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About the author

To a Skylark

Better than all measures
Of delightful sound -
Better than all treasures
That in books are found -
Thy skill to poet were, thou scorner of the ground!

Teach me half the gladness
That thy brain must know,
Such harmonious madness
From my lips would flow,
The world should listen then – as I am listening now.

P.B. Shelley (To a skylark, 1820)

Chapter 1

General introduction

Farmland birds

Birds are found everywhere on earth, from the tropics to the poles and from the high mountains to the oceans. Over the course of a more than 100 million year evolutionary history, birds have adapted to climatic differences, changes in food availability, numerous predators and diseases, seasonality, living alone or in flocks, walking, flying and swimming. And, not unimportantly, all bird species that have survived until today have to a greater or lesser degree been able to handle anthropogenic influences. One could argue that presently there is no place left in this world that is not to some extent influenced by humans, but in some habitats this influence is most pronounced. One of these habitats is farmland, where people control practically all circumstances, from ground water levels and soil fertility to vegetation composition and landscape structure.

At present, farmland is one of the world's most widespread habitats. In the European Union, 45% of the land surface is covered by agricultural land, more than half of which is arable (FAOSTAT 2014). In the Netherlands, the percentage of agricultural land even comprises 56%. Despite, or perhaps thanks to, the large human influence on agricultural habitats, a substantial part of all bird species can be found on farmland. Some of them live on farmland during almost all phases of their life cycle, while others occasionally turn to farmland to breed or to find food or shelter. All birds that depend partially or fully on agricultural land for their existence are commonly called farmland birds.

In the light of evolution, the development of farming in Europe is only very recent (Colledge et al. 2005) and farmland birds have not evolved as farmland birds. The species that we call farmland birds originally occurred in natural ecosystems, such as raised bogs, grassland plains, wetlands and steppes (Beintema et al. 1995). When more and more natural land was converted to farmland, they were able to find a new living environment on agricultural fields. Due to the similarities between their original habitat and the open agricultural landscape, these birds were 'pre-adapted' to inhabit this man-made habitat (Van der Weijden et al. 2010). Some species were even able to extend their ranges and became more numerous than ever before (Beintema et al. 1995). However, this development changed abruptly in the second half of the 20th century, when agricultural practices intensified and most species of farmland passerines started to decline. The natural habitats of these bird species had in the meantime been degraded or even disappeared, so that their existence is now dependent on farmland. For these 'farmland specialists', farmland is their last resort.

Agricultural intensification

After World War II, several fundamental changes took place in Western-European agriculture (Stoate et al. 2001, Stoate et al. 2009). After the food shortages during and shortly after the war, European countries sought ways to increase agricultural production and meet the demands of the growing population. To realise this goal, political involvement was considered necessary. In 1957, the Common Agricultural Policy was adopted by the then six member states of the European Economic Community (Belgium, France, Italy, Luxembourg, West Germany and The Netherlands). The CAP realised an open market for the trade of agricultural products between the member states, while the principle of community preference ensured that products of member states had priority over those from other countries (Ackrill et al. 2008). Price support mechanisms and export subsidies secured a good and stable income for farmers, so that their standard of living could improve and technical progress could be made. The aim of the CAP was to stabilise food prices and increase agricultural productivity in order to ensure the availability of sufficient supplies for consumers at reasonable prices (Ackrill et al. 2008).

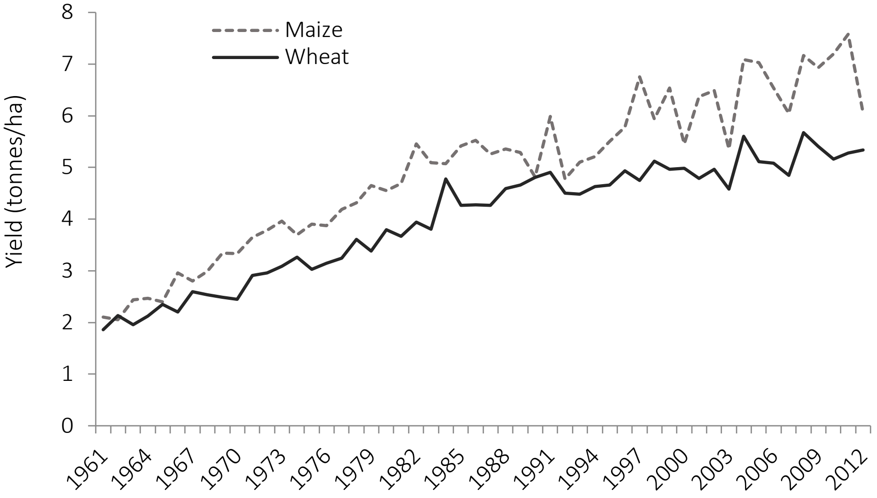


Figure 1. Trends in the average annual production of wheat and maize in the European Union between 1961 and 2012 (FAOSTAT 2014).

Since its introduction, the CAP has often been amended and reformed, but the strong coupling between payment and production was only relinquished to some extent after 1992 (Stoate et al. 2009). In particular during the 1960s, 1970s and 1980s, the CAP was the driver behind the process of agricultural intensification. Agricultural changes included for example the increased use of pesticides and fertiliser, the enlargement of fields by the removal of semi-natural boundary structures such as hedges and margins, and the reduction of crop diversity at the farm and landscape scale (Fuller et al. 1995, Chamberlain et al. 2000). In grassland areas, improved drainage combined with the use of fertilizers and grass-monocultures made earlier and more frequent harvesting of silage grass possible (Newton 2004). All these and other changes resulted in a mass increase in agricultural production (Figure 1). Despite an increase of the human population, the amount of food produced per capita increased by 25% between 1970 and 2000 (Krebs et al. 1999).

Effects on farmland birds

Soon after the first post-war agricultural changes, the environmental consequences became visible. Public awareness of the adverse effects of pesticides was raised by the publication of the soon famous book *Silent Spring* by Rachel Carson (1962). Fifty years later, the link between farming intensification, environmental degradation and the loss of species has been studied extensively, and is now widely acknowledged (Krebs et al. 1999, Stoate et al. 2001, Benton et al. 2002, Robinson and Sutherland 2002, Geiger et al. 2010). Farmland species from various taxa have been affected by agricultural intensification, including vascular plants (Thomas et al. 2004, Andreasen and Streibig 2011), arthropods (Benton et al. 2002, Attwood et al. 2008), mammals (Macdonald et al. 2007) and birds (Donald et al. 2006, Wretenberg et al. 2006, Herzon et al. 2008). Although birds are not the most sensitive species group and often respond to changes with a time lag because of their relatively long life span (Chamberlain et al. 2000, Thomas et al. 2004), birds are useful as indicators of the overall state of biodiversity within an ecosystem (Renwick et al. 2012). Birds are high up in the food chain and therefore likely to respond to changes further down (Hallmann et al. 2014). Birds are also widespread and diverse, their ecology is well understood, and fluctuations in bird diversity seem to mirror those in other species groups (Gregory 2006, Renwick et al. 2012).

