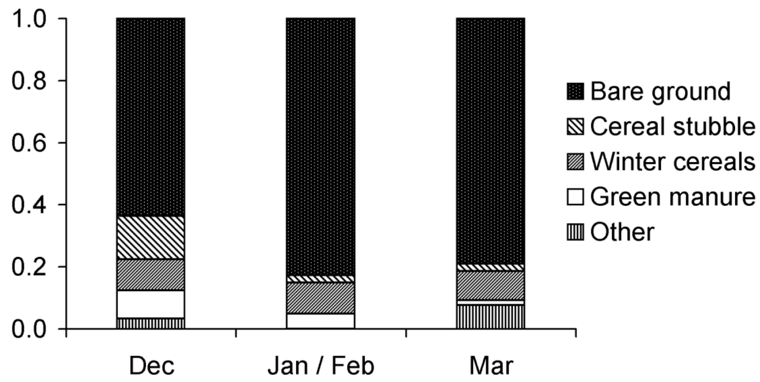

Figure 5.5 *Proportion of wheat fields covered by different vegetation types (bare ground, cereal stubble, winter cereals, green manure crops, other) per survey round.*

Remarkably, we did not observe small-bodied species that rely on early detection of predators by sight and that prefer to forage in short vegetation, such as yellowhammers (*Emberiza citrinella*) and chaffinches (*Fringilla coelebs*) (Whittingham & Evans, 2004). When a predator is spotted, these species are likely to flee into tall boundary vegetation, such as hedgerows and shrubs. The lack of tall boundary vegetation in our study area, might explain these species' absence in the survey plots (Whittingham & Evans, 2004).

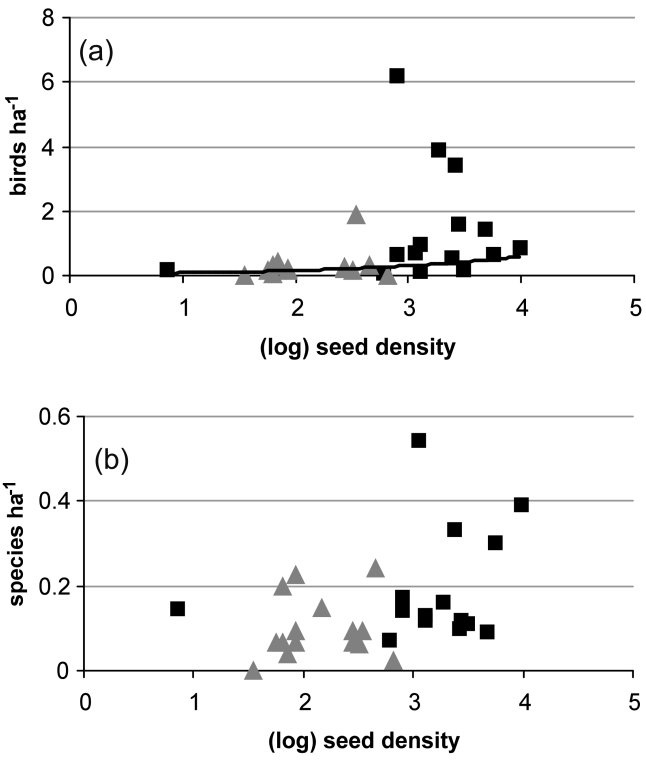

Figure 5.6 *(a) Number of birds (ha^{-1}) and (b) species richness (ha^{-1}) at field scale (averaged over the three survey rounds) in relation to (log of) soil seed density (m^{-2}) on organic (black squares) and conventional (grey triangles) farms. Trend lines have been plotted for fitted values if relations were significant.*

Table 5.4 *At the field scale, the effects of food abundance (seed density and vegetation biomass), vegetation cover and height on species richness and bird abundance were analysed using generalized linear mixed models with repeated measures and forward selection. Models always included the polder as a fixed effect. Final models are presented. F stat: F statistics, p: p-value, Std effect: standardized effect.*

	Field size			Polder		Seed density			Bare ground		
	F stat	*p*	Std effect	F stat	*p*	F stat	*p*	Std effect	F stat	*p*	Std effect
Bird abundance	1.32	0.262	0.126	0.88	0.426	7.35	**0.012**	0.140			
Species richness	0.08	0.781	0.04	0.25	0.778				4.99	**0.035**	-0.059

Over 90% of the wheat fields had been ploughed, and vegetation cover was sparse during the winter. In agreement with our second hypothesis, more birds were observed on wheat fields with higher seed densities. Interestingly, even at the survey plot scale, total bird abundance and species richness were positively related to the soil seed densities of the wheat fields. These findings are in line with those of other studies, which found foraging birds aggregating on fields with high seed densities (Donald et al., 2001a; Moorcroft et al., 2002; Robinson & Sutherland, 1999).

Soil seed densities were sampled only once, in February. Seed densities in soils have been shown to decrease during the winter, and depletion rates might differ between fields, with highest depletion rates in the fields most frequently visited by birds (Butler et al., 2005a; Robinson & Sutherland, 1999). As bird abundance and species richness were positively related to soil seed densities in February throughout the survey rounds, we suppose that soil seed densities in frequently visited fields were even higher at the beginning of the winter. Most fields had been ploughed before the first bird survey and were thus comparable in terms of cultivation practices during the winter.

The only individually analysed species whose abundance was positively related to seed densities was the starling, which however feeds mainly on invertebrates. Since starling abundances have been shown to be higher on organic farms than on conventional farms (Chamberlain et al., 2010), it is likely that starlings were also more abundant on the organic farms in our study. A possible explanation for the positive relation between starlings and seed densities found in this study is the higher starling abundance on organic fields, which comprise higher soil seed densities.

Effects of farm management on food abundance

Our finding that soil seed densities were higher in organically than in conventionally managed fields confirms our third hypothesis. Fields on organic farms contained on average more than 2500 seeds m^{-2}, compared to just 200 seeds m^{-2} on conventional fields. On the other hand, we also found that seed densities on organic farms were decreased by frequent mechanical weeding, which may have reduced the probability of seed setting for various weed species (Andreasen & Stryhn, 2008). The effects of other farming practices on food abundance for wintering birds remained unclear. Pesticides and artificial fertilizers were used almost consistently on conventional farms and not on organic farms. Single effects of artificial fertilizer and some pesticides were negatively related to soil seed density. However, when farm type was considered in the analyses (i.e. included as a fixed effect), none of the farming practices proved to be related to seed density anymore. Furthermore, when conventional farms alone were included in the analyses, none of the farming practices were related to seed density. This implies either that the difference in seed densities between the two farm types was due to the difference between use or no use of pesticides and artificial fertilizers, or that an ad-

Table 5.5 *Explanatory variables were tested for differences between farm types (organic vs. conventional) using nonparametric Mann-Whitney U tests. Differences between the two farm types in terms of field cover types (survey plot scale) were tested using generalized linear mixed models with repeated measures including farm type as a fixed effect. No. of applications: number of applications, amount of a.i.: amount of active ingredients, Sign.: significance levels are shown: ns for p > 0.05, * for p < 0.05, ** for p < 0.01, *** for p < 0.001.*

		Organic		**Conventional**		
		Mean	**(stdev)**	**Mean**	**(stdev)**	**Sign.**
	Field size (ha)	7.7	(4.0)	10.9	(6.5)	ns
Farming practices (previous growing season)	Herbicide (no. of applications y^{-1})	0.0	(0.0)	1.8	(0.9)	***
	Herbicide (amount of a.i. y^{-1})	0.0	(0.0)	2.1	(1.2)	***
	Insecticide (no. of applications y^{-1})	0.0	(0.0)	0.7	(0.5)	***
	Insecticide (amount of a.i. y^{-1})	0.0	(0.0)	0.1	(0.1)	***
	Fungicide (no. of applications y^{-1})	0.0	(0.0)	1.3	(0.5)	***
	Fungicide (amount of a.i. y^{-1})	0.0	(0.0)	0.5	(0.3)	***
	Artificial fertilizer (kg N ha^{-1} y^{-1})	0.0	(0.0)	160.3	(50.8)	***
	Organic fertilizer (kg ha^{-1} y^{-1})	17503.3	(14971.7)	8336.0	(13816.3)	*
	Ploughing depth (m)	0.2	(0.0)	0.3	(0.1)	*
	Mechanical weed control (frequency y^{-1})	2.9	(2.4)	0.0	(0.0)	***
Landscape characteristics	Mean field size (ha)	28.3	(10.7)	31.0	(14.9)	ns
	Habitat diversity (Shannon diversity index)	0.4	(0.3)	0.5	(0.3)	ns
Food abundance and vegetation cover (field scale)	Soil seed density (m^{-2})	2527.1	(2447.1)	199.9	(179.8)	***
	Total weed biomass (g m^{-2})	4.2	(9.7)	2.0	(7.6)	**
	Grass biomass (g m^{-2})	3.1	(10.5)	2.7	(7.8)	*
	Dicotyledonous biomass (g m^{-2})	1.8	(4.4)	0.1	(0.2)	*
	Green manure biomass (g m^{-2})	2.3	(7.2)	0.1	(0.2)	ns
	Vegetation height (cm)	11.7	(14.5)	4.1	(5.0)	ns
	Total weed cover (%)	2.4	(3.6)	0.7	(1.4)	*
	Grass cover (%)	0.4	(0.5)	0.2	(0.4)	ns
	Dicotyledonous cover (%)	1.9	(3.5)	0.6	(1.3)	ns
	Green manure crop cover (%)	14.8	(32.8)	9.2	(26.1)	ns
	Bare ground (%)	79.3	(38.0)	90.5	(25.5)	ns
Field cover type (survey plot scale)	Bare ground (%)	68.7	(28.3)	70.5	(18.7)	ns
	Cereal stubble (%)	2.8	(7.4)	0.3	(2.0)	ns
	Winter cereals (%)	9.3	(10.4)	18.4	(17.2)	ns
	Green manure crops (%)	8.1	(17.2)	1.3	(5.3)	ns
	Permanent grassland (%)	4.7	(10.4)	1.2	(3.3)	*
	Grassy field margins (%)	0.5	(0.6)	0.5	(0.7)	ns

Table 5.6 *Mann-Whitney U tests were used to analyse differences in landscape characteristics between the three polders: Southern (SF), Eastern (EF) and Northeastern Flevoland (NEF). Mean field size and habitat diversity were measured within 500m-radius circles around bird survey plot centres. Asterisks indicate significant differences relative to Eastern Flevoland.*

	NEF		**EF**		**SEF**	
	Mean	**(stdev)**	**Mean**	**(stdev)**	**Mean**	**(stdev)**
Mean field size (ha)	19.89*	(0.44)	23.73	(0.30)	45.37*	(0.61)
Habitat diversity	0.44	(0.28)	0.30	(0.22)	0.61*	(0.40)

ditive effect of the use of artificial fertilizer and pesticides resulted in lower soil seed densities on conventional farms. Another plausible explanation is that seed densities are mainly influenced by post-harvest operations on farmland (Moreby & Southway, 1999; Robinson & Sutherland, 1999; Wilson et al., 1999). Thus, it remains difficult to determine which of the farming practices was decisive as regards the higher seed densities on organic farmland.

Previous work has shown that fields under non-inversion tillage supported more birds than fields under conventional ploughing regimes, possibly due to higher seed densities (Cunningham et al., 2005; Field et al., 2007a). In the present study, ploughing to depths ranging from 0.18 to 0.47 m during the crop growing season had no effect on soil seed densities in February. However, the reduced seed densities due to deep tillage (1.2 m) in autumn on one of the organic fields illustrates the huge impact that tillage operations may have on seed availability for wintering birds.

Moorcroft et al. (2002) rarely found linnets or reed buntings in stubble fields with less than 250 dietary seeds m^{-2} in the upper 3 mm of arable soils. In our study, average soil seed densities in February even in the upper 10 mm of conventional fields fell below this threshold, implying food shortage on these fields for purely seed-eating species. Although Diaz & Telleria (1994) found no relation between bird abundance and seed densities in an area with sufficient seed supply, the scarcity of food might account for the strong positive relation between seed densities and bird abundance found in our and other studies (Robinson et al., 2004). As about 92% of the arable land in Flevoland is cultivated conventionally (CBS, 2010), much of the agricultural land in this province might not provide sufficient food for birds in late winter.

Population declines of several species have been shown to be related to high winter mortality due to food shortage (Peach et al., 1999; Siriwardena et al., 2008). Moreover, previous work has shown that providing supplementary food in winter may positively influence population developments (Robb et al., 2008; Siriwardena et al., 2007). We therefore conclude that food shortage in winter might be a bottleneck for birds foraging on farmland. At a local scale, agri-environment schemes, such as the provision of cereal stubble or field margins with seed-bearing crops, might increase the food supply for wintering farmland birds (Henderson et al., 2004b; Perkins et al., 2008). However, to increase food availability in winter at a larger scale, which is probably necessary to support bird populations (Gillings et al., 2005; Siriwardena et al., 2008), farm management that enhances food availability in winter should be encouraged. This might include the further expansion of organic farming with reduced pesticide use (Bradbury et al., 2008; Chamberlain et al., 2010; Wilson et al., 1996) and shallow or non-inversion tillage (Cunningham et al., 2005; Cunningham et al., 2004).

Acknowledgements

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Chapter 6

Boundary characteristics, vegetation cover and food abundance determine habitat selection by wintering skylarks (*Alauda arvensis*)

Flavia Geiger, Maurits Gleichman, Heiner Flinks, Geert R. de Snoo, Sebastian Prinz, Arne Hegemann, B. Irene Tieleman, Frank Berendse

Abstract

In recent decades, skylark populations in Europe have declined sharply due to agricultural intensification. The two main proximate reasons for the decline are an insufficient reproduction rate and an increased winter mortality. Research so far focused mainly on the breeding ecology of skylarks. Research in winter is generally scarce and mostly limited to the UK. Yet, little is known about the habitat selection and diet of skylarks wintering on farmland. This study investigated what habitat characteristics (field and boundary characteristics, vegetation cover and food abundance) influence field selection by foraging skylarks in winter. Moreover, skylark diet based on faecal contents was analysed in relation to season and foraging habitat. Skylarks wintering in a Dutch agricultural region were surveyed nine times between November and March. Simultaneously, food abundance (flying and ground-dwelling invertebrates, soil seed density and weed cover) was estimated on 35 arable fields and permanent grasslands. Skylarks avoided fields with tall boundary vegetation, and 90% of all groups were observed on fields larger than 4.3 ha. Skylarks preferred cereal stubble fields and fields with high densities of dietary seeds. Skylark group densities were low on permanent grasslands and on maize fields. At the end of the winter, skylarks selected larger fields and fields with taller vegetation. We analysed the contents of 158 faecal pellets collected on potato and cereal fields. Faeces collected on potato fields contained more seeds of dicotyledonous weed species, while faeces collected on cereal fields contained more cereal grains. The proportion of grains in the diet of skylarks fell sharply at the end of November, indicating that birds had to switch to less energy-rich food sources, such as weed seeds and leaves. The proportion of invertebrates in the diet was positively related to temperature, but remained of minor importance throughout the winter. We conclude that field selection by foraging skylarks in winter is affected by field and boundary characteristics (potential predator avoidance), as well as food abundance (energy intake). Therefore, conservation measures in winter, such as food provision by over-winter stubbles, should be concentrated on fields situated in open landscapes.

Introduction

In western Europe, agricultural landscapes have been altered by agricultural intensification in the last century (Stoate et al., 2009; Stoate et al., 2001). In the same period, populations of many farmland birds have declined (Benton et al., 2002; Donald et al., 2001c; van Dijk et al., 2010). The skylark (*Alauda arvensis*) is a typical farmland bird that has suffered from changes in agricultural practices and whose populations have been decreasing sharply. In the Netherlands, breeding populations dropped by almost 95% since the 1970s (van Dijk et al., 2009).

Insufficient reproduction rates and increased winter mortality are main proximate reasons for population declines of skylarks (Chamberlain & Crick, 1999; Newton, 2004; Siriwardena et al., 2008; Willems et al., 2008). Reasons for a decreased reproductive success are well studied in the UK (e.g. Chamberlain et al., 1999; Donald et al., 2001b; Donald et al., 2001c; Field et al., 2007b; Henderson et al., 2001) and received attention as well in other countries (e.g. Jenny, 1990; Kragten et al., 2008; Ottens et al., 2003; Willems et al., 2008). In contrary, research about wintering skylarks (e.g. Donald et al., 2001a; Gillings & Fuller, 2001; Wakeham-Dawson & Aebischer, 1998) and their diet (Donald et al., 2001a; Green, 1978) is mainly limited to the UK and yet, little is known about skylark winter ecology in other parts of Europe.

The Dutch breeding population of skylarks consists of partial migrants and locally wintering birds are additionally accompanied during the wintering months by birds from more northern and eastern populations (Hegemann et al., 2010). Thus, the Netherlands serve as wintering grounds for different populations and wintering conditions are not only important for the Dutch breeding population itself, but also for birds from a wide geographical range.

Insight in the habitat selection of foraging skylarks in relation to energy intake and expenditure can help to understand the factors that determine winter mortality and to improve conservation measures taken on their wintering grounds.

During habitat selection, birds experience a trade-off between minimizing predation risk and maximizing energy intake (Butler et al., 2005b; Erichsen et al., 1980; Lima & Dill, 1990). Habitat characteristics that optimize this trade-off are likely to be preferred by foraging birds (Butler et al., 2005b). Predation risk is minimized by an early detection of predators, as well as optimal shelter preventing the discovery by predators (Lima & Dill, 1990). Therefore, the vegetation structure of foraging habitats and their boundaries largely influences the risk of predation (Donald et al., 2001a; Lazarus & Symonds, 1992; Lima & Dill, 1990).

Energy intake depends on a species' diet composition and on food availability, i.e. food abundance and accessibility. Food accessibility and thus searching time are influenced by the vegetation structure within fields (Butler et al., 2005a; Whittingham et al., 2006). Hence, the selection of foraging habitats is likely to depend on field and boundary characteristics, within-field vegetation structure and food abundance.

The diet of many bird species changes between seasons due to the availability of different food types (Diaz, 1996). While skylarks feed mainly on invertebrates during the breeding season, they switch to cereal grains, weed seeds and plant leaves in winter (Green, 1978). Variation in the availability of different food types in time and space is likely to determine not only habitat selection, but also the composition of the diet (Donald et al., 2001a; Robinson, 2004). Green (1978), for example, showed that the proportion of cereal grains in the diet of skylarks was primarily correlated with the availability of grains (estimated on the basis of the area under cereal stubbles and sowings).

In this study, we investigated whether field selection by skylarks wintering in an agricultural region in the northern Netherlands was influenced by field and boundary characteristics, within-field vegetation structure or food abundance. In addition, we examined the characteristics of winter foraging habitats for skylarks regarding these three aspects. Finally, we analysed the contents of skylark faeces to investigate their winter diet in relation to seasonal differences and to foraging habitat.

Materials and methods

Study area

The study area was situated on the border of the provinces Drenthe and Friesland in the northern Netherlands (N 52°57', E 6°19'). Within an area of about 130 km^2, we selected 10 survey plots ranging from 35 to 75 ha and covering in total 480 ha (Table 6.1). The 10 survey plots comprised in total 77 different arable fields and permanent grasslands. Selection criteria ensured that the survey plots included at least six replicates of former cereal, former potato and former maize fields (referred to below as cereal, potato and maize fields), and permanent grasslands.

Bird surveys

Birds were surveyed nine times between the first week of November 2008 and mid-March 2009. Surveys were repeated every two to three weeks and done between one hour after sunrise and one hour before dusk. Rainy, windy and foggy weather was avoided. The order in which the survey plots were visited alternated at each survey round to minimize time of day effects. All fields within survey plots were walked zigzag and bird observations were mapped. We marked landing positions of flushed birds in maps to prevent double counting.

Table 6.1 *Field characteristics are listed per crop type: cereal fields; potato fields; maize fields; grasslands; and unknown former crop, i.e. at the time of the surveys covered by green manure crops. Number of fields (no. fields); total area; number of fields occupied by skylarks at least once during the survey rounds (no. of fields occupied); mean skylark group density averaged over all survey rounds; mean, standard deviation (stdev) and range of the field size; mean, standard deviation (stdev) and range of the field boundary index.*

	Cereals	**Potato**	**Maize**	**Grassland**	**Unknown**	**Total**
No. fields	22	20	15	18	2	77
Total area (ha)	153.2	137.4	96.8	63.6	29.2	480.3
No. of fields occupied (%)	17 (77)	12 (60)	11 (73)	2 (11)	1 (50)	43 (56)
Skylark group density (ha^{-1})	0.121	0.063	0.054	0.005	0.067	0.070
Field size						
Mean (ha)	6.97	6.87	6.05	3.53	14.61	6.24
Stdev (ha)	4.38	4.12	2.67	2.22	7.40	4.06
Range (ha)	0.4 - 16.9	0.6 - 14.1	2.3 - 13.4	0.5 - 10.1	9.4 - 19.8	0.4 - 19.8
Field boundary index						
Mean	1.09	0.91	1.14	1.18	0.00	1.03
Stdev	1.06	1.01	1.39	0.78	0.00	1.05
Range	0 - 4.38	0 - 3.07	0 - 3.82	0 - 2.77	0 - 0	0 - 4.38

Field and boundary characteristics

Field size and perimeter-to-area ratio of all fields within the survey plots were estimated using GPS. All vertical objects along the field boundaries were mapped in the field. Object length was measured using ArcGIS 9 (ESRI Inc.) and object height was estimated in the field. A field boundary index was calculated similar to the one developed by Wilson et al. (1997). The perimeter of each field was divided into sections according to different categories of boundary objects: 0, no vertical structure; 1, fences with poles (< 1m high); 2, low vegetation (< 2m high); 3, medium vegetation (2-5m high); 4, high vegetation (tree rows and single large trees, > 5m high); 5, forest. The length of each object type was multiplied by its object score (0-5), summed and divided by the field perimeter. This resulted in a field boundary index for each field ranging from 0 (no vertical structure) to 5 (surrounded by forest).

Food abundance and vegetation cover

To relate food abundance to bird presence, food sampling was conducted at the same day as the bird surveys had taken place. Food abundance was sampled on six fields of each of the following four field types: potato, cereal, maize, and permanent grassland. The six fields of each type were distributed across six of the 10 survey plots. We extrapolated data about food abundance and vegetation cover from measured fields to adjacent fields if they were cultivated in the same way. In total, food and vegetation cover data was available for 24 sampled and 11 adjacent fields.

Vegetation cover and height, invertebrate biomass, and soil seed densities were sampled within three sampling plots of 1×2 m. These plots were selected 5 m distant from each other out at a distance of approximately 10 m from one of the field borders. The location of the sampling plot was different at each sampling round to prevent overlap of soil sampling.

Vegetation cover was estimated for each of the following vegetation types: total weed cover; grassy weed cover; dicotyledonous weed cover; cereal, potato or maize stubbles, respectively; winter cereals; volunteer cereals; and bare ground. In addition, the height of the tallest plant within a sampling plot was measured.

Invertebrates were caught during 24 h with one pitfall and one sticky trap per sampling plot. Pitfall traps had a diameter of 90 mm and were filled with 4% formaldehyde. Invertebrates were fixed in 70% ethanol and identified to suborder (Hymenoptera, Diptera) or family level (Coleoptera). Sticky traps (Pherobank ®, 100×210 mm, excluding margins) were placed on a stick, at about 50 cm height (Kragten et al., 2010). Invertebrates on both sides of the sticky traps were identified to order, suborder (Hymenoptera, Diptera, Araneae) or family level (Coleoptera). Lengths of all invertebrates were measured with a digital caliper and invertebrate biomass (dry weight) was calculated using the regression equations and parameter estimations of Hodar (1996).

Soil seed densities were estimated by taking 10 soil samples per sampling plot with a bulb planter (60 mm diameter). Samples were taken to a depth of 10 mm, as seeds up to this depth were potentially available for foraging skylarks. The 10 sub-samples were mixed into a composite sample. Soil samples were stored at 4°C before processing to prevent seed germination. The soil was sieved through two sieves with mesh widths of 1 and 0.5 mm, respectively. These mesh sizes ensured that the majority of seeds taken by skylarks were caught (Green, 1978). The remainder from sieving (e.g. seeds, small stones, vegetation remnants) was dried (48 h, 70°C) and sorted by hand. Weed seeds were identified to species level and counted. All or a maximum of 25 seeds per species were weighted to derive average seed weights per species.

Only seed species that were found in the faeces and seeds of *Ranunculus* sp., *Lamium* sp. and *Digitaria* sp., described as Skylark diet by Cramp et al. (1988), were included in the analyses. As seed densities and seed weights were strongly correlated (Pearson correlation coefficient = 0.88), only seed densities were used for further analyses. Food abundance and vegetation cover were averaged over the three sampling plots within one field for further analyses.

Analysis of skylark faeces

During the bird surveys, faeces were collected at locations where foraging skylarks had been observed. Faecal pellets were mixed with some table salt to prevent mouldering and subsequently frozen. On both cereal and potato fields, 8 to 12 faecal pellets were analysed per survey round, except for the last one. A total of 158 faecal pellets, 80 from cereal fields and 78 from potato fields, were analysed. Droppings were dispersed by soaking them in water for 30 min and then analysed under a binocular microscope (20× magnification). Invertebrate remains were used to assess the minimum number of invertebrate individuals in the faeces. Invertebrate length was estimated using a reference collection and information from literature (Calver & Wooller, 1982; Flinks & Pfeifer, 1987; Jenni et al., 1990; Ralph et al., 1985). The quantity of ingested plant remains (epidermis of leaves or testa) was measured using a millimetre screen. The number of ingested seeds was estimated by dividing the measured area of the remains (seed coat) of the ingested seeds by the estimated surface of the reference seeds. If the ingested plant remains could not be identified by direct comparison with the reference collection, they were compared with other reference plant material under a microscope at 100 to 400 × magnification (Rogers & Gorman, 1995).

The dry weight composition of faecal pellets was calculated for the following food types using correction factors estimated by Green (1978): invertebrates; cereal grains; dicotyledonous seeds (including fruit inflorescence and flowers); monocotyledonous seeds (including fruit inflorescence and flowers); dicotyledonous leaves; and monocotyledonous leaves. Four faecal pellets collected on potato fields contained potato tuber remains, four faecal pellets collected on cereal fields contained bryophytes and two contained dicotyledonous fruits. Green (1978) does not give correction factors for these food types. As the area of bryophytes in the faeces was relatively low (< 3.5%), it was neglected. The other six samples containing tuber and fruit remains were excluded from further analyses.

Data availability

Pitfall trapping and the use of sticky traps were hampered by grazing animals and low temperatures. No sticky traps and pitfalls were placed when cows or sheep were grazing. Furthermore, frozen soil in the beginning of January prevented digging pitfalls into the ground. At both sampling periods in January the glue of the sticky traps was frozen and did not stick anymore. Moreover, frozen soil in the beginning of January prevented the collection of soil samples. In total, data from 228 sticky traps and 259 pitfall traps, as well as soil samples, were included in the analyses.

Statistics

As skylarks often forage in large flocks in winter, we assumed that groups of skylarks and not individual birds were distributed randomly across fields (Cramp et al., 1988; Donald et al., 2001a). Therefore, skylark group density was used as response variable.

To investigate which variables were associated with field selection by wintering skylarks, firstly, we analyzed separately the effects of field and boundary characteristics, food abundance, and vegetation cover on the density of skylark groups. In a second step, all variables were combined in one single analysis.