Although farmland birds at first profited from the expanding agriculture, this effect was soon reversed when agricultural practices continued to intensify (Chamberlain and Fuller 2000, Chamberlain et al. 2000, Donald et al. 2001b, Donald et al. 2006). Today, agricultural intensification and expansion are considered to be among the largest extinction threats to birds (Tilman et al. 2002, Green et al. 2005). Fuller et al. (1995) calculated that in the United Kingdom, 15 out of 18 analysed farmland bird species had become less abundant in 1990 compared to 1970, seven of which had declined by more than 50%. Additionally, the distribution ranges of 24 out of 28 species of farmland birds had contracted during this period. Although the attention for biodiversity in agricultural areas increased after 1990, bird populations continued to decline (Donald et al. 2006, Wretenberg et al. 2007). In the Netherlands, approximately 6,6 to 11,4 million farmland birds have disappeared since the 1960s (Sovon 2012). The population declines and range contractions of farmland birds are directly related to the degree of agricultural intensification within a landscape (Herzon et al. 2008) or within a country (Donald et al. 2001b, Wretenberg et al. 2007, Geiger et al. 2010). Cereal yield, milk production and fertilizer use significantly correlate negatively with bird population trends in Europe; cereal yield alone explaining as much as 31% of the variation in population trends (Donald et al. 2001b).

Various aspects of agricultural intensification have contributed to bird population declines. Present-day agricultural landscapes are simplified and homogenised, lacking not only semi-natural landscape elements such as field margins and hedgerows, but also the former diversity in crops (Stoate et al. 2001, Benton et al. 2003). Traditional crop rotation schemes have been shortened and simplified with help of fertiliser to restore soil nutrients and pesticides to suppress disease, so that farmers can specialise in crops that are economically most profitable. For birds, this has reduced habitat diversity both spatially and temporally and diminished the area of suitable breeding and foraging habitat (Chamberlain et al. 2000). Reduced habitat diversity has, in combination with increased herbicide and pesticide applications, also reduced the availability of important invertebrate and plant food resources (Wilson et al. 1999, Benton et al. 2002). On silage grassland, earlier and more frequent mowing resulted in great losses of eggs and chicks of waders and other grassland species (Wilson et al. 1997, Tyler et al. 1998, Roodbergen et al. 2012). Seed resources for wintering birds have decreased due to herbicide use, improved harvesting techniques and the shift from spring-sown to autumn-sown cereals and the associated loss of winter stubbles, driving the population declines of seed-eating birds (Wilson et al. 1999, Newton 2004, Taylor et al. 2006).

Agri-environmental management

The increase in agricultural production that was realised over the past decades is not expected to level off yet. The human population is projected to grow by 50% over the next 30 years and human dietary preferences are shifting towards a larger proportion of animal protein, requiring even more cereals, maize and soy beans for animal fodder (Tilman et al. 2001, Green et al. 2005). At the same time, there is a growing awareness of the detrimental effects of the human population and its agricultural demands on the planet. Society calls for a more sustainable agriculture, that reduces its environmental impacts and tries to reverse past losses of biodiversity (Firbank 2009). Over the past years, societal concern was for example related to the decreases in pollinator diversity and abundance that threaten food production (Meffe 1998, Kremen et al. 2002). But also regarding the large-scale farmland bird declines, today is seen as a pivotal moment for bird conservation in Europe (Wilson et al. 2010).

From the early 1980s onwards, organised attempts have been made in Western Europe to counteract the effects of modern agriculture on biodiversity and environment. So-called agri-environment schemes have been operated by many European countries, inviting farmers to participate in formal agreements to change their management practices (Berendse et al. 2004). In return, farmers receive payments that compensate them for income losses and for any management actions that need to be performed. The choice to adopt agri-environment schemes is usually voluntary for individual farmers, but since 1992 it is compulsory for EU member states to participate in agri-environmental programmes (De Snoo et al. 2012a, European Commission 2014). Already from the start of these programmes there was a large variety in agri-environmental prescriptions. They ranged from being very specific, for example prescriptions aimed at increasing the Cirl bunting *Emberiza cirlus* in south Devon, UK (Ovenden et al. 1998), to being very general, such as pesticide-free strips at the borders of cropped fields to reduce surface water pollution and to enhance the diversity of plants, invertebrates and birds (De Snoo et al. 1994). Between 2007 and 2013, the EU expenditure on agri-environmental measures amounted nearly 20 billion euro, which was 22% of the expenditure for rural development (European Commission 2014).

This thesis is mainly concerned with one specific form of agri-environmental management, which is the establishment of arable field margins. Arable field margins are uncropped strips of land on which no fertiliser or pesticides are applied, usually sown with seed mixtures containing grasses, forbs and flowers.

They can be very narrow, but also reach widths up to 50 meters (Field et al. 2007, Conover et al. 2009). Field margin management can have many different objectives, including the conservation of plant and invertebrate diversity (Asteraki et al. 2004, Noordijk et al. 2010), enhancement of pollination (Rands and Whitney 2011), pesticide reduction through biological pest control (Collins et al. 2002), improvement of water quality (De Snoo and De Wit 1998) and landscape restoration (Donald and Evans 2006). In many regions, field margins are aimed at supporting populations of breeding and wintering birds, for which they can provide foraging habitat, shelter or a breeding site (Rands 1987, Sparks et al. 1996, Vickery and Fuller 1998, Vickery et al. 2002).

Debates about the tense relationship between food production and nature often centre around the theme of 'land sparing or land sharing' (Green et al. 2005). 'Land sharing' integrates conservation and production on the same surface area of land, while 'land sparing' aims to increase yields to minimise demands for agricultural land. Both approaches have benefits and limitations, depending on factors such as the current level of farming intensity, the demand for agricultural products, land scarcity, current local environmental status and the relationship between agricultural yield and biodiversity (Green et al. 2005, Fischer et al. 2014). For improving food security and preserving ecosystem services that have direct benefits for agriculture, the option of land sharing is the obvious choice (Tscharntke et al. 2012). In the Netherlands, land sharing has also been the most common conservation route for the protection of farmland birds, although farmland reserves also exist. However, the distinction between land sharing and land sparing is not absolute and may change depending on the spatial scale considered. Field margins, for example, can be regarded as a land sparing option at a fine spatial grain, because they separate the productive land and the non-productive land. On a larger spatial resolution, however, a network of field margins and agricultural fields may result in a landscape that would be regarded as an example of land sharing (Fischer et al. 2014).

Effectiveness of agri-environmental management

Considering the large sums of money spent on agri-environmental management, it is surprising that research on this subject came to a slow start. In 2003, Kleijn and Sutherland concluded that the total number of studies evaluating the effectiveness of agri-environmental management was not only low, but also originated from only six European countries, while agri-environment schemes were active in 26 countries at the time. Furthermore, the research design of most studies was inadequate to reliably assess the effectiveness of the schemes. Fortunately, in the first two decades of the 21th century, the number of studies on agri-environmental management increased rapidly.