Effects of field and boundary characteristics (i.e. field size, perimeter-to-area ratio, field boundary index) and their interactions with survey round were investigated using generalized linear mixed models (GLMM) with repeated measures and the method of residual maximum likelihood in GenStat 12.1 (Payne et al., 2008). Fields nested within survey plots were included as random effect. Forward selection was applied to select variables significantly affecting skylark group density. This was done starting with an empty model and including at each following step the variable with the most significant effect based on Wald tests ($p < 0.05$). This procedure was reiterated until variables no longer added significant effects to the model. The selection of two strongly correlated explanatory variables (Pearson correlation > 0.7, see Appendix Table 6.6) within one model was prevented. This was done by including only the most significant variable and subsequently excluding correlated variables from the forward selection. The variables that significantly affected skylark group density in this analysis were included as fixed effects in subsequent analyses to account for influences of field and boundary characteristics on field selection by skylarks.

Next, we analysed whether the skylark group density was related to food abundance, including interactions between food abundance and survey round. In this analysis, only the 35 fields, for which data about food abundance was available, were included. We used repeated measures in GLMM and forward selection as described above, including eight food variables (Table 6.2). Firstly, effects of biomass of flying and ground-dwelling invertebrates on skylark group density was analysed excluding one or both sampling rounds in January, respectively, as data about invertebrate biomass was missing for these sampling rounds (see *Data availability*). If there was a significant relation between invertebrate biomass and skylark group density, further analyses were done with the reduced dataset. If there was no significant relation, all sampling rounds were included in the analyses to test the effects of other (food) variables on skylark groups.

Table 6.2 *Differences of response and explanatory variables between crop types were analysed using GLMM with repeated measures. F statistics (F) and p-values (p) are listed. Fields nested within survey plots were included as random effect. The first survey round in January was excluded from the analyses (except for [a,b]) due to missing data. Categories (Cat) of field and boundary (fb), food (f) and vegetation cover (c) variables and mean values per crop type are given. [a] All surveyed fields are included. [b] Both January survey rounds are excluded.*

Variable	**Cat**	***F***	***p***	**Cereal**	**Potato**	**Maize**	**Grassland**
Skylark group density (ha^{-1})[a]		12.26	<0.001	0.12	0.06	0.06	0.00
Field boundary index[a]	fb	16.19	<0.001	6.97	6.87	6.45	3.53
Perimeter-to-area ratio[a]	fb	26.96	<0.001	2.34	2.36	2.27	2.44
Field size (ha)[a]	fb	51.22	<0.001	1.04	0.91	1.14	1.18
Bare ground (%)	c	465.70	<0.001	76.48	91.93	89.78	5.43
Cereal stubbles (%)	c	81.20	<0.001	10.29	0.00	0.00	0.00
Volunteer cereals (%)	f/c	28.53	<0.001	4.34	0.00	0.00	0.00
Maize stubbles (%)	c	20.13	<0.001	0.00	0.00	8.21	0.00
Potato stubbles (%)	c	161.82	<0.001	0.00	3.00	0.00	0.00
Total weed cover (%)	f/c	1011.77	<0.001	8.20	6.06	1.43	92.71
Dicotyledonous weeds (%)	f/c	29.72	<0.001	2.34	2.49	1.17	12.20
Grassy weeds (%)	f/c	893.35	<0.001	6.34	3.67	0.43	82.16
Winter cereals (%)	f/c	58.42	<0.001	0.00	0.00	2.13	0.00
Seed density (m^{-2})	f/c	30.70	<0.001	1757.25	4609.18	1163.21	1332.19
Vegetation height (cm)	c	72.93	<0.001	16.80	4.17	9.95	11.27
Flying invertebrates (mg $trap^{-1}$)[b]	f	1.75	0.158	4.95	2.81	3.33	5.38
Ground-dwelling invertebrates (mg $trap^{-1}$)	f	46.93	<0.001	9.15	5.36	4.48	26.49

The effects of vegetation cover and height and their interaction with survey round on wintering skylarks were examined in the same way as the latter analysis, but instead of food related variables, 11 vegetation cover variables were used for the forward selection procedure (Table 6.2).

Finally, the effects of field and boundary, as well as food and vegetation cover variables and their interaction with survey round on skylark groups were similarly analysed in one analysis. At first, the previously selected field and boundary variables were included in the model. Then, forward selection using all food and cover variables was applied.

Significant interactions between explanatory variables and survey round were further investigated by analysing the effect of the respective explanatory variable on skylark group density per survey round. This was done using GLMM, fields nested within survey plots as a random effect and the explanatory variable as a fixed effect.

To test for relations between season, foraging habitat and skylark diet, the effects of survey round, temperature and crop type on skylark diet were examined. Single effects of crop type, survey round and mean temperature (of the three days preceding the collection of the faeces) were analyzed on the proportion of dry weight of different food types in the skylark faeces. Temperature data were available from a weather station approximately 20 km distant from the study area (Hoogeveen, Dutch national weather station KNMI). GLMM with repeated measures were applied, including survey plot, survey round and crop type (for the analyses regarding the effects of survey round and temperature) as random effects.

Results

More than half of the in total 77 fields and 23 of the 35 fields, where food abundance and vegetation cover was available, were occupied by skylarks at least once during the bird surveys (Table 6.1). In total, more than 2000 skylarks assembled in 304 groups were observed during the nine survey rounds. On fields, where food was sampled, 1107 skylarks and 153 groups were counted (Fig. 6.1).

Food abundance on sampled fields

The most abundant invertebrate groups caught with sticky traps, referred to below as flying invertebrates, were from the orders Brachycera (83%) and Nematocera (7%). Biomass of flying invertebrates differed significantly between survey rounds, with highest biomass in the first round and lower biomass in subsequent rounds ($F = 212.8$, $p < 0.001$). Almost no flying invertebrates were caught between the beginning of December and late February.

Coleoptera larvae, including 38% Carabidae and 12% Staphylinidae, accounted for more than half of the invertebrate biomass caught in pitfall traps, referred to below as ground-dwelling invertebrates. Coleoptera imagos accounted for 22% of the biomass in pitfalls and Diptera for 13%. Biomass of ground-dwelling invertebrates differed significantly between crop types, with highest biomass caught in grassland (Table 6.2). Biomass of ground-dwelling invertebrates differed also significantly between survey rounds and was highest in the first survey round and subsequently lower, but increased again slightly at the end of the winter ($F = 17.8$, $p < 0.001$).

The most abundant seed species including all seeds found in the soil samples belonged to the family Chenopodiaceae (44%), followed by *Poa annua* (12%), *Stellaria media* (9%), *Solanum* sp. (9%) and *Polygonum persicaria* (7%), all of which were part of the skylark diet. Cereal grains accounted for less than 0.1% of the sampled seeds. Average densities of seeds belonging to the diet of skylarks declined significantly in grasslands, while densities in potato fields declined almost significantly ($F = 14.89$, $p < 0.001$ and $F = 3.45$, $p = 0.063$, respectively). Soil seed densities on maize fields increased in the course of the winter ($F = 13.32$, $p < 0.001$), while it did not change significantly on cereal fields ($F = 0.45$, $p = 0.503$).

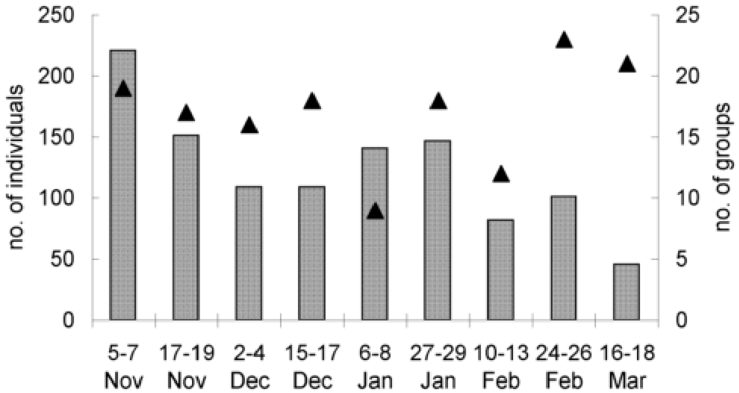

Figure 6.1 *Skylark numbers (grey bars, primary y-axis) and numbers of skylark groups (black triangles, secondary y-axis) per survey round. The figure includes only skylarks observed on fields for which data about food abundance and vegetation cover was available.*

Table 6.3 *Effects of field and boundary characteristics on skylark group density. Generalized linear mixed models (GLMM) with repeated measures including fields nested within survey plots as random effect were applied. Forward selection of field and boundary variables (see Table 6.2) resulted in the presented model. F statistics (F), p-values (p) and standardized effects (β) are listed. Effects of field size on skylark group density were analysed per survey round applying GLMM.*

Variable	***F***	***p***	***β***
Survey round	2.95	**0.003**	
Field size	2.30	0.130	-0.010
Survey round* field size	3.25	**0.001**	
Field size (5-7 Nov)	0.25	0.620	-0.007
Field size (17-19 Nov)	0.01	0.907	0.002
Field size (2-4 Dec)	0.44	0.507	-0.009
Field size (15-17 Dec)	1.12	0.294	-0.019
Field size (6-8 Jan)	0.26	0.610	-0.005
Field size (27-29 Jan)	3.15	0.080	0.020
Field size (10-13 Feb)	1.41	0.238	0.017
Field size (24-26 Feb)	10.20	**0.002**	0.057
Field size (16-18 Mar)	4.64	**0.031**	0.055
Field boundary index	8.31	**0.004**	-0.019

Habitat selection

Skylark group densities differed significantly between fields of different crop types (Table 6.2). Densities were highest on cereal fields and lowest on permanent grasslands.

To investigate the selection of foraging habitats by wintering skylarks, the effects of field and boundary characteristics, food abundance and vegetation cover on the density of skylark groups were analyzed separately, as well as simultaneously.

First, we analysed the effects of field and boundary characteristics on skylark group density. The interaction between field size and survey round had the strongest single effect, followed by the field boundary index (Appendix Table 6.7). Skylark group density was only significantly positively related to field size in the last two survey rounds (Table 6.3). Skylark group density was negatively related to the field boundary index. The smallest field occupied by skylarks was 1.8 ha in size and 90% of the skylark groups were observed on fields larger than 4.3 ha. The highest field boundary index of occupied fields was 3.7 and 90% of all skylark groups were found on fields with a boundary index smaller than 1.5. Such a value can be interpreted as for example a field with a forest along a third of its perimeter.

Secondly, we investigated relations between the density of skylark groups and food abundance. As single effects of the biomass of ground-dwelling invertebrates significantly affected skylark group density (Appendix Table 6.7), all further analyses were performed without the first survey round in January. Skylark group density was positively related to the interaction between the cover of volunteer cereals and survey round and negatively to the biomass of ground-dwelling invertebrates (Appendix Table 6.8). Density of skylark groups was positively related to the cover of volunteer cereals in mid-December and late-February.

Next, we analysed the effects of vegetation cover on skylarks. Skylark group density was negatively related to the vegetation height in early November, but positively from February onwards (Table 6.4). On average, vegetation was tallest on cereal fields and shortest on potato fields (Table 6.2). Additionally, skylarks were negatively related to maize stubbles and total weed cover. Total weed cover was highest on grasslands with on average more than 93% in comparison to 8%, 6% and 1% on cereal, potato and maize fields, respectively (Table 6.2). Weed cover was no longer significantly related to skylark group density when grassland was excluded from the analysis ($F = 1.45$, $p = 0.231$). The effect of volunteer cereals differed between survey rounds. Finally, skylark group density was positively related to cereal stubbles.

Simultaneous investigation of all explanatory variables resulted in a model including the same cover variables as described above and additionally seed density, which positively affected skylark group density (Table 6.4). 90% of the skylark groups were observed on fields with more than 860 dietary seeds m^{-2} (Fig. 6.2). Densities of di-

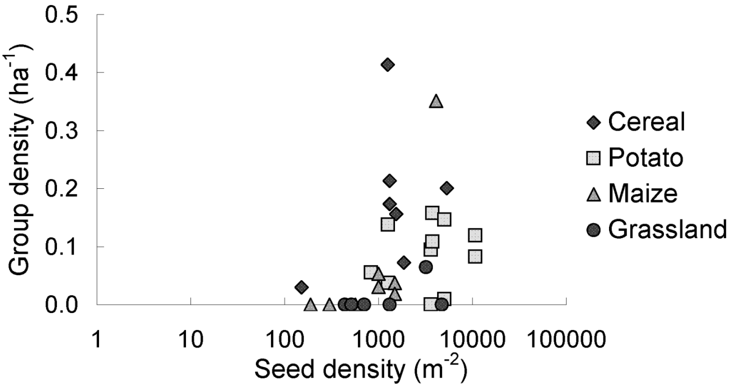

Figure 6.2 *Relation between the density of dietary seeds (m^{-2}, log-scale) and skylark group density (ha^{-1}) averaged over all survey rounds.*

Table 6.4 *Effects of field and boundary characteristics, vegetation cover and food abundance on skylark group density. Generalized linear mixed models (GLMM) with repeated measures including fields nested within survey plots as random effect were applied. Field and boundary variables were included a priori. Forward selection of cover variables (see Table 6.2) resulted in the presented model excluding seed density (below dashed line). Forward selection including all explanatory variables resulted in the presented model (including seed density). F statistics (F), p-values (p) and standardized effects (β) are listed. Effects of vegetation height and volunteer cereals on skylark group density were analysed per survey round applying GLMM.*

Variable		***F***	***p***	***β***
Survey round		0.45	0.870	
Field size		3.25	0.074	-0.017
Survey round* field size		0.60	0.755	
Field boundary index		6.31	**0.014**	-0.024
Vegetation height		5.89	**0.016**	-0.055
Survey round* Vegetation height		5.08	**<0.001**	
	Vegetation height (5-7 Nov)	7.90	**0.005**	-0.059
	Vegetation height (17-19 Nov)	0.07	0.793	0.007
	Vegetation height (2-4 Dec)	0.01	0.926	-0.002
	Vegetation height (15-17 Dec)	0.76	0.389	0.025
	Vegetation height (27-29 Jan)	0.02	0.886	-0.004
	Vegetation height (10-13 Feb)	6.65	**0.016**	0.090
	Vegetation height (24-26 Feb)	3.81	**0.061**	0.057
	Vegetation height (16-18 Mar)	7.10	**0.012**	0.115
Maize stubble		14.94	**<0.001**	-0.035
Total weed cover		14.29	**<0.001**	-0.051
Volunteer cereal		0.20	0.655	-0.032
Survey round* Volunteer cereal		2.65	**0.012**	
	Volunteer cereal (5-7 Nov)	0.45	0.504	-0.011
	Volunteer cereal (17-19 Nov)	1.08	0.309	0.033
	Volunteer cereal (2-4 Dec)	5.31	**0.021**	0.068
	Volunteer cereal (15-17 Dec)	3.31	0.080	0.085
	Volunteer cereal (27-29 Jan)	0.13	0.718	-0.011
	Volunteer cereal (10-13 Feb)	17.84	**<0.001**	-0.273
	Volunteer cereal (24-26 Feb)	0.27	0.606	-0.065
	Volunteer cereal (16-18 Mar)	3.32	0.080	-0.211
Cereal stubble		6.56	**0.011**	0.042
Seed density		7.36	**0.007**	0.031

etary seeds were highest in soils of potato fields followed by cereal fields, grasslands and maize fields (Table 6.2).