Analyses of scheme effectiveness in a number of European countries returned highly variable results. Invertebrate diversity and abundance were seemingly easier to enhance than those of birds and plants (Kleijn and Sutherland 2003). But also within species groups, effects of management were variable and many studies showed both positive and negative effects of agri-environmental management, depending on the species or the area under consideration (Kleijn and Sutherland 2003, Kleijn et al. 2006). There are various reasons behind the failure of some agri-environment schemes to promote target species. Sometimes measures are too simple and do not address the key variables that underlie population declines (Kleijn et al. 2004, Van Dijk et al. 2013, Meichtry-Stier et al. 2014). Measures can also differ in effectiveness depending on the characteristics of the region or landscape where they are applied (Whittingham et al. 2007), for example due to differences in landscape complexity and habitat diversity (Wretenberg et al. 2010, Concepción et al. 2012). On arable land, the use of pesticides has strong detrimental effects on birds that are difficult to reverse by agri-environmental management (Potts 1986, Geiger et al. 2010, Hallmann et al. 2014).

In the Netherlands, research into the effects of agri-environmental management on birds has mainly focussed on meadow birds, because the Netherlands has an international responsibility for several meadow bird species that have their main breeding grounds in this country (Beintema et al. 1995, Berendse et al. 2004). Nest protection and postponed mowing were among the first initiatives (implemented from 1981 onwards, Kleijn et al. 2001), but turned out to be ineffective when no other measures were taken (Kleijn and van Zuijlen 2004, Kragten et al. 2008a). In some cases, population densities were even lower on fields with agri-environmental measures than on those without (Kleijn et al. 2001, Breeuwer et al. 2009). Over the years, the ecological and behavioural knowledge of meadow birds increased and it became evident that additional measures were needed, such as raising groundwater levels, reducing fertilisation and restoring landscape openness (Melman et al. 2008, Schekkerman et al. 2008, Breeuwer et al. 2009, Van der Vliet 2013).

Within arable areas, research on birds and agri-environmental management in the Netherlands often concentrated on the effects of organic farming (Kragten and de Snoo 2007, 2008, 2008b, Kragten et al. 2011). Although a number of studies exist on the effects of arable field margins on birds, for example from Switzerland (Weibel 1999, Zollinger et al. 2013) and the UK (Douglas et al. 2009, Davey et al. 2010a, Baker et al. 2012), this topic has received relatively little scientific attention in the Netherlands.

Research aims

The central aim of this thesis is to evaluate the effectiveness of field margins as a form of agri-environmental management to aid the conservation of arable farmland birds. Several areas of study were connected to gain a good understanding of the value of field margins for birds. Monitoring data from a northern province of the Netherlands was used to explore whether field margins affect the abundance and population development of a number of farmland bird species. The large-scale census data were supplemented with behavioural and ecological studies that focused on the Skylark, a farmland bird that is declining over most of Europe. By studying the effects of field margins on the foraging behaviour, diet, nestling condition and reproduction of the Skylark, the benefits and limitations of field margin management became apparent.

The study species: the Skylark

The main study species in this thesis is the Eurasian Skylark *Alauda arvensis* (Linnaeus 1758), hereafter simply called Skylark. The Skylark, a passerine of about 18 cm length, was the most widespread and one of the most abundant birds in the Netherlands in the 1970s, but it has suffered greatly from agricultural intensification (Van 't Hoff 2002). The Skylark has a long breeding season that starts early April and continues into August, during which time most breeding pairs undertake three nesting attempts (Donald 2004). Clutches usually contain 3-5 eggs, which are incubated by the female for 12-14 days. After hatching, the chicks are fed by both parents. It takes around 8 days before the chicks leave the nest and around 6 days more before fledging. It is often seen that the male is still feeding the chicks of the previous nest while the female is already incubating the next clutch (Delius 1965). The Skylark is rather short-lived and return rates for juveniles are low, therefore a good reproduction rate is essential to maintain population levels (Donald 2004, Hegemann 2012).

With a distribution that includes entire Europe, parts of Asia, the Middle East and the north of Africa, the Skylark can be called very widespread (Donald 2004). Skylarks are typical of open landscapes and avoid nesting close to tall structures like trees or buildings (Chamberlain and Gregory 1999). They are strongly associated with farmland throughout much of their range, but also occur in a range of (semi-) natural habitats, such as steppes, edges of marshes, dunes, heathland, moorland and grassland plains (Donald 2004). In the Netherlands, the Skylark has decreased by 96% since the 1960s, a loss of approximately 750,000 to 1,1 million breeding pairs (Sovon 2012). It has become rare in large parts of the country, especially in areas that mainly consist of production grassland (Figure 2, Van 't Hoff 2002). Also in other western European countries the Skylark is in steep decline (Chamberlain and Crick 1999, Wretenberg et al. 2006, EBCC 2013). BirdLife International has marked the species' population status as Depleted (BirdLife International 2004). Due to its large geographical range, the Skylark is currently not of conservation concern according to the IUCN red list (IUCN 2014). However, it is more than likely that local and regional extinctions have occurred and will occur, given the rate of the decline and the fact that the declines continue even at low population densities.

Different aspects of agricultural intensification have contributed to the population declines of Skylarks on farmland. The amount of suitable breeding habitat that is available to Skylarks has been reduced because of the lower crop diversity at the farm and landscape level (Chamberlain and Vickery 2000, Geiger et al. 2010, Henderson et al. 2012). Also the switch from spring-sown to autumn-sown cereals is believed to be an important factor. The growth of autumn-sown cereals requires the ploughing and sowing of the land in October or November, thereby reducing the availability of overwintering stubble fields that are rich in cereal and weed seeds (Donald et al. 2001a, Siriwardena et al. 2008, Geiger et al. 2013). Also, autumn-sown cereals start their growing season earlier than spring-sown cereals and thereby become too tall for nesting already early in the breeding season, which can reduce the number of breeding attempts per season (Chamberlain et al. 1999, Chamberlain and Vickery 2000, Donald et al. 2002). A last important factor that may have contributed to population declines is the decreased availability of key invertebrate and seed foods on present-day farmland, which is associated with pesticide and herbicide applications, increasing specialisation of farmland and loss of uncropped habitat (Wilson et al. 1999, Geiger et al. 2010).

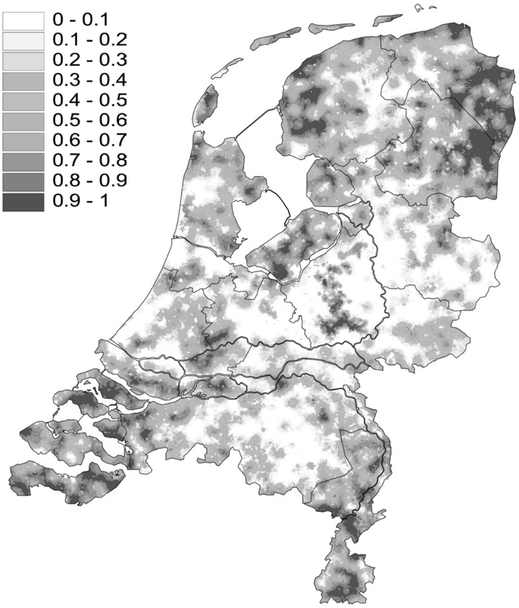


Figure 2. Relative densities of the Skylark in the Netherlands (SOVON Vogelonderzoek Nederland, 2002).

The study area: Groningen

The research was conducted in Groningen, one of the northern provinces of the Netherlands. Arable agriculture is the main land use in large parts of this province, and field margins have been present here for more than 15 years. The total surface area of agricultural land exceeded 169,000 ha in 2012, which is 71% of the total land surface of the province (Dienst Regelingen 2012). Less than half of the agricultural land is in use as grassland, mostly in the western part of the province that is not considered in this thesis. On cropped land, cereals and root and tuber crops (mostly sugar beet and potato) are the most abundant crops, followed by maize, lucerne, rape seed, onion and hemp (Figure 3).

Most research for this thesis was performed in the north-eastern part of the province of Groningen, in the current municipality Oldambt, which is located on fertile marine clay soil (see Figure 1 in Chapter 2). In this region fields are relatively large and semi-natural habitat elements relatively scarce. Wheat has since long been the most important crop in this region, although the proportion of crops related to cattle farming has increased steadily over the past decades. Since 1980, the relative surface area of grassland has increased from ca. 12% to 22% and maize from ca. 1% to 5%, mostly at the expense of lucerne and rape seed (Wiersma et al. 2014). In this same period therelative surface area of spring-sown cereals decreased from ca. 15% to 3% at the expense of a larger proportion autumn-sown cereals (Wiersma et al. 2014). Within the Netherlands, eastern Groningen is one of the regions with a relatively high density of Skylarks (Figure 2).

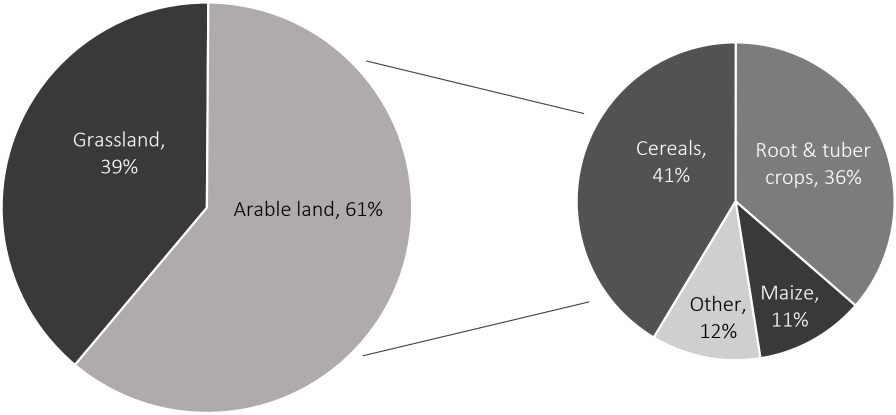


Figure 3. Relative surface area of grassland, arable land and the most abundant crops in 2012 in the province of Groningen, the Netherlands.

Agri-environmental management in Groningen

Compared to other provinces, the province of Groningen has a relatively long history in the conservation of arable farmland birds (Wiersma et al. 2014). In 1985, the province of Groningen issued the first systematic farmland breeding bird inventory (De Rooij 1987), followed by a second inventory in 1989 (Koks 1989). In 1990, the province initiated the Akkervogelproject (arable farmland bird project) that was aimed at gaining more insight in the ecology and habitat preferences of arable farmland birds, but also at exploring possibilities for conservation and policy development (Van Scharenburg et al. 1990). Two species received special attention in this project: the Partridge *Perdix perdix* and the Montagu's Harrier *Circus pygargus*.

Around that same time, the European Economic Community introduced the set-aside incentive scheme to help reduce the large and costly agricultural surpluses that were produced in Europe (Regulation 1272/88). On the basis of this scheme, farmers could receive compensatory payments if they voluntarily set aside arable land. In Groningen, the response was large, in particular in areas where wheat was a prominent crop because wheat prices were low at the time. Set-aside became compulsory in 1992 as part of the reforms of the Common Agricultural Policy under agricultural commissioner R. McSharry of the European Union. Large arable farms were obliged to set aside 15% of their land, later reduced to 10%. After a few years, unexpected positive effects of set-aside on biodiversity were observed. Different birds of prey, such as Montagu's Harrier, Hen Harrier *Circus cyaneus* and Barn Owl *Tyto alba* showed marked population increases (Vermeer 1993, Koks and Van Scharenburg 1997). From 1992, all member states of the European Union were required to develop agri-environment programmes for which they would receive 50-75% funding by the EEC in order to reduce pollution and to improve the environment, the countryside, the landscape, the soil, genetic diversity and natural resources (Regulation 2078/92). The Dutch Ministry of Agriculture, Nature and Fisheries launched a 'Nature set-aside' programme in 1995 and evaluated the effects on several species groups, among which mammals and birds (Ellenbroek et al. 1998a, b). From 1997, also strips of set-aside, called 'fauna margins', became available to farmers as an option specifically aimed at the conservation of arable farmland birds.

The set-aside regulations were abolished by the European Commission in November 2008 because surpluses had been reduced and prices had risen. Ecological considerations were of minor importance in this decision. Over the years, however, programmes that stimulated 'wildlife-friendly farming' on arable farmland had become general practice, so that farmland bird conservation could continue, albeit at a much smaller scale than was achieved with the set-aside regulations. With the start of the agri-environmental support system Subsidiestelsel Natuur- en Landschapsbeheer (SNL) in 2010, management agreements were only allowed in 'core areas' that were appointed by the government. The idea behind the clustering of measures was that a larger part of the total bird population would be reached and that measures would be more effective in higher densities (Bos et al. 2010). Within the SNL support system there are two schemes for arable farmland birds, called 'arable farmland with breeding birds' and 'arable farmland with wintering birds'. Fauna margins and natural set-aside are options within the scheme for breeding birds; the scheme for wintering birds comprises patches of winter seed resources and cereal stubble. The ratio between winter and summer measures is approximately 1:2.5 (Figure 3). To follow international terminology, fauna margins are called field margins in this thesis.