Neither field size nor its interaction with survey round was related to skylark group density in the dataset including only the 35 fields, for which food data was available.

Skylark diet (faecal analysis)

The skylark diet was analysed based on the content of faeces collected throughout the winter on potato and cereal fields. The most frequent food types found in faeces col-

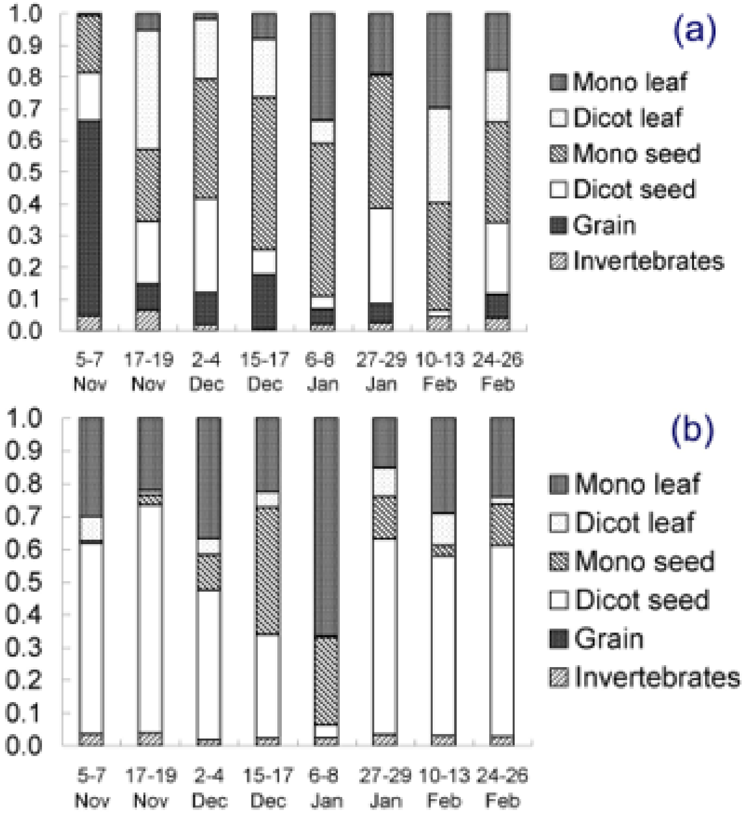

Figure 6.3 *Average proportion of different food types in skylark faeces collected on former (a) cereal and (b) potato fields: mono leaf: monocotyledonous leaf; dicot leaf: dicotyledonous leaf; mono seed: monocotyledonous seed, including flowers and fruit inflorescence; dicot seed: dicotyledonous seed, including flowers and fruit inflorescence; cereal grains and invertebrates.*

Table 6.5 *Single effects of crop type (potato and cereal), temperature (mean of the 3 days preceding faeces collection) and survey round on the proportion of different food types in faecal pellets: invertebrates; dicotyledonous leaves (dicot leaf); dicotyledonous seeds, fruit inflorescence and flowers (dicot seed); cereal grains; monocotyledonous leaves (mono leaf); monocotyledonous seeds, fruit inflorescence and flowers (mono seed). Generalized linear mixed models with repeated measures were applied, including survey plot, survey round and crop type (for the analyses regarding the effects of survey round and temperature) as random effects. F statistics (F), p-value (p) and standardized effects (β) are listed. Mean proportions of the different food types in skylark faeces are given per crop type (cereal and potato).*

	Variable	***F***	***p***	$\boldsymbol{\beta}$	**Cereal**	**Potato**
Invertebrates	Crop type	0.2	0.641	0.014	0.03	0.03
	Temperature	10.2	**0.001**	0.010		
	Survey round	1.4	0.185			
Dicot leaf	Crop type	2.3	0.133	-0.130	0.16	0.05
	Temperature	0.0	0.945	-0.001		
	Survey round	1.2	0.353			
Dicot seed	Crop type	6.1	**0.016**	0.258	0.16	0.48
	Temperature	3.6	0.072	0.025		
	Survey round	2.3	0.090			
Grain	Crop type	14.9	**<0.001**	-0.215	0.14	0.00
	Temperature	3.3	0.082	0.017		
	Survey round	3.3	**0.035**			
Mono leaf	Crop type	4.1	0.063	0.181	0.15	0.30
	Temperature	3.1	0.090	-0.024		
	Survey round	1.6	0.187			
Mono seed	Crop type	0.7	0.399	-0.087	0.35	0.14
	Temperature	0.9	0.394	-0.013		
	Survey round	0.7	0.700			

lected on potato fields were seeds of *Atriplex* sp., present in 65% of the pellets, followed by leaves and seeds of *Poa annua* (58% and 35%, respectively), seeds of *Solanum* sp. (33%) and *Stellaria media* (32%). This reflects roughly the order in the abundance of seed species found in the soil samples. On cereal fields, seeds of *Atriplex* sp. were found in most of the faecal pellets (53%), too. Furthermore, 45% of the faecal pellets contained seeds of *Polygonum convolvulus*, 42% seeds of *Echinochloa crus-galli* and 40% cereal grains.

73% of all droppings contained a very low percentage (on average 3%) of small invertebrates ($\geq$ 5mm) (Fig. 6.3). The most important prey types were from the order Coleoptera (89% of all pellets) and Araneae (25%).

The contents of skylark faeces differed between the two habitat types, cereal and potato fields (Fig. 6.3). The proportion of dicotyledonous seeds was significantly higher in faecal pellets collected on potato fields, whereas the proportion of cereal grains was significantly higher in faeces collected on cereal fields (Table 6.5). Furthermore, the proportion of invertebrates in the faeces was positively related to temperature (Table 6.5). Only the proportion of cereal grains in the faeces was related to sampling round, i.e. its proportion was highest in the first sampling round and lower in subsequent rounds.

Discussion

Habitat selection by skylarks in winter

Habitat selection by skylarks was influenced by field and boundary characteristics, as well as vegetation cover and food abundance. Higher densities of skylark groups were observed on larger than on smaller fields only at the end of the winter. Yet, 90% of the skylark groups observed across the winter foraged on fields larger than 4.3 ha. A preference for large fields is also found in other studies (winter: Donald et al., 2001a; Gillings & Fuller, 2001; Robinson & Sutherland, 1999; summer: Wilson et al., 1997). Furthermore, skylarks avoided fields surrounded by high boundary vegetation. For 90% of the skylarks, the minimal distance to field borders without vertical objects was 11 m, to borders with small structures (poles, shrubs, single trees < 5m) 50 m and to forest edges 250 m (data not shown). Accordingly, skylarks showed a clear avoidance of high boundary vegetation, which might be explained by their predator avoidance strategy. Depending on a species' predator avoidance strategy, vegetation cover might be both protective and obstructive (Lima & Dill, 1990). In contrast to many other granivorous passerines that fly to protective cover after predator detection, the skylark is a cryptic species and avoids predation by crouching (Butler et al., 2005a). Vigilance of skylarks is likely to increase in the proximity of high field boundary vegetation, such as tree lines and forest edges, which obstruct their view (Lazarus & Symonds, 1992). Consequently, avoidance of large boundary structures saves time spent on vigilance (Lima & Dill, 1990) and increases the time available for foraging. Preference of skylarks for open areas with large fields and low boundary vegetation is supported by other studies (winter: Donald et al., 2001a; Robinson & Sutherland, 1999; summer: Berg & Pärt, 1994; Donald et al., 2001b).

Although dietary seeds were more abundant on potato fields and skylark group density was positively related to seed density, the average skylark group density was higher on cereal fields. As skylarks rely on crouching to avoid detection by a predator, the experienced predation risk on potato fields was possibly higher than on cereal fields. Potato fields contained more bare soil in contrast to cereal fields, which were mostly covered by stubbles. Skylarks have been shown to prefer some vegetation cover above bare soil and taller over shorter stubbles (Gillings & Fuller, 2001; Whittingham et al., 2006). In the present study, skylark numbers were positively related to cereal stubble cover, which is likely to offer suitable shelter, as is shown by other studies, too (Donald et al., 2001a; Gillings & Fuller, 2001). Particularly, at the end of the winter when birds started to behave territorially, they were more abundant in taller vegetation. While foraging skylarks have been shown to select fields with stubbles of approximately 15 cm in winter (Butler et al., 2005a; Whittingham et al., 2006), Kragten et al. (2008) found an optimal vegetation height of 20-50 cm during the breeding season. The results of these studies indicate that breeding skylarks might select even taller vegetation as foraging skylarks in winter, possibly as the former are less flexible in changing between habitats and more dependent on optimal shelter.

It remains unclear, why the relation between skylark group densities and volunteer cereals was inconsistent. A possible explanation might be that there was an interfering effect of vegetation height on volunteer cereals in the analyses, as vegetation height and volunteer cereals were weakly correlated.

Skylarks avoided maize fields and grasslands. Half of the maize fields and grasslands contained less than 860 seeds m^{-2}. On fields with seed densities below this threshold, skylark group density decreased rather clear and steep. On these fields, searching time may increase and consequently, energy intake rate may be reduced to a suboptimal level. Furthermore, in most grasslands, food was probably hardly accessible due to the dense vegetation impeding bird movement (Wakeham-Dawson & Aebischer, 1998; Whittingham & Markland, 2002). Both occasions, at which skylarks have been observed in grassland, was after grazing by sheep and cattle, respectively, which caused open areas in the grass sod. Moreover, as the average grassland size (3.5 ha) was smaller than the field size preferred by most skylarks (4.3 ha), grasslands might have been avoided because of their small size (Wakeham-Dawson & Aebischer, 1998). The combination of lower seed densities and the lack of suitable vegetation cover on maize fields, might explain the relatively low skylark group densities found on these fields.

Skylark diet

Analyses of faeces collected on potato and cereal fields revealed differences between the diet of skylarks foraging on the two field types. Cereal grains were only found in faeces collected on cereal fields. In the beginning of November, the proportion of cereal grains in the faeces was about 60%, but dropped below 20% in December and in subsequent months below 10%. Cereal grains were just found in three of the soil samples collected throughout the winter. Thus, despite the meagre cereal grain abundance in the soil samples, the grain content was relatively high in faeces collected at the beginning of November. A possible explanation might be that cereal grains were highly aggregated within fields and that skylarks have a strong preference for cereal grains. Nonetheless, as the proportion of grains in the skylark faeces declined sharply at the end of November, cereal grains on arable fields were probably depleted already at the beginning of the winter and birds had to switch to other food types.

Green (1978) found similar declines in the proportion of cereal grains in skylark faeces in the course of the winter. He compared the energy gain between skylarks feeding on weed seeds in ploughed fields, on cereal grains in stubble fields and sowings, and on wheat leaves in winter wheat fields. The metabolizable energy of weed seeds was highest with 3.71 kcal g^{-1}, compared to 3.49 kcal g^{-1} and 2.38 kcal g^{-1} of grains and wheat leaves, respectively. However, due to differences in size and feeding rates per food type, the metabolizable energy intake rate was highest for cereal grains with on average 7.29 cal s^{-1}, followed by weed seeds (0.83 cal s^{-1}) and wheat leaves (0.78 cal s^{-1}). Therefore, skylarks probably take cereal grains as long as they are available and switch only to other food types when grain supply is depleted (Green, 1978). As harvesting techniques have been improved and less grain is spilled, the composition of the diet of granivorous birds might have changed during the last decades (Wilson et al., 1999).

In the present study, dicotyledonous and monocotyledonous seeds were an important part of the skylark diet throughout the winter. A higher proportion of dicotyledonous seeds were eaten by skylarks foraging on potato compared to cereal fields. Remarkably, soil seed densities were on average higher on potato than on cereal fields. Moreover, seeds were possibly better accessible on potato fields due to a higher percentage of bare earth (Whittingham & Markland, 2002). Strikingly and on the contrary to studies that found seed depletion in soils of cereal stubble fields (Butler et al., 2005b; Moorcroft et al., 2002; Robinson & Sutherland, 1999), seed densities decreased significantly only in grasslands and slightly, but non-significant in potato fields. The marginal seed decline on potato fields coincides with the higher proportion of seeds eaten on these fields.

Interestingly, in early January when the soil was frozen and probably most seeds were unavailable for foraging birds, skylarks fed almost exclusively on monocotyledonous leaves and seeds. Both, leaves and seeds, were possibly taken from grassy weeds that had been setting seeds throughout the winter.