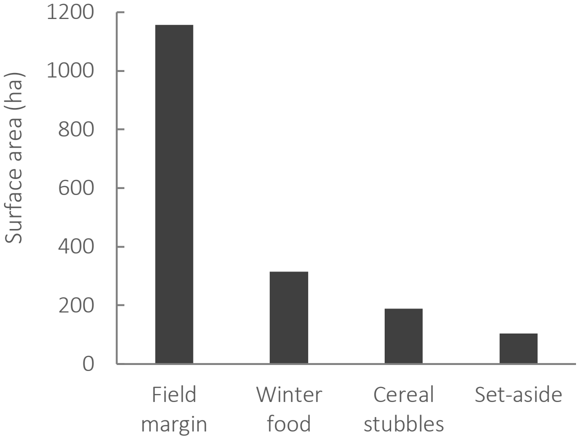


Figure 4. Mean surface area over 2011 and 2012 of the four most common forms of agri-environmental management in the province of Groningen, the Netherlands (Wiersma et al. 2014).

Thesis outline

In this thesis, the effectiveness of field margins as a conservation measure for arable farmland birds is evaluated. To achieve a good overview of the effects of field margins on birds, a larger-scale population study that considers multiple species is combined with several detailed studies that zoom in on the breeding biology and foraging behaviour of one species, the Skylark.

In chapter 2, the relationship between field margins and the occurrence of ten farmland birds is explored. First the habitat associations of the bird species are determined and their abundance is related to the surface area of field margins. Then the development of bird abundance through time is analysed to compare possible differences in population trends in areas with and without field margins. Based on the results of both analyses, the impact of field margins on the distribution and population development of the ten bird species is assessed.

Chapters 3, 4 and 5 focus on the effects of field margins on Skylarks. Chapter 3 aims to answer one of the first questions that come to mind when studying the effects of agri-environmental measures on birds: are the measures indeed used by the species they are intended for? In this chapter, the foraging behaviour of Skylarks that provide for their young is studied in detail to quantify the use of field margins as a foraging habitat compared to other common habitats and crops. The foraging observations are supplemented with measurements of invertebrate availability to help explain the observed behaviour. Based on the typical foraging distances of the Skylark in the study area, some conclusions are drawn on the appropriateness of the placement of field margins within the landscape.

The next two chapters explore if and how Skylark breeding success is affected when adult Skylarks use field margins as a foraging habitat. In Chapter 4, the diet composition of nestlings that were or were not provided with food from field margins is compared. Although this subject has received relatively little attention in previous research, diet diversity and composition can have profound effects on the weight and health of young birds. Finally, chapter 5 investigates the effects of field margins on clutch size, nestling condition and survival. Increasing the reproductive success of the Skylark is one of the pillars under population recovery and therefore one of the main goals of agri-environmental management. Clutch size, nestling condition and survival are important components of overall productivity that should be improved in order for field margins to be a successful conservation instrument.

The thesis ends with a general discussion (chapter 6), in which the findings from the previous chapters are synthesised. I will discuss the effects of field margins on Skylarks and other farmland birds and give suggestions for improvement of agri-environmental management in intensively farmed arable areas in the Netherlands. Based on my research and research previously performed by others, certain requisites and circumstances are derived that have proven to be essential for successful agri-environmental management.

Hail to thee, blithe Spirit!
Bird thou never wert,
That from Heaven, or near it,
Pourest thy full heart
In profuse strains of unpremediated art.

Higher still and higher
From the earth thou springest
Like a cloud of fire;
The blue deep thou wingest,
And singing still dost soar, and soaring ever singest.

P.B. Shelley (To a skylark, 1820)

Chapter 2

The impact of field margins on farmland bird abundance, species richness and population growth rates in the north of the Netherlands

Marije W. Kuiper, Popko Wiersma, Henk Jan Ottens, Jasper van Ruijven,
Geert R. de Snoo, Frank Berendse, Ben J. Koks

Abstract

Biodiversity on European farmland has been under pressure for several decades and agri-environmental management takes a central place in the conservation of species. Arable field margins are a common management option, aiming to provide foraging and breeding habitat for a range of farmland birds. Although field margins are the main management instrument for breeding birds in arable landscapes in the Netherlands, it is unclear if, and which, species profit from this measure. Here we assessed the influence of field margins on the abundance, species richness and population development of ten bird species, using monitoring data collected between 2009 and 2013 in the northeast of the Netherlands. Bird species richness was positively related to field margin surface area. This effect was consistent across different geographical regions within the province. The abundance of most study species, in particular Bluethroat, Lapwing, Pheasant, Quail and Whitethroat, increased with field margin area, although the effect varied across regions. The population densities of two species increased during the study period (Lapwing and Yellowhammer) and one decreased (Yellow wagtail). The species' population growth rates did not differ between areas with and without field margins, except for Skylark and Meadow pipit, that exhibited more negative growth rates in areas with field margins. The results indicate that field margins improve bird species richness and abundance, but since population growth rates are not affected this seems to be caused by the establishment of field margins in areas that already had higher bird densities beforehand, or by the relocation of birds to areas with field margins through habitat selection.

Introduction

Historically, field margins and other border structures had true agricultural functions, such as defining field boundaries and fencing crops from wildlife (Marshall and Moonen 2002). During the second half of the 20th century, the process of agricultural intensification called for field enlargement and larger machinery, prompting the removal of field margins and hedgerows from the landscape (Arnold 1983). A few decades later, the interest in field margins and their functions for wildlife, environment and ecosystem services has returned. With the increased use of fertiliser and pesticides, field margins can act as buffer strips against drift deposition and run-off of pollutants into the surface water (De Snoo and De Wit 1998). Also the role of field margins as a habitat for beneficial insects that provide services such as pollination and pest control, was increasingly acknowledged (Kremen et al. 2002, Geiger et al. 2009, Hof and Bright 2010, Rands and Whitney 2011). Lastly, it was recognised that field boundaries are one of the principal resources for wildlife in intensively farmed areas, as well as being vital for the connectivity of natural habitats (Sparks et al. 1996, Marshall and Moonen 2002, Donald and Evans 2006).

It is likely that the removal of natural field boundaries has contributed to the substantial population declines that were observed among farmland birds in the northwest of Europe over the past 50 years (Fuller et al. 1995, Donald et al. 2001). Currently, policy initiatives aimed at reversing the negative bird population trends often include the establishment of field margins: uncropped strips of land that are either allowed to regenerate naturally or sown with seed mixtures containing grasses, forbs and flowers (Vickery et al. 2009, Baker et al. 2012, Kuiper et al. 2013). Field margins are widely advocated for their positive effects on biodiversity and ecosystem services, and they are a common agri-environmental prescription in many European countries (Denys and Tscharntke 2002, Marshall et al. 2006, Smith et al. 2008, Vickery et al. 2009, Noordijk et al. 2011, Rands and Whitney 2011, Cordeau et al. 2012, Zollinger et al. 2013).

Field margins are an example of a ‘broad-and-shallow’ agri-environmental measure: a “low-level environmental enhancement through modest farmer effort” (Baker et al. 2012). Broad-and-shallow options generally operate at the national scale and are designed to deliver general biodiversity or environmental benefits, rather than being shaped to fit the specific needs of certain species. For birds, field margins may provide foraging habitat, shelter from predators and for some species a breeding site (Sparks et al. 1996, Vickery and Fuller 1998, Stoate and Szczur 2001, Vickery et al. 2002, Aschwanden et al. 2005, Kuiper et al. 2013). Positive effects of field margins on bird densities have been found in Switzerland (Meichtry-Stier et al. 2014), but in the United Kingdom the effect of field margins on bird population growth rates was negative for several species (Baker et al. 2012) and varied regionally (Davey et al. 2010a). In the Netherlands, field margins are the main instrument by which government and farmers aim to support bird populations in arable areas (Provincie Groningen 2008), but it is unclear whether, and which, species benefit from this type of management.

Here we use the data from a large-scale farmland bird monitoring programme (Roodbergen et al. 2011b) to study the effects of arable field margins on ten bird species that use farmland (i.e. agricultural fields and semi-natural habitat elements commonly found on farmland) for breeding or foraging. The aim of this study was to assess whether arable field margins had a positive effect on the abundance and species richness of farmland birds during the breeding season and on their population development between 2009 and 2013. The main research questions were (1) is the abundance and species richness of farmland birds positively related to the surface area of field margins, and (2) do field margins have a positive influence on bird population growth rates? To answer these questions we conducted two series of analyses. First, we studied the habitat associations of the ten bird species to assess whether abundance and species richness correlated positively with a larger surface area of field margins. The advantage of this method is that the relation with field margins can be tested taking into account the effects of other habitat types and crops that may influence bird distributions (Whittingham et al. 2009), but the disadvantage is that habitat associations give no information about temporal processes. Also, there is a risk of bias when field margins were preferentially placed in areas or at farms where bird abundances were higher a priori (Kleijn and Sutherland 2003). Therefore, we also compared bird population growth rates on locations with and without field margins to assess the effect of field margins on population development. Since species' responses to conservation measures are dependent on spatial context, regional differences in the efficacy of measures are often observed (Whittingham et al. 2007, Davey et al. 2010a). To assess whether such regional variation also exists in our study area, bird habitat associations were studied separately for three regions that differed in soil type and cropping plan.

Methods

The study was conducted in the province of Groningen, the Netherlands (Figure 1). Bird monitoring took place in areas with arable and mixed farming, excluding the predominantly pastoral areas in the southwestern part of the province. Agri-environmental management was introduced to the province more than 15 years ago, with field margins currently being the prime management option (Wiersma et al. 2014). Field margins generally are 12 m wide, sown with different mixtures of grasses and herbs. Mowing regulations have varied over the years, in most years margins were partially mown (20-70% of the surface area) twice a year. Of the 1769 census points that were monitored over the five years, 579 (33%) contained at least 0.01 ha of field margins. The average relative surface area of field margins within the census circles that contained a field margin was 5.4% (SD ±6.3).

Within the province of Groningen, several regions can be distinguished that differ in soil type, cultivation history and cropping plan (Figure 1). To assess whether the effect of field margins on bird abundance and species richness varied across regions, separate analyses were carried out for three regions with sufficient data points: Hogeland (region 1), Oldambt (region 2) and Veenkoloniën (region 3). Region 1 comprises the northernmost part of the province, where the soil consists of light marine clay. Onion and vegetables (mainly carrots and Brussels sprouts) are characteristic crops, as well as autumn-sown cereals, potatoes and grassland (table 1). Region 2 is situated on the heavy marine clay soils in the eastern part of the province. Here, autumn-sown cereals, rapeseed and lucerne are characteristic crops, while spring-sown cereals and maize are markedly low in surface area. The third region is located in the south of the province, where the soil consists of sand and peat. This region is characterised by a large proportion of spring-sown cereals, potato, maize, sugar beet and hemp.

Bird monitoring

Birds were monitored by professionals and experienced volunteers using a point count method, as part of a farmland bird monitoring programme called MAS (Meetnet Agrarische Soorten), set up by the Dutch Montagu's Harrier Foundation, the provinces of Groningen and Flevoland, the CBS and Sovon, the Dutch Centre for Field Ornithology (Roodbergen et al. 2011b). The census points were randomly distributed over the province, but only located on farmland (Figure 1). To avoid crop damage, census points in fields were moved to the nearest field border. Following Baker et al. (2012), only points comprising > 50% agricultural land were included in this study. Between 2009 and 2013, 640 unique points were surveyed 1769 times in total. 62 points were counted once, 241 were counted twice, 175 three times, 110 four times and 52 five times.

During a survey, all birds seen or heard within a radius of 300 m from the census point were drawn on a map with a code indicating breeding status. Surveys took place between 30 minutes before and five hours after sunset (Roodbergen et al. 2011a). The duration of the surveys was 5 minutes in 2009 and 2010, and 10 minutes in 2011, 2012 and 2013. Bird abundances observed in 2009 and 2010 were corrected for the shorter survey time to enable comparison with later

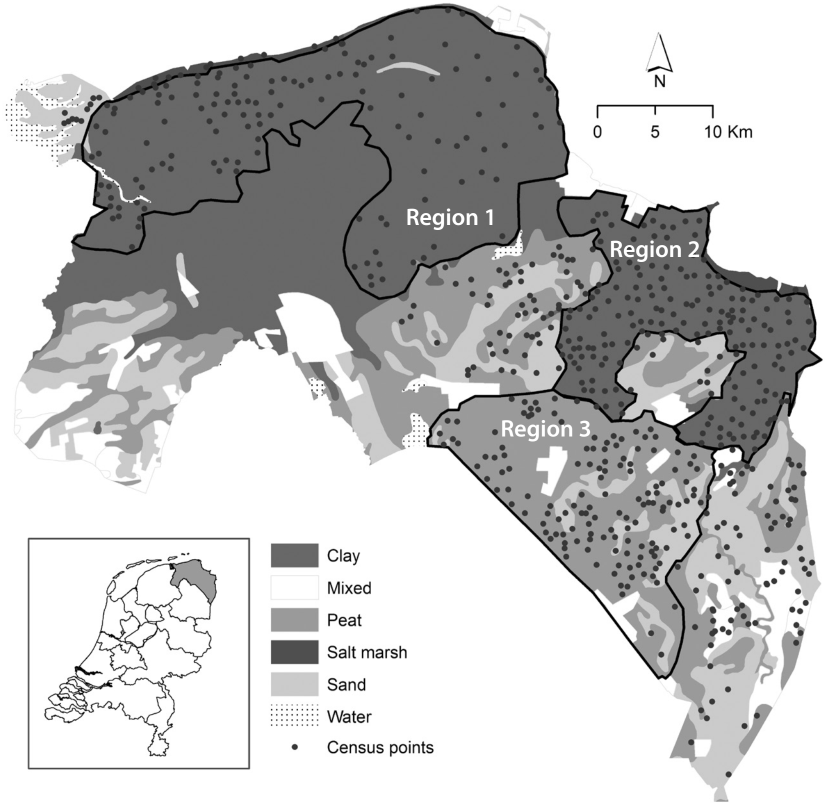


Figure 1 Soil types and location of the census points in the province of Groningen, the Netherlands (inset: location of Groningen in the Netherlands). Separate analyses were carried out for the three regions indicated in the figure.

years: species-specific correction factors were calculated and applied to the 2009 and 2010 data by dividing the duration of the counts in 2013 in two 5-minute sections, and calculating the difference in bird numbers between the first 5 minutes and the full 10-minute count. The 5 minutes extra counting time resulted in approximately 20-30% higher abundances for the species considered.