Invertebrates were of minor importance in the winter diet of skylarks. Similarly, Green (1978) found a very low proportion of invertebrates in the winter compared to the summer diet of skylarks. The higher proportion of invertebrates in the faecal samples during November and February, when temperatures were higher in comparison to the other winter months, might reflect a small but higher abundance and mobility of invertebrates.

Our findings suggest that skylarks roughly feed on the food types that are most abundant and most easily accessible in a certain habitat (Green, 1978; Robinson, 2004). As cereal grains, one of the most profitable food types in winter (Green, 1978), were already depleted by the end of November, weed seeds and leaves were the main component of the skylark diet. However, foraging on weed seeds increases searching time and reduces energy gain compared to foraging on cereal grains (Green, 1978). Therefore, birds wintering in Dutch agricultural landscapes possibly suffer from a lack of energy-rich food sources throughout the winter and might experience difficulties in meeting their daily energy requirements.

Conclusions

We conclude that field selection by foraging skylarks in winter is determined by a trade-off between maximizing energy intake and minimizing predation risk. Most skylarks have been observed on fields with characteristics that probably optimize this trade-off, i.e. field and boundary characteristics and within-field vegetation cover that reduce predation risk and high food abundance. Cereal stubble fields larger than 4.3 ha, surrounded by no or low boundary vegetation and a density of dietary seed species of more than 860 seeds m^{-2} were most suitable for wintering skylarks. Therefore, conservation measures targeted at wintering skylarks, such as over-winter stubble fields and additional seed supply, should be focused on large fields in open areas.

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Appendix

Table 6.6 *Correlations of food and cover variables. Variables include: % cover bare ground, % cover dicotyledonous weed cover (Dicot), % cover monocotyledonous weed cover (Monocot), % cover total weed (Total weed), % cover volunteer cereal, % cover winter cereals, % cover maize stubbles, % cover potato stubbles, % cover cereal stubbles, (log) soil seed density (m^{-2}), vegetation height (cm).*

	Ground-dw.inv	Bare ground	Dicot	Monocot	Total weed	Volunteer cereals	Winter cereals	Maize stubbles	Potato stubbles	Cereal stubbles	Seed density
Bare ground	-0.57										
Dicot	0.54	-0.54									
Monocot	0.57	**-0.93**	0.44								
Total weed	0.61	**-0.94**	0.60	**0.98**							
Volunteer cereals	0.04	-0.04	-0.03	-0.05	-0.05						
Winter cereals	-0.17	0.24	-0.13	-0.21	-0.21	-0.09					
Maize stubbles	-0.12	-0.10	-0.11	-0.13	-0.14	-0.06	-0.02				
Potato stubbles	-0.18	0.35	-0.17	-0.29	-0.30	-0.15	-0.20	-0.12			
Cereal stubbles	0.00	-0.01	-0.10	-0.15	-0.16	0.37	-0.12	-0.08	-0.20		
Seed density	-0.01	0.08	0.06	-0.10	-0.08	0.01	-0.30	-0.02	0.42	-0.04	
Vegetation height	0.14	-0.39	0.05	0.22	0.20	0.54	-0.10	0.37	-0.36	0.28	-0.06

Table 6.7 *Single effects of explanatory variables on skylark group density. Generalized linear mixed models with repeated measures were applied always including the interaction between field size and survey round (SR) and field boundary index as fixed effects (except a) and fields nested within survey plots as random effect. F statistics (F), p-values (p) and standardized effects (β) are listed. [a] All surveyed fields (n = 77) are included. [b] Both January survey rounds are excluded.*

Variable	***F***	***p***	**β**
Field size[a]	1.95	0.163	0.008
SR*Field size[a]	3.24	**0.001**	
Perimeter-to-area ratio[a]	0.93	0.335	-0.006
SR*Perimeter-to-area ratio[a]	1.18	0.306	
Field boundary index[a]	8.28	**0.004**	-0.019
SR*Field boundary index[a]	0.31	0.961	
Crop type	7.14	**<0.001**	
SR*Crop type	1.41	0.118	
Flying invertebrates[b]	1.07	0.303	-0.020
SR*Flying invertebrates[b]	1.40	0.217	
Ground-dw. invertebrates	5.13	**0.025**	-0.032
SR*Ground-dw. invertebrates	0.38	0.911	
Bare ground	0.36	0.546	0.008
SR*Bare ground	1.75	0.098	
Dicot weed	0.65	0.422	-0.010
SR*Dicot weed	0.46	0.862	
Monocot weed	3.88	0.050	-0.026
SR*Monocot weed	0.54	0.804	
Seed density	3.48	0.063	0.023
SR*Seed density	0.31	0.951	
Total weed	4.45	**0.037**	-0.029
SR*Total weed	0.58	0.768	
Vegetation height	4.42	**0.037**	0.022
SR*Vegetation height	4.48	**<0.001**	
Cereal stubbles	5.35	**0.022**	0.028
SR*Cereal stubbles	4.48	**<0.001**	
Maize stubbles	0.73	0.394	-0.010
SR*Maize stubbles	0.40	0.902	
Potato stubbles	0.86	0.354	-0.011
SR*Potato stubbles	2.25	**0.031**	
Winter cereals	0.02	0.899	-0.001
SR*Winter cereals	0.48	0.822	
Volunteer cereals	4.72	**0.031**	0.023
SR*Volunteer cereals	3.19	**0.003**	

Table 6.8 *Effects of food abundance on skylark group density. Generalized linear mixed models (GLMM) with repeated measures including fields nested within survey plots as random effect were applied. Field and boundary variables were included a priori. Forward selection of food variables (see Table 6.1) resulted in the presented model. F statistics (F), p-values (p) and standardized effects (β) are listed. Effects of volunteer cereals on skylark group density were analysed per survey round applying GLMM.*

Variable		***F***	***p***	**β**
Survey round		0.37	0.918	
Field size		3.01	0.084	-0.007
Survey round* field size		0.50	0.836	
Field boundary index		4.26	**0.043**	-0.030
Volunteer cereal		5.35	**0.022**	-0.018
Survey round* Volunteer cereal		3.23	**0.003**	
	Volunteer cereal (5-7 Nov)	1.31	0.262	-0.018
	Volunteer cereal (17-19 Nov)	1.55	0.223	0.026
	Volunteer cereal (2-4 Dec)	3.08	0.079	0.038
	Volunteer cereal (15-17 Dec)	9.37	**0.005**	0.093
	Volunteer cereal (27-29 Jan)	1.02	0.321	0.030
	Volunteer cereal (10-13 Feb)	0.89	0.345	0.038
	Volunteer cereal (24-26 Feb)	16.62	**<0.001**	0.268
	Volunteer cereal (16-18 Mar)	0.20	0.655	0.064
Ground-dwelling invertebrates		5.36	**0.022**	-0.032

Chapter 7

Agricultural intensification and farmland birds - a synthesis

In recent decades, many populations of farmland birds have declined dramatically. These declines are clearly linked to agricultural intensification. To halt these declines, it is essential to unravel the underlying causal factors. Knowledge about impacts of various components of agricultural intensification on birds, including their resources, their behaviour and various demographic parameters, is necessary. This synthesis chapter elaborates on the effects of farm management on farmland birds, focussing on bird foraging ecology. In this context, adaptations of farm management to improve breeding and wintering habitats for birds are discussed. In addition, suggestions are made to increase the effectiveness of conservation measures taken on farmland.

Effects of farm management on habitat selection by foraging birds

When selecting a foraging habitat, birds face a trade-off between predation risk and energy intake as described by the optimal foraging theory (Parker & Stuart, 1976). Foraging birds will therefore choose a habitat where predation risk is minimized and energy intake is maximized (Lima & Dill, 1990).

Predation risk

To avoid predation, foraging birds have to spot approaching predators in time and they have to prevent being detected by predators. Species have evolved different predator avoidance strategies and adopted different foraging behaviour. There are at least three different predator avoidance strategies regarding farmland birds. For example, yellowhammers (*Emberiza citronella*), chaffinches (*Fringilla coelebs*) and tree sparrows (*Passer montanus*) forage close to cover, such as hedgerows, and fly into this cover when a predator is detected (Lazarus & Symonds, 1992; Robinson & Sutherland, 1999). For these species, hedgerows offer protection and the experienced predation risk increases with distance to cover. At the same time, vegetation cover within foraging patches, such as stubbles, might obstruct their view and retard predator detection. Another strategy is adopted by skylarks (*Alauda arvensis*) and grey partridges (*Perdix perdix*). They rely on camouflage and avoid foraging near tall boundary vegetation, such as hedges and tree rows, which possibly hides predators (Lima & Dill, 1990). For these species, vegetation cover within foraging patches might increase crypsis. Finally, when a predator is approaching, larger-bodied species, such as golden plovers (*Pluvialis apricaria*), lapwings (*Vanellus vanellus*) and starlings (*Sturnus vulgaris*), fly away in large flocks to reduce the risk of predator attacks (Thompson & Barnard, 1983; Zoratto et al., 2009). To minimize the time spent on vigilance, flocking behaviour is also adapted by smaller species that forage in open areas, such as skylarks and corn buntings (*Miliaria calandra*)

(Beauchamp, 2002). Predator avoidance and foraging behaviour have been shown to be influenced by flock size, as well as the structure of vegetation cover (Lima & Dill, 1990). Additionally, predator avoidance behaviour might also be adapted to increased predator densities or to different predator types (e.g. raptor vs. mammalian).

Due to these individual predator avoidance strategies, species have evolved preferences for different landscape types regarding openness and the structural arrangement of linear elements. For example, wintering skylarks prefer large fields and avoid high boundary vegetation (chapter 6), while yellowhammers prefer areas with small fields (chapter 3, 4) and tall boundary vegetation (Bradbury et al., 2000). Different predator avoidance strategies have resulted in species-specific preferences for within-field vegetation structures, too (chapter 5). Skylarks, for example, prefer to forage in tall cereal stubble, as tall vegetation probably enhances camouflage for this species (chapter 6; Butler et al., 2005a). In contrast, many other species, such as yellowhammers, goldfinches (*Carduelis carduelis*), corn and reed buntings (*Emberiza schoeniclus*), have been shown to prefer foraging habitats with low vegetation, which enhances the opportunity to spot approaching predators (Butler et al., 2005a; Whittingham et al., 2006; Whittingham & Evans, 2004).

The above described specific and distinct habitat preferences of farmland birds might be the reason why the reduction in habitat heterogeneity by agricultural intensification has decreased species richness on farmland (Benton et al., 2003). Habitat heterogeneity at landscape, farm, as well as field scale offers different habitats and provides a variety of resources, such as food and shelter (Benton et al., 2003). Therefore, it is likely that species richness is increased in more diverse habitats. More species have been observed in landscapes alternated with arable crops and grasslands compared to either arable- or grassland-dominated landscapes (Atkinson et al., 2002; Robinson et al., 2001). At the farm scale, the spatial and temporal variation of crops may offer various foraging and breeding habitats and therefore increase species richness and bird abundance (chapter 3; Benton et al., 2003; Chamberlain & Gregory, 1999).

Although habitat heterogeneity increases species richness, most farmland bird species prefer a certain landscape type, such as open or complex landscapes, in accordance with their predator avoidance strategy (see Table 7.1).

Energy intake rate

In addition to minimize predation risk, foraging birds have to maximize energy gain. Energy gain is the difference between energy expenditure and energy assimilation. Birds spend energy on, for example, predator avoidance, searching food and handling preys, and they assimilate energy through food intake. Energy intake rates are influenced by food abundance and accessibility (Smart et al., 2008; Stillman & Simmons, 2006), crypticity of seeds, inter- and intra-specific competition (Norris & Johnstone, 1998), feeding strategy and diet (Whittingham & Markland, 2002).

Food abundance and accessibility, as well as seed crypticity affect a bird's searching time for preys. Searching time is reduced and thus intake rate increased by food sources that are abundant, easy accessible and detectable (Smart et al., 2008; Stillman & Simmons, 2006; Whittingham & Markland, 2002). A species' diet and traits, such as bill structure and body size, determine whether a food source is suitable and accessible (Butler & Gillings, 2004; Diaz, 1990; Richman & Lovvorn, 2009; Soobramoney & Perrin, 2007). Furthermore, energy intake rates vary largely between different food types, due to differences in energy-content, assimilation rate and the size of food items (Green, 1978). Therefore, the available food greatly influences the time spent on foraging.

Densities of wintering farmland birds have been shown to be positively related to food abundance (chapter 5, 6; Robinson et al., 2004; Tucker, 1992), which is largely influenced by farm management. In general, organically managed fields offer more food for farmland birds than conventionally managed fields (chapter 5; Kragten et al., 2010; Moreby & Sotherton, 1997). On conventional farms, the use of pesticides reduces the abundance and diversity of invertebrates, as well as weed species (this thesis, unpublished results; Stoate et al., 2009) and is possibly the most important reason for the difference in food abundance between the two farm types (McKenzie & Whittingham, 2009). Furthermore, ploughing reduces seed densities in the upper centimetres of arable soils (Cunningham et al., 2005; Field et al., 2007a) and after deep ploughing (1.2 m) hardly any seeds are left (chapter 5). Moreover, within organic systems, frequent mechanical weeding negatively affects soil seed densities probably through a decreased weed cover (chapters 4, 5; Andreasen & Stryhn, 2008).

In Flevoland (land recently reclaimed from the Sea, mainly clay soils, chapter 5), we found 10 times higher soil seed densities and two times higher weed biomass on organic compared with conventional wheat fields. Interestingly, soil seed densities sampled in February 2009 in conventionally managed cereal fields in northern Netherlands (mainly sandy soils) were almost as high as soil seed densities sampled in February 2008 in organically managed fields in Flevoland (on average 2461 seeds m^{-2} and 2527 seeds m^{-2}, respectively). These similar seed densities might be explained by a different ploughing regime between the two study sites. While the majority of the arable fields in northern Netherlands were left unploughed until the end of the winter, most arable fields in Flevoland were ploughed at the beginning of the winter, which decreased soil seed densities significantly. Other reasons for similar seed densities might be the difference in land age and duration of weed dispersal, soil type and crop type (spring wheat vs. probably spring barley).