The maximum number of individuals that was recorded over all visits was taken as the annual value per census point, taking into account only territorial and breeding birds. In 2011 through 2013, census points were visited four times between and April 1 and July 15. In 2009 and 2010, the census points were visited three times, omitting the first round. To correct for the effect of the extra visit in the later years, a correction factor was calculated based on the data collected in 2013, by comparing the maximum number of individuals recorded during all four visits and the maximum number of individuals recorded during the last three visits. The correction factor was small for all species, because the maximum number of individuals was generally not recorded during the first visit.

The employed point count method is not suitable to study habitat associations of rare species and species with a small sighting chance, because these are likely to be missed during short counts at random locations. This led to the exclusion of Grey partridge (*Perdix perdix*), European stonechat (*Saxicola rubicola*) and Eurasian curlew (*Numenius arquata*) from the analyses. Birds of prey were excluded because of their large home ranges. The following species were used for analyses: Bluethroat (*Luscinia svecica*), Common linnet (*Linaria cannabina*), Common pheasant (*Phasianus colchicus*), Common quail (*Coturnix coturnix*), Common whitethroat (*Sylvia communis*), Meadow pipit (*Anthus pratensis*), Northern lapwing (*Vanellus vanellus*), Skylark (*Alauda arvensis*), Yellowhammer (*Emberiza citrinella*) and Western yellow wagtail (*Motacilla flava*). For convenience, the additions Common, Northern and Western to the common bird names are not further used in this chapter. Total bird species richness per census point was calculated by counting all species of which at least one individual was observed during the visits, taking into account only the ten species listed above.

Habitat composition

The occurrence and abundance of birds is expected to correlate to a large extent with the crops and semi-natural habitat elements that are present at a certain location (Whittingham et al. 2005, Whittingham et al. 2009, Gilroy et al. 2010). Therefore, we modelled the relation between field margins and bird abundance taking into account the surface areas of the most common crops and semi-natural habitat elements. The habitat composition within a distance of 300 m around each census point was mapped using ArcMap 10.1 (ESRI, Redlands, California). Maps of the Ministry of Economic affairs from 2009 through 2013 were used to calculate the surface area of agricultural habitat types (crops, grassland, agri-environmental management). In some areas, additional field margins were established that were derived from the Portal for Nature and Landscape (Portaal Natuur en Landschap 2014).

The surface areas of semi-natural habitat types were derived from a nature element map of the Netherlands, created by Cormont et al. (in prep.). This map combines information from a topographical map (Top10NL, 2010), two land use maps (Bestand Bodemgebruik, 2008 and Landelijk Grondgebruikbestand Nederland 6, 2008) and a nature type map (Basiskaart Natuur, 2009) This map was used for all study years, assuming that the position and surface area of the semi-natural habitat elements under consideration had not changed significantly over the five-year study period. Semi-natural habitat types included in this study were road verges, wet ditches, dry ditches and vertical structures. Road verges were strips of grassy and herbaceous vegetation alongside roads. Wet ditches carry water year-round, are bordered by grassy and herbaceous vegetation and sometimes contain reed. Dry ditches only carry water during periods of high precipitation and often contain a relatively coarse and tall herbaceous vegetation. Vertical structures included buildings, forest patches and tree rows.

In order to reduce the number of explanatory variables in the models, crops with similar vegetation characteristics and agricultural management were clustered. All autumn-sown cereals (barley and wheat) were clustered, as well as all spring-sown cereals (barley, wheat, rye and oats). All types of grassland were clustered; the great majority consisting of high-input silage or grazed grasslands. In all regional models, potato and sugar beet were clustered. Habitat types that occurred in less than 10% of the census circles were excluded from the analyses. All habitat types included in the models are listed in Table 1.

Data analyses

Bird abundances in relation to habitat types were analysed using the R program for statistical computing, version 2.15.2 (R Development Core Team 2013). To account for the fact that surveys performed at the same census point in different years are not independent, the data were analysed using Generalised Linear Mixed Models

Table 1 Habitat composition within the census circles, expressed as mean proportional surface area and frequency of occurrence (percentage of census points), in the entire province of Groningen and in three regions within the province. Habitat types indicated with an asterisk were not present in sufficient frequencies to be included in the analyses.

	Province (n = 1769)		**Region 1** (n = 374)		**Region 2** (n = 590)		**Region 3** (n = 393)	
	Mean area (%)	Frequency (%)	Mean area (%)	Frequency (%)	Mean area (%)	Frequency (%)	Mean area (%)	Frequency (%)
Beet	8.7	55	8.2	57	7.0	44	11.5	71
Cereals, autumn-sown	27.1	68	27.5	90	50.5	91	8.3	38
Cereals, spring-sown	7.4	45	5.7	46	2.6	19	12.6	73
Field margin	1.7	33	1.5	26	2.0	38	2.3	44
Grassland	15.2	65	17.4	75	16.6	67	7.8	52
Hemp	0.8	5*	0.2	2*	0.1	2*	2.3	17
Lucerne	0.8	7*	0.3	4*	1.7	14	0.2	2*
Maize	5.0	33	3.1	26	2.2	18	7.4	49
Onion	0.6	5*	2.2	19	0.3	2*	0.2	3*
Potato	18.0	62	20.7	84	4.0	19	30.7	90
Rapeseed	1.5	10	0.3	3*	3.3	19	0.4	3*
Vegetables	0.5	5*	1.3	11	0.1	3*	0.3	4*
Dry ditch	0.3	58	0.2	57	0.1	37	0.5	81
Road verge	0.5	76	0.4	70	0.6	75	0.6	77
Vertical structures	2.8	66	2.0	78	1.7	55	4.9	73
Wet ditch	1.1	95	1.5	100	0.8	93	1.2	92

with census point as a random variable. Year was added as a random variable to account for differences in census technique between the years and for any other differences in bird abundances between years. The annual maximum bird count per species per census point was entered as the dependent variable, applying a Poisson-distribution and log-link function. Total bird species richness per census point followed a normal distribution and was therefore analysed using a General Linear Mixed Model. The surface areas in hectares of the selected habitat types around the census points were used as predictor variables. The effects of all predictors were explored as main effects only. All models were performed using the R package lme4 (Bates 2007). Separate analyses were carried out for the whole province of Groningen, including all 1769 counts, and for three regions within the province, comprising 374 counts for region 1, 590 counts for region 2 and 393 counts for region 3.