Table 7.1 *Species-specific landscape preferences according to Dochy & Hence (2005) (small-scale landscapes, landscapes of intermediate complexity, open landscapes; black = strong preference, grey = tolerated, white = no preference or avoidance). Effects of landscape characteristics (field size, habitat diversity and the % land planted with arable crops) and farm management (mech. = mechanical) on individual species, total bird abundance and species richness based on this research. Study period indicates in which season the species was studied (b = breeding season, w = winter). Signs between brackets indicate non-significant trends (0.05 < p < 0.1) or an effect interlinked with farm type (organic vs. conventional).*

				Landscape preference						Effects of farm management (this thesis)									
				Dochy et al. 2005			This thesis			Yield		Organic							
			Study period	Small-scale	Intermediate	Open	Field size	Habitat diversity	% arable land	Breeding season	Winter	Breeding season	Winter	Number of crops	Mech. weeding	Ploughing	Pesticide use	Artificial fertilizer	Organic fertilizer
C	Carrion crow	*Corvus corone corone*	w																
CB	Corn bunting	*Miliaria calandra*	b/w							-	ns	ns					-		
GP	Golden Plover	*Pluvialis apricaria*	w																
GO	Goldfinch	*Carduelis carduelis*	w																
GR	Greenfinch	*Carduelis chloris*	w				-	+			ns		+						-
P	Grey partridge	*Perdix perdix*	b																
JD	Jackdaw	*Corvus monedula*	w																
L	Lapwing	*Vanellus vanellus*	b				+			-		+			+			-	
MG	Magpie	*Pica pica*	w																
MW	Marsh warbler	*Acrocephalus palustris*	b				-			-		+						-	
MP	Meadow pipit	*Anthus pratensis*	b/w						+	(+)	ns	-	ns					(+)	
PH	Pheasant	*Phasnaius colchicus*	b																
Q	Quail	*Coturnix coturnix*	b							(-)		ns		+			-		
RB	Reed bunting	*Emberiza schoeniclus*	w																
S	Skylark	*Alauda arvensis*	b/w				-/+		+	(-)	ns	ns	ns						
SD	Sock dove	*Columba oenas*	w																
SG	Starling	*Sturnus vulgaris*	w																
TS	Tree sparrow	*Passer montanus*	w																
WH	Whinchat	*Saxicola rubetra*	b							-		ns					-		
WW	White wagtail	*Motacilla alba*	w																
WP	Wood pigeon	*Columba palumbens*	w																
YW	Yellow wagtail	*Motacilla flava*	b							ns		(-)					-		
Y	Yellowhammer	*Emberiza citrinella*	b/w				-	+	-	(-)	ns	(+)	ns			-			
	Species richness		b/w				-	+		-	(-)	ns	+		-		-		
	Bird abundance		b/w				-		+	-	(-)	ns	+	+	(-)		-		

Skylark densities on cereal fields differed between these two regions, too. Average skylark densities in Flevoland were 0.05 and 0.36 birds ha^{-1} on conventional and organic farms, respectively. In the same months, however a year later, average skylark densities on conventional cereal fields in northern Netherlands were 0.75 birds ha^{-1}. Possibly, wintering skylarks were attracted by an overall higher food abundance in the study area situated in the northern Netherlands. However, other differences between the study areas, such as landscape characteristics, or a year effect cannot be excluded.

There might be a threshold of food abundance below which searching efficiency of foraging birds and thus energy intake rates decrease rapidly and birds select other foraging habitats (Moorcroft et al., 2002; Richman & Lovvorn, 2009). In this study, skylark density decreased rapidly on fields with seed densities below 860 seeds m^{-2} (chapter 6). Probably, such a threshold is not fixed and might shift if external factors change. Birds might leave a foraging habitat earlier if resource competition (Dolman, 1995) or predator pressure are high (Martinez-Padilla & Fargallo, 2008). Nonetheless, seed densities on conventional farms in Flevoland were far below 860 seeds m^{-2}. Hence, foraging birds, especially purely granivorous species, are likely to avoid fields where foraging efficiency is too low.

Food accessibility and detectability are mainly influenced by vegetation structure (Whittingham & Markland, 2002). Mechanization, increased competitive ability of modern crop types, and the use of artificial fertilizers and pesticides have homogenized sward structures and increased crop density, which hampers the accessibility of food during the breeding season (Benton et al., 2003; Butler & Gillings, 2004; Stoate et al., 2001; Wilson et al., 2005). Lower sowing densities and unsown plots may increase the accessibility of food in crops. In winter, the reduction of vegetation height and the scarification of the soil surface have been shown to be an effective measure to increase food accessibility for many farmland bird species (Butler et al., 2005a; Whittingham et al., 2006).

Diets differ between species, as well as between seasons due to variations in food availability (Dochy & Hens, 2005; Holland et al., 2006). For example, the diet of yellow wagtails (*Motacilla flava*) consists mainly of invertebrates during the breeding season, as well as in winter (Cramp et al., 1988). In contrast, the proportion of invertebrates in the diet of skylarks is much higher in summer than in winter, when they feed mainly on seeds and other plant material (chapter 6; Green, 1978). Agricultural intensification has not only affected the abundance, but also the composition of bird food (McCracken & Tallowin, 2004; Moorcroft et al., 2006; Vickery et al., 2001; Wilson et al., 1999). For granivorous birds, cereal grains are an important food source due to their size and high energy content resulting in high energy intake rates (Green, 1978; Perkins et al., 2007). In recent decades, however, the availability of cereal grains on arable fields in winter has decreased dramatically due to more efficient harvesting and improved seed cleaning techniques, and tillage after harvest (Newton, 2004; Stoate et al., 2009; Wilson et al., 1999). In our study, the cereal grain content in the diet of wintering skylark fell below 10% already in the beginning of the winter (chapter 6). In addition, we found hardly any cereal grains in and on the soil throughout the winter. In the absence of cereal grains, birds have to switch to other food types, which probably have a lower energy content. Therefore, birds are likely to spend more time on foraging or to take higher predation risks to meet daily energy requirements.

Summarizing, agricultural intensification has altered foraging habitats of farmland birds, and thus probably affected energy intake rates, as well as predation risk. As habitat selection and foraging behaviour are species-specific, farmland birds are differently affected by farm management (see Table 7.1). Therefore, bird conservation measures taken on farmland should consider these species-specific requirements.

Bird conservation on farmland

Agri-environment schemes have been designed to reduce environmental risks associated with modern farming and to preserve biodiversity and cultural landscapes (European Commission, 2005). In 2002 about 44% (2 billion EUR) of the EAGGF[1]-Guarantee expenditure for rural development was spent on agri-environment schemes and about 20% of the agriculturally used land was covered by agri-environment schemes (European Commission, 2003). They have been shown to enhance local species richness and abundances of some species groups (chapter 2; Kleijn et al., 2006; Kleijn & Sutherland, 2003) and to provide various food sources for farmland birds (Vickery et al., 2002). However, their effectiveness in reversing population declines is limited (Berendse et al., 2004; Kleijn & Sutherland, 2003). Only few schemes based on intensive research and monitoring programmes and in combination with additional measures have been effective in reversing species declines of grey partridge (*Perdix perdix*), corncrake (*Crex crex*), stone-curlew (*Burhinus Burhinus oedicnemus*) and cirl bunting (*Emberiza cirlus*) in the UK (Aebischer et al., 1983; Berendse et al., 2004; Wilson et al., 2010).

Several reasons have been suggested why many agri-environment schemes are not effective in halting bird population declines: schemes focus only on one part of a species' life cycle; schemes are inflexible regarding adaptations to variable weather conditions; schemes are not implemented in accordance with agreements; the scale of schemes is too small; and schemes are implemented in unsuitable areas, i.e. outside a species' core area or in areas with constraints, such as disturbances or a high predation pressure (Evans & Green, 2007; Melman et al., 2008; Schekkerman et al., 2008; Whittingham,

[1]EAGGF: European Agricultural Guidance and Guarantee Fund

2007; Wilson et al., 2007). Moreover, many schemes are likely to be too broad, i.e. targeting many species, and not specific enough to support declining species (Wilson et al., 2007).

The effects of organic farming on biodiversity vary between studies and species, too (see chapters 1 - 5). There is a fast growing amount of literature on the effectiveness of agri-environment schemes and organic farming in relation to landscape heterogeneity (e.g. Concepción et al., 2008; Dänhardt et al., 2010; Smith et al., 2010). These studies have shown that the effectiveness of agri-environment schemes and organic farming depends on landscape composition (chapter 4; Tscharntke et al., 2005).

Therefore, if population declines of farmland birds are to be halted, farming practices have to be adapted and bird conservation on farmland has to be more effectively implemented. The results of the research presented in this thesis emphasise the necessity of reducing the use of pesticides at large scale, of increasing on-farm habitat diversity and of taking landscape composition and species-specific requirements into account when designing agri-environment schemes. These measures will be discussed in more detail in the following paragraphs.

The findings of chapter 2 and 3 indicate that the use of pesticides is the most important farming practice assessed in this study that negatively affects species richness and abundance of breeding farmland birds at large scale, i.e. across several European study areas (see also Table 7.1). Therefore, the use of pesticides on arable land has to be reduced to improve habitats for breeding and wintering farmland birds. A reduction in the area sprayed with pesticides could be achieved on the one hand by decreasing the use of pesticides on cropland and on the other hand by increasing the area of non-crop and thus unsprayed habitat on farmland. First of all, the use of pesticide could be reduced on conventional farms. Furthermore, as organic farming does not use synthetic pesticides, extending the area under organic farm management would increase the extent of unsprayed cropland. Food abundance for birds has been shown to be higher on organic than on conventional farms during the breeding season, as well as in winter (chapter 5; Kragten et al., 2010; Mäder et al., 2002; Moreby, 1997). However, in our study, species richness as well as abundance of breeding farmland birds were not higher on organic compared to conventional farms. Reasons for this might be the differences in crop types grown on the two farm types (Kragten & de Snoo, 2008), a high disturbance frequency on organic farms through crop management (Kragten et al., 2008), or the negative effects of pollution associated with the use of pesticides at surrounding conventional farms. Especially for bird species that use areas larger than single farms for foraging, like yellow wagtails, such large-scale effects might be relevant. Fox (2004) hypothesized that a reduction of the use of pesticides and artificial fertilizers and an increased area under organic farming in Denmark in the 1980s (5.2% in 2005; Eurostat, 2007b) has resulted in more stable Danish farmland bird populations compared to the UK. 5% of the agriculturally used area covered by organic farms might be the minimal area required to effectively reduce the negative impact of pesticides. Therefore, it would be interesting to study the effects of organic farming on farmland birds varying the level of coverage of organic agriculture, but keeping landscape characteristics constant.

Another way to extend the unsprayed area on farmland is to increase the area of non-crop habitats. An extended area of field margins has been shown to increase densities of breeding skylarks (van t' Hoff & Koks, 2008). In the northern Netherlands, densities of skylarks were three times higher in agricultural areas with more field margins (on average 3.7%) compared to control areas (on average 2.1%) (van t' Hoff & Koks, 2008). The creation of at least 6 m wide field margins covering an area of 3-10%, depending on the scale of implementation, has been suggested to effectively increase numbers of breeding skylarks and grey partridges (Bos et al., 2010; Dochy & Hens, 2005).

Both measures, organic farming, as well as the creation of field margins are likely to increase food abundance for many bird species and offer breeding habitats for at least some species (e.g. Kragten & de Snoo, 2008; Moreby, 1997; Vickery et al., 2009; Whittingham et al., 2009).

Moreover, the results of this research show that farmland birds might benefit from an increased crop diversity at the farm scale (chapter 3). The spatial and temporal heterogeneity of different crops and vegetation structures offers various foraging and breeding habitats. This enables individual birds to change breeding habitats in the course of the breeding season. Additionally, due to differences in species' predator avoidance strategies and preferences for different crop structures, more species may benefit from farms growing diverse crops (see *Predation risk*).

The effectiveness of agri-environment schemes might be improved by taking landscape composition into account. Before conservation measures are taken on farmland, the target area should be investigated in the context of a number of prerequisites, which should minimally be satisfied to provide suitable foraging or breeding habitats for farmland birds. For example, target areas should meet minimal distances to urban areas and other disturbing infrastructure. This approach might substantially reduce the unsuitable area under agri-environment schemes, as has been shown by a study of Melman et al. (2008). They estimated that approximately 10% of the area under meadow bird management was unsuitable due to road traffic noise.

Next, since several studies have shown that the effectiveness of conservation measures depends on landscape composition, conservation measures should be adapted to the level of landscape complexity. Although landscape complexity is a continuous measure, I propose a classification based on empirical data (Andrén, 1994; Tscharntke et al., 2005), which may be used as a rough indication of different landscape types: cleared landscapes with less than 1% semi-natural habitats; simple landscapes with 1-20% semi-natural habitats; and heterogeneous landscapes with more than 20% semi-natural habitats (see chapter 4). In this research, organic farming had no effect on birds in cleared landscapes. Field margins and other semi-natural habitats, which may function as source habitat for bird food, lack in these landscapes. Therefore, colonisation of arable fields by invertebrates and weeds may be too low to attract birds. In cleared landscapes, first of all, the percentage of unsprayed field margins should be increased. Manhoudt & de Snoo (2003) showed that the average area of semi-natural habitats on Dutch arable farms is approximately 2%. The average area of semi-natural habitats on farms participating in field margin projects (18 farms in two distinct regions) was increased to more than 5% (Manhoudt & de Snoo, 2003). After increasing the area of field margins, i.e. a source habitat of weeds and invertebrates, other (in-field) conservation measures might become more effective.

As many species are associated with a certain landscape type (Table 7.1), distinct measures should be designed for species that prefer either simple or heterogeneous landscapes. For example, wintering skylarks are likely to benefit from weedy cereal stubble fields in open landscapes (chapter 6). In contrast, wintering yellowhammers might benefit from unharvested cereal margins in heterogeneous, small-scale landscapes (Vickery et al., 2002). In addition, the concentration of conservation measures in areas with high densities of the target species is likely to be more successful and cost-effective than spreading the measures over large areas, possibly including areas that do not satisfy the above mentioned prerequisites (Bos et al., 2010; Whittingham, 2007).

I conclude that if we wish to halt the decline of bird species diversity on farmland, the use of pesticides has to be reduced at large scale and crop diversity has to be increased at farm scale. In addition, the effectiveness of agri-environment schemes has to be increased by tailoring them to individual species and to different landscape types.

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Summary

Introduction

In 1957, the Common Agricultural Policy was adopted by the member states of the European Economic Community (EEC) to stabilize food markets, to ensure farmer's income and to increase food production. As a consequence, many agricultural production practices have been intensified simultaneously, which have affected farmland at different spatial scales. Yields have been increased, fields have been enlarged, farms have become more specialized and agricultural land has been homogenized. This has resulted in the decline of many farmland species. Many populations of farmland birds, an intensively studied group and often used as indicator species, have suffered from agricultural intensification.

As many components of agricultural intensification have been intensified simultaneously, the disentanglement of their effects on farmland birds remains difficult. Therefore, one of the main goals of the research reported on in this thesis was to investigate and unravel the effects of different components of agricultural intensification, such as yield, the use of pesticides and fertilizers, mechanical weeding, field and farm layout, and landscape characteristics, on farmland birds during the breeding season, as well as in winter.

Organic farming and agri-environment schemes are the most widespread measures taken on farmland to mitigate the negative effects of agricultural production practices. Organic farming does not use synthetic pesticides and artificial fertilizers and is meant to produce more environment-friendly and to enhance biodiversity on farmland. Agri-environment schemes are measures taken on farmland with diverse goals, such as the creation of field margins as shelter for fauna or the decrease in the use of pesticides to reduce environmental pollution. However, many studies show limited success of organic farming and agri-environment schemes in enhancing biodiversity on farmland. Hence, a second goal of this thesis was to investigate the effects of organic farming, in some countries an agri-environment scheme, on farmland birds.

During habitat selection, foraging birds face a trade-off between minimizing predation risk and maximizing energy gain. We studied the effects of farming practices on habitat characteristics that influence predation risk and energy intake, i.e. food abundance and vegetation cover. In addition, we were interested in habitat selection by farmland birds in winter in respect of vegetation cover and food abundance.

Summary of research

The studies presented in chapter 2, 3 and 4 include up to nine different European study areas. In each study area, 30 arable farms were selected so as to represent an intensity gradient, using wheat yield as a proxy for agricultural intensity. Bird surveys were conducted during the breeding season, as well as in winter in survey plots of 500×500 m^2 around a focal cereal field, mostly winter wheat. Sampling of vegetation cover and bird food, i.e. plants, carabids and weed seeds, was limited to the cereal fields within the survey plots. Information about farm management was collected by means of a questionnaire sent out to all participating farmers. Landscape characteristics were calculated within a 500-m radius circle around the centre of the focal cereal fields.

In chapter 2 we show that species richness of ground-breeding farmland birds, as well as species richness of plants and carabids, were negatively related to wheat yield, a variable related to many farming practices and often used as proxy for agricultural intensity. In addition, the biological control potential of predators was reduced at farms with higher yields. The use of pesticides affected consistently and negatively the species richness of all studied taxa and the biological control potential. Organic farming and the area covered by agri-environment schemes increased species richness of carabids and plants, but not that of birds.

Chapter 3 describes the effects of agricultural intensity on the total abundance of ground-nesting farmland birds including 30 species and on the abundance of nine individually investigated species. Total breeding bird abundance, as well as the abundances of four species were higher on low-yielding farms. Interestingly, yellow wagtails (*Motacilla flava*) and meadow pipits (*Anthus pratensis*) were slightly more abundant on high-yielding farms. Again, the use of pesticides had the most consistent negative effect on total breeding bird abundance and on the abundance of yellow wagtails, whinchats (*Saxicola rubetra*), corn buntings (*Miliaria calandra*) and quails (*Coturnix coturnix*). Furthermore, total breeding bird abundance and the abundance of quails were positively related to crop diversity. Organic farms supported more lapwings (*Vanellus vanellus*) and less meadow pipits compared to conventional farms. Responses to landscape characteristics were species-specific, too, but the majority of species was more abundant in landscapes comprising a higher percentage of arable crops or small fields.

In chapter 4, we investigated the effects of organic farming on wintering farmland birds in relation to landscape composition. Three landscape types were distinguished differing in the amount of agriculturally used area: complex landscapes (< 80% agriculturally used land), simple landscapes (80-99% agriculturally used land), and cleared landscapes (> 99% agriculturally used land). Bird abundance and species richness were higher on organic farms only in simple landscapes. In cleared landscapes, there was no difference in bird abundance and species richness between the two farm types, whereas bird abundance in complex landscapes was even higher on conventional farms. Furthermore, frequent mechanical weeding reduced the number of bird species on organic farms. In addition, birds were more abundant on farms with more land covered by cereal stubble, pasture and green manure crops. Species richness was higher on farms with more land covered by pasture.

The research described in chapter 5 was limited to the 30 arable farms situated in the Dutch study area, Flevoland. The effects of farm management on the abundance of food, i.e. soil seed density, for farmland birds and vegetation cover were studied in winter. Furthermore, the relation between bird abundance, vegetation cover and food abundance was investigated. Average soil seed densities were approximately 10 times higher on organic compared to conventional wheat fields. On organic farms, soil seed density was reduced by frequent mechanical weeding. Farmland birds were more abundant on fields with higher seed densities. Species richness was negatively related to the percentage bare earth on wheat fields. Field selection in respect of vegetation cover differed between species, probably due to differences in species' diets and predator avoidance strategies.

In chapter 6, we investigated which habitat characteristics, i.e. field and boundary characteristics, vegetation cover and food abundance, influenced field selection by foraging skylarks in winter. In addition, we were interested in seasonal variation in the diet of skylarks and whether the diet differed between foraging habitats.

Skylarks were surveyed nine times between November and mid-March in an agricultural region in northern Netherlands. Food abundance, i.e. soil seed densities and invertebrate biomass, was sampled and vegetation cover was estimated on former cereal, maize and potato fields, and on permanent grassland. Skylark faeces was collected on potato and cereal fields and analysed to obtain the proportion of different food types in the diet of skylarks.

Foraging skylarks avoided fields with tall boundary vegetation and preferred large fields. Skylark flocks were more abundant on cereal stubble fields and avoided permanent grasslands and maize fields. They were positively related to soil seed densities and their abundance decreased steeply on fields with soil seed densities below than 860 seeds m^{-2}. The proportion of invertebrates in the skylark faeces was low throughout the winter, but increased with increasing temperature. The proportion of dicotyledonous seeds was higher in faecal pellets collected on potato fields, whereas the proportion of cereal grains was higher in faeces found on cereal fields. The proportion of grains in the faecal pellets already decreased sharply at the end of November and was mainly replaced by weed seeds.

Conclusions

The results of this research show that the majority of ground-nesting farmland bird species are negatively affected by agricultural intensity, particularly by the use of pesticides.

However, species respond differently to farm management, i.e. farming practices and farm type. The abundance of breeding birds is increased by a high crop diversity at the farm scale and foraging birds in winter are more abundant on mixed farms, i.e. comprising arable crops as well as pastures.

I suppose that the availability of cereal grains on arable land in the Netherlands is already depleted at the beginning of the winter and that granivorous birds have to forage on other food types with lower energy intake rates. Foraging time of birds and therefore also predation risk might have increased due to diminished food availability throughout the winter.

We show that food abundance for birds in winter is increased by organic farming. However, birds benefited from organic farming only in simple landscapes, implying that the effectiveness of conservation measures depends on landscape composition.

To conserve birds on farmland, we therefore suggest

- to drastically reduce the use of pesticides by increasing the area of unsprayed field margins or the area under organic farming, or by a reduction of the use of pesticides on conventional farms.
- to increase crop diversity at the farm scale.
- to increase the area of field margins, particularly in cleared landscapes.
- to make agri-environment schemes species-specific and landscape dependent and to concentrate on the core areas of species' distributions.
- to increase food abundance in winter by for example overwinter stubble, non-inversion tillage, or less frequent mechanical weeding.

Samenvatting

Inleiding

De start van een gemeenschappelijk landbouwbeleid door de Europese Economische Gemeenschap in 1957 heeft in de daarop volgende decennia geleid tot een intensivering van de landbouw. De opbrengsten zijn gestegen, het gebruik van gewasbestrijdingsmiddelen en kunstmest is sterk toegenomen, door ruilverkaveling werden akkers vergroot, bedrijven werden gespecialiseerd en veel landschapselementen zijn uit het cultuurlandschap verdwenen. De intensivering van de landbouw bestaat dus uit verschillende componenten die op meerdere ruimtelijke schaalniveaus plaatsgevonden hebben.

De veranderingen op het boerenland hebben geleid tot een afname van de diversiteit van planten en dieren. Broed- en foerageerhabitats van veel boerenlandvogels zijn door de intensivering van de landbouw veranderd of zelfs verdwenen. Daardoor zijn veel populaties van boerenlandvogels sterk achteruitgehold.

Een aantal landbouwpraktijken zijn gelijktijdig geïntensiveerd en zijn onderling verweven. Daardoor is het moeilijk om hun afzonderlijke effecten op boerenlandvogels te bestuderen. Het bepalen van de afzonderlijke effecten van de verschillende componenten van de landbouwintensivering op boerenlandvogels is één van de doelen van dit proefschrift.

Biologische landbouw en agrarisch natuurbeheer zijn twee wijdverbreide maatregelen om de schadelijke effecten van de landbouwintensivering op het milieu tegen te gaan. De biologische landbouw stelt zich ten doel om milieuvriendelijk te produceren door zich aan bepaalde eisen op het gebied van milieu, natuur en landschap te houden. Er worden dan ook geen chemische gewasbeschermingsmiddelen en kunstmest op biologische bedrijven gebruikt. Binnen het agrarisch natuurbeheer worden beheersovereenkomsten met boeren afgesloten, waarbij de boeren financieel gecompenseerd worden voor gederfde inkomsten en inspanningen. Deze beheersovereenkomsten verschillen in ontwerp en doelen. Voorbeelden van beheersovereenkomsten zijn het creëren van akkerranden als habitat voor akkervogels en het laten staan van granen in de winter als voedsel voor doortrekkende akkervogels. Onderzoek laat echter uiteenlopende resultaten zien als het om de toename van de biodiversiteit op biologische bedrijven en het succes van agrarisch natuurbeheer gaat. Het vergelijken van het voorkomen van boerenlandvogels op biologische en op gangbare akkerbouwbedrijven, is het tweede doel van dit proefschrift.

Habitatkenmerken, zoals vegetatiebedekking en voedselaanbod, beïnvloeden enerzijds de predatiekans en anderzijds de energieopname van foeragerende vogels. Daarom zijn de effecten onderzocht van verschillende landbouwpraktijken op habitatkenmerken die de predatiekans en energieopname van vogels beïnvloeden. Daarnaast is de habitatkeuze van boerenlandvogels in relatie tot vegetatiebedekking en voedselaanbod in de winter onderzocht.

Samenvatting van het onderzoek

Het onderzoek dat in de hoofdstukken 2 tot en met 4 beschreven is, werd tegelijkertijd uitgevoerd in zeven tot negen verschillende studiegebieden verdeeld over een aantal Europese landen. Binnen elk studiegebied werden 30 akkerbouwbedrijven van verschillende intensiteit geselecteerd. Als maat voor intensiteit werd de graanopbrengst van het voorgaande jaar gebruikt. Per bedrijf werd één vogeltelgebied van 500×500 m^2 met daarin minstens één graanveld gekozen. Binnen dit telgebied werden in 2007 broedvogels en in de winter van 2007/2008 overwinterende vogels gekarteerd. Vegetatiebedekking en voedselaanbod werden op het graanveld binnen het telgebied bemonsterd. Informatie over de bedrijven en de daarop toegepaste landbouwpraktijken werd door middel van een enquête onder de deelnemende agrariërs verkregen. Binnen een cirkel met een straal van 500 m rondom het centrum van het telgebied werden een aantal landschapskenmerken, zoals gemiddelde veldgrootte en habitatdiversiteit, berekend.

Uit het onderzoek beschreven in hoofdstuk 2 bleek dat een hogere graanopbrengst leidt tot een lagere soortenrijkdom van grondbroedende boerenlandvogels, planten en loopkevers. Daarnaast bleek de capaciteit van biologische bestrijding door natuurlijke vijanden kleiner te zijn op bedrijven met hogere opbrengsten. De gewasopbrengst wordt beïnvloed door de meeste intensiveringsmaatregelen en wordt daarom vaak als maat voor landbouwintensiteit gebruikt. Daarnaast verminderde het gebruik van gewasbeschermingsmiddelen de soortenrijkdom van alle onderzochte taxa en de mogelijkheden voor biologische bestrijding. De soortenrijkdom van planten en loopkevers, maar niet van boerenlandvogels, was hoger op biologische bedrijven vergeleken met gangbare bedrijven. Ook nam de soortenrijkdom van planten en loopkevers toe met een toenemend oppervlak aan beheersovereenkomsten.

In hoofdstuk 3 zijn de effecten van landbouwintensiteit in Europa op de dichtheid van boerenlandvogels (in totaal 30 soorten) en afzonderlijk op de dichtheid van negen soorten onderzocht. De dichtheid van alle soorten en ook de dichtheid van vier afzonderlijk onderzochte soorten was lager op bedrijven met een hoge graanopbrengst. Gele kwikstaarten (*Motacilla flava*) en graspiepers (*Anthus pratensis*) waren juist talrijker op bedrijven met een hoge opbrengst. Wederom waren de dichtheden van alle soorten bij elkaar en ook van gele kwikstaarten, paapjes (*Saxicola rubetra*), grauwe gorzen (*Miliaria calandra*) en kwartels (*Coturnix coturnix*) afzonderlijk lager op bedrijven waar meer bestrijdingsmiddelen gebruikt werden. Het aantal gewassen dat op de bedrijven verbouwd werd had een positief effect op de totale dichtheid van boerenlandvogels en op de dichtheid van kwartels. Meer kieviten (*Vanellus vanellus*), maar minder graspiepers broedden op biologische bedrijven. Soorten reageerden verschillend op landschapskenmerken, maar de meeste soorten hadden een voorkeur voor landschappen met kleine velden en veel bouwland.

Hoofdstuk 4 beschrijft de effecten van biologische bedrijfsvoering in Europa op boerenlandvogels in de winter en hoe deze effecten binnen verschillende landschapstypen varieerden. Aan de hand van het percentage oppervlak gebruikt voor agrarische productie werd er onderscheid gemaakt tussen drie landschapstypen: complex (< 80% landbouw), simpel (80-99% landbouw) en 'opgeruimd' (> 99% landbouw). Soortenrijkdom en abundantie van boerenlandvogels was alleen hoger op biologische bedrijven in simpele landschappen. Er was geen verschil in soortenrijkdom en dichtheid van boerenlandvogels tussen biologische en gangbare bedrijven in opgeruimde landschappen. In complexe landschappen waren er zelfs meer vogels op gangbare bedrijven. Vergeleken met biologische bedrijven met minder frequente mechanische onkruidbestrijding, waren dichtheid en soortenrijkdom lager op biologische bedrijven waar onkruid frequenter bestreden werd. Op bedrijven met een grotere oppervlakte aan graanstoppels, grasland en groenbemester werden meer overwinterende vogels geteld. Op bedrijven met een grotere oppervlakte aan grasland waren ook meer soorten aanwezig.

Het onderzoek dat in hoofdstuk 5 beschreven is beperkte zich tot de 30 akkerbouwbedrijven in Flevoland (Nederland). In deze studie zijn de effecten van verschillende landbouwpraktijken op het voedselaanbod voor boerenlandvogels en de vegetatiebedekking in de winter onderzocht. Daarnaast is gekeken in hoeverre vegetatiebedekking en voedselaanbod het voorkomen van foeragerende vogels beïnvloedt. De zaaddichtheid in de bovenste centimeter van biologische akkers was 10 keer hoger dan die van gangbare akkers. De zaaddichtheid op biologische bedrijven met frequente mechanische onkruidbestrijding was lager dan de zaaddichtheid op biologische bedrijven met minder frequente onkruidbestrijding. Op akkers met veel zaden werden ook meer soorten en meer vogels geteld. Verder waren er weinig soorten op akkers met veel kale grond. De voorkeur voor een bepaald type vegetatiebedekking, bijvoorbeeld grasland, graanstoppels of akkerrand, verschilde per soort. Deze voorkeur wordt waarschijnlijk door het dieet en de strategie om predatoren te ontvluchten bepaald.

In hoofdstuk 6 zijn de kenmerken van foerageerhabitats van overwinterende veldleeuweriken onderzocht. Verder is de samenstelling van het dieet van de veldleeuwerik gedurende de winter geanalyseerd. Het dieet van vogels die op aardappelakkers foerageerden is vergeleken met het dieet van vogels die op graanakkers hun voedsel zochten.

In een agrarisch gebied in Noord-Nederland werden tussen november en half maart om de twee à drie weken veldleeuweriken geteld. Op geoogste aardappel-, graan- en maïsakkers en op graslanden werd het voedselaanbod (zaaddichtheid en biomassa van evertebraten) bemonsterd en de vegetatiebedekking geschat. Op de aardappel- en graanakkers werden uitwerpselen van veldleeuweriken verzameld, om het aandeel van verschillende soorten voedsel in de uitwerpselen te kunnen analyseren.

Veldleeuweriken meden kleine velden en velden met hoge begroeiing langs de randen. De meeste veldleeuweriken werden op akkers met graanstoppels geteld en er zaten weinig vogels op maïsakkers en grasland. Veldleeuweriken hadden een sterke voorkeur voor akkers met meer dan 860 zaden m^{-2}. Het aandeel evertebraten in de uitwerpselen van veldleeuweriken was laag gedurende de hele winter, maar positief gerelateerd aan de temperatuur. Het aandeel zaden van dicotylen was hoger in uitwerpselen die op aardappelakkers gevonden waren, terwijl het aandeel granen hoger was in uitwerpselen die op graanakkers verzameld waren. Het aandeel granen in het dieet van de veldleeuwerik nam echter al eind november sterk af en werd met name door onkruidzaden vervangen.

Conclusies

De resultaten van dit proefschrift laten zien dat de intensivering van de landbouw negatieve gevolgen heeft voor de meeste boerenlandvogels. Soortenrijkdom en dichtheid van broedvogels was vooral laag op bedrijven waar veel gewasbeschermingsmiddelen gebruikt waren. Wel profiteerden veel soorten broedvogels van een hoge diversiteit aan gewassen. Bovendien waren de meeste boerenlandvogels in de winter op gemengde bedrijven, d.w.z. met grasland en akkerbouw, te vinden. De positieve effecten van biologische landbouw op soortenrijkdom en abundantie van alle soorten bij elkaar waren beperkt tot simpele landschappen. Afzonderlijke soorten reageerden echter verschillend op de effecten van verschillende landbouwpraktijken. Ook waren de dichtheden van de meeste soorten op biologische en gangbare bedrijven gelijk en had maar een enkele soort een voorkeur voor één van de twee bedrijftypen.

Het onderzoek laat zien dat het graanaanbod op Nederlandse akkers tegenwoordig waarschijnlijk al in het begin van de winter minimaal is en dat graanetende vogels op ander, minder energierijk voedsel moeten omschakelen. Hierdoor moet een vogel mogelijkerwijs meer tijd besteden aan het zoeken van voedsel en is het gevaar voor predatie voor boerenlandvogels gedurende de hele winter toegenomen.

Op biologische bedrijven was het zaadaanbod in de winter hoger dan op gangbare bedrijven. Er zaten echter alleen meer vogels op biologische bedrijven in simpele landschappen, wat erop duidt dat de effectiviteit van beschermingsmaatregelen afhankelijk is van het landschapstype.

De resultaten beschreven in dit proefschrift wijzen erop dat boerenlandvogels alleen behouden kunnen blijven:

- als op grote schaal het gebruik van gewasbeschermingsmiddelen drastisch gereduceerd wordt door een verdere reductie van het gebruik van pesticiden op gangbare bedrijven, door een toename van onbespoten akkerranden of door grotere oppervlakten met biologische productie.
- als de gewasdiversiteit binnen akkerbouwbedrijven toeneemt.
- als de oppervlakte van akkerranden, met name in de opgeruimde landschappen, toeneemt.
- als het agrarisch natuurbeheer aan specifieke soorten en aan verschillende landschapstypen aangepast wordt. Dit is o.a. mogelijk door het concentreren van beheersovereenkomsten in kerngebieden van doelsoorten.
- als het voedselaanbod voor boerenlandvogels in de winter toeneemt. Dit kan gedaan worden door akkers met graanstoppels te laten staan, ondiep te ploegen of minder frequent mechanisch onkruid te bestrijden.

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Acknowledgements

In the past four years, I have often wondered whether I was taking a detour on my path of life or whether I was climbing a huge mountain. Probably, it was a detour on the way to the top of a mountain.

Imagine: While climbing, the next hill hides the path in front of you. You never know what comes beyond that hill and you often encounter something unexpected. A while later, you might discover a beautiful mountain pasture, but between yourself and this pasture there is a deep ravine and you have to go a long way round before you will be able to reach it. When you finally do reach this mountain pasture, you may rest for a while, thinking back to the path you left behind and enjoying your achievement. When you think you are nearly at the summit, however, there is another rise and another incline. The last metres below a mountain top are the steepest, most slippery and exhausting ones. And you never know what to expect when you finally reach the top. How is the view? Is the view obstructed by waft of mist? What to expect at the other side of the mountain?

In the past four years, I experienced literally and figuratively high altitudes and deep valleys. I enjoyed the many challenges that form part of a PhD, the discussions with fellow researchers and contacts with project partners. While I encountered many unexpected, sometimes unwelcome obstacles, I got an enormous amount of help to surmount these obstacles. I was not alone on my climb and I was accompanied by many friends, colleague's and my family. Without the support of patient friends and many encouraging words of companions during misfortunes, I never would have been able to finish this thesis. Finally, I have the chance to thank all of you who helped me along this journey.

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About the author

Curriculum vitae

Flavia Geiger was born on October 19, 1980 in Affoltern am Albis, Switzerland. In Obfelden, a small village south of Zürich, she grew up and attended primary school. In January 2000, she obtained her high school degree at the Gymnasium Urdorf, after which she moved to Wageningen to study biology. During her Masters she did two MSc theses in Wageningen and an internship in Switzerland. In her first MSc thesis, she investigated the abundances of hibernating natural enemies of insect pests in different semi-natural habitat types. In her second MSc thesis, she studied the differences in insect abundance of cow dung pats between organic and conventional diary farms and nature conservation areas under grazing management. During her internship at the WSL Institute for Snow and Avalanche Research SLF in Davos, Switzerland, she investigated weather effects on the mortality of Alpine chamois. Although she did not spot any chamois during her stay in Davos, she enjoyed hiking through the Swiss Alps and living between the mountains. After obtaining her MSc degree in Biology (Ecology) in January 2006, she worked for two more months at the SLF to finish her report about the chamois study.

Thereafter she moved to Zürich, where she did an internship at the visitor centre Neeracherried of Birdlife Schweiz. In this nature conservation area, she counted birds, led excursions, compiled a flora database and organised exhibitions and special events. In October 2006, she moved back to Wageningen to start her PhD research at the Nature Conservation and Plant Ecology Group. Her research was part of the EuroDiversity AgriPopes programme. In this European research project she focused on the effects of agricultural intensification on farmland birds. Furthermore, in 2007 she became a member and in 2009 the chair of the PhD Council of the C.T. de Wit Graduate School for Production Ecology & Resource Conservation (PE&RC) and held position on the Board of PE&RC.

Since November 2010 she has been working as a research associate at the research station Agroscope Changins-Wädenswil ACW in Switzerland.

List of publications

Geiger, F., de Snoo, G.R., Berendse, F., Guerrero, I., Morales, M.B., Oñate, et al. (2010). Landscape composition influences farm management effects on farmland birds in winter: a pan-European approach. Agriculture, Ecosystems & Environment, in press.

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PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

The C.T. De Wit Graduate School PE&RC PRODUCTION ECOLOGY & RESOURCE CONSERVATION

Review of literature (4.5 ECTS)

- Agriculture and biodiversity

Post-graduate courses (8.9 ECTS)

- Crossing the frontier between below and above; Soil Ecology (2007)
- Trends in biodiversity: European ecosystems and policy; ALTER-Net Summer School (2007)
- Biodiversity and ecosystem services in a sustainable world (2008)
- A practical post-graduate GIS course; iGIS (2009)

Invited review of (unpublished) journal (1 ECTS)

- How edge distance affects biological pest control and pollination; Journal Agriculture, Ecosystems and Environment (2010)

Competence strengthening / skills courses (5.1 ECTS)

- Competence assessment (2007)
- Personal efficacy (2007)
- Multivariate analysis (2008)
- Scientific writing (2010)

PE&RC Annual meetings, seminars and the PE&RC weekend (2.7 ECTS)

- PE&RC Day (2007, 2008 and 2009)
- PE&RC Weekend (2007 and 2009)

Discussion groups / local seminars / other scientific meetings (9.8 ECTS)

- Project meeting; Agripopes, Chizé (2006)
- PhD Discussion group Forest and Conservation Ecology; FEM-NCP-REG (2006-2010)
- Project meeting; Agripopes, Wageningen (2007)
- Project meeting; Agripopes, Paris (2007)
- Project meeting; Agripopes, Wageningen (2008)
- Project meeting; Agripopes, Uppsala (2008)
- Project meeting; Agripopes, Uppsala (2009)
- Project meeting; Agripopes, Madrid (2009)

International symposia, workshops and conferences (9.4 ECTS)

- 10th INTECOL 2009 'Ecology in a Changing Climate'; Brisbane, Australia (2009)
- 2nd European Congress of Conservation Biology 'Conservation Biology and Beyond: From Science to Practice'; Prague, Czech Republic (2009)
- ESCORT 3 Workshop 'Linking Testing and Risk Assessment with Protection Goals'; Egmond aan Zee, the Netherlands (2010)
- GfÖ Meeting 'The Future of Biodiversity - Genes, Species, Ecosystems'; Giessen, Germany (2010)

Lecturing / supervision of practical's / tutorials (4.4 ECTS)

- Ecology of communities; Ecosystems and Landscapes; 6 days (2008)
- Guest lecture Agrobiodiversity course; (2009)
- Ecology of communities; Ecosystems and Landscapes; 5 days (2009)
- Ecology I; 2.5 days (2010)

Supervision of 3 MSc students (30 days)

- Food abundance and habitat use of Yellow wagtail (*Motacilla flava flava*) and Skylark (*Alauda arvwensis*) in wheat plots on farms in Flevoland
- Food availability for farmland birds in different cereal types in the Netherlands throughout the winter
- Field use of wintering Skylarks in the surrounding of the Drents-Friese Wold

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