To avoid the variability of model outcomes that is associated with stepwise regression and other methods relying on a single best model, an information-theoretic approach was employed (Whittingham et al. 2006). Information theoretic analyses identify all models that can describe the data equally well, providing weighted parameter coefficients and a variable importance ranking (Burnham and Anderson, 2002). For each analysis, a model set with all possible combinations of predictor variables was generated and ranked by corrected AIC (AICc) using the R package MuMIn (Bartón 2013). The parameter coefficients that are presented in this chapter were averaged across all models that differed <2 in AICc value compared to the best fitting model, using zeroes as coefficients when variables did not enter a particular model. The relative importance of each predictor variable was calculated by summing the Akaike weights of all models including that variable (Posada and Buckley 2004).

When considering a large number of habitat types, it can hardly be avoided that some are correlated. Field margins were significantly correlated with a few other habitat types, but Pearson's correlation coefficients did never exceed 0.1 in the provincial model or 0.2 in the regional models. Correlations among other habitat types with Pearson's correlation coefficients exceeding 0.4 were between grassland and autumn cereals (-0.48, $P < 0.01$) and between grassland and beet/potato (-0.52, $P < 0.01$) in region 1, between grassland and autumn cereals (-0.60, $P < 0.01$) and between vertical structures and dry ditches (0.50, $P < 0.01$) in region 2, between autumn cereals and beet/potato (-0.43, $P < 0.01$) in region 3, and between autumn cereal and potato (-0.49, $P < 0.01$) in the whole province. Since modelaveraging techniques are relatively robust to collinearity between predictors, no predictor variables were excluded from the models (Freckleton 2011).

Bird population growth rates were analysed using Generalised Linear Mixed Models in SPSS 21 (IBM, Armonk, New York). The annual maximum bird count per species per census point was entered as the dependent variable, applying a Poisson-distribution and log-link function. Bird species richness followed a normal distribution and was analysed using a General Linear Mixed Model with a normal distribution and log link. Only census points that were counted in at least three of the five census years or points that were counted in two years with at least four years in between were included in the analyses. Census points were divided into two groups, one group that continuously had a field margin within the 300m census circle during the study period (n=95, counted 341 times), and one group that continuously had no field margin (n=199, counted 682 times). Census points that gained or lost a field margin over the course of the study period were omitted, because they were too small in number to analyse separately. Field margin presence and year were entered as predictor variables, as well as the interaction term 'field margin × year' to assess whether changes in maximum count over the years were affected by field margin presence. Census point was entered as subject (random factor) and year as repeated factor, so that each observation of the same census point was considered a repeated observation. Region was entered as a random variable to account for possible regional differences in population growth rates.

Results

Yellow wagtail was the most frequently counted species in the province of Groningen, followed by Skylark, Lapwing and Meadow pipit (Table 2). The densities of Bluethroat, Skylark, Whitethroat and Yellowhammer differed markedly between the three considered geographical regions. Yellowhammer was almost exclusively found on the sandy peat soils in the southern part of the province (region 3) and also Whitethroat was far more abundant in this area. Skylark was less abundant in region 1.

Table 2. The mean number of individuals per 28.3 ha census circle (±SE) in the whole province of Groningen and in three regions within the province, and total bird abundance in the province. n gives the number of census points counted in each geographic area between 2009 and 2013.

	Province (n = 1769)		**Region 1** (n = 374)	**Region 2** (n = 590)	**Region 3** (n = 393)
	Abundance	Average	Average	Average	Average
Bluethroat	517	0.29 (±0.01)	0.59 (±0.04)	0.13 (±0.02)	0.39 (±0.03)
Lapwing	1998	1.13 (±0.04)	1.46 (±0.09)	0.71 (±0.05)	1.13 (±0.03)
Linnet	450	0.25 (±0.02)	0.31 (±0.04)	0.20 (±0.02)	0.35 (±0.03)
Meadow pipit	1753	0.99 (±0.03)	0.92 (±0.04)	1.12 (±0.05)	0.87 (±0.05)
Pheasant	987	0.56 (±0.02)	0.59 (±0.04)	0.40 (±0.03)	0.71 (±0.04)
Quail	618	0.35 (±0.02)	0.22 (±0.03)	0.46 (±0.03)	0.35 (±0.04)
Skylark	2834	1.60 (±0.04)	0.60 (±0.05)	1.46 (±0.06)	2.06 (±0.07)
Whitethroat	1163	0.66 (±0.02)	0.26 (±0.03)	0.33 (±0.03)	1.41 (±0.06)
Yellowhammer	1161	0.66 (±0.03)	0.01 (±0.00)	0.08 (±0.01)	1.81 (±0.06)
Yellow wagtail	3636	2.06 (±0.04)	1.54 (±0.06)	2.32 (±0.07)	2.04 (±0.07)
Total abundance	15117	0.85(±0.03)	0.65 (±0.04)	0.72 (±0.04)	1.11 (±0.05)
Species richness		4.5 (±0.05)	4.0 (±0.09)	4.0 (±0.08)	5.5 (±0.09)

Bird abundances

Considering the data from the whole province, the abundances of five of the ten bird species were significantly positively associated with field margin surface area (Table 3). In the three separately analysed regions, four of the ten species in region 2 and 3 and three of eight species in region 1 (only eight species were analysed in region 1 because the abundances of Yellowhammer and Quail were too low) increased with an increasing area of field margins. Species that were positively associated with field margin surface area were Bluethroat, Lapwing, Pheasant, Quail, Whitethroat, Linnet, Skylark and Yellowhammer, of which the latter three species were only associated with field margins in one of the three regions but not in the entire province. Meadow pipit and Yellow wagtail were not associated with field margin area in any of the geographic areas. Total bird species richness was positively associated with field margin surface area in the whole province and in all regions (Figure 2).

In all analyses, multiple models could describe the variation in abundance or species richness equally well. The number of best-fitting models ranged between two and 41 per analysis. The model-averaged parameter estimates of the associations with other habitat types than field margins are listed in Appendix A - J. The correlations between habitat types and bird species richness can be found in Appendix K.

Table 3. Correlations between field margin surface area and the abundance of ten bird species and overall species richness in the whole province of Groningen and in three regions within the province. Average results are given of the information-theoretic model selection based on Akaike information criterion (i) for all models with Δi < 2. Rank indicates the importance of field margins relative to the other habitat types, based on the sum of the Akaike weights of all models including field margins, where 1 is the most important habitat type and 12 the least important (11 in region 3). Empty cells mean that the variable was not included in any of the best models. When the abundance of a species was too low for analysis this is marked with a '-'.

	Province			Region 1		
	B	Z	Rank	B	Z	Rank
Bluethroat	0.144	3.55***	3	0.116	2.20*	1
Lapwing	0.077	2.80**	6	0.140	3.38***	2
Linnet	0.039	0.86	9	0.114	1.10	10
Meadow pipit	-0.020	0.83	9	0.019	0.49	8
Pheasant	0.103	4.17***	2	0.061	1.29	5
Quail	0.095	2.70**	4	-	-	-
Skylark	0.028	1.13	8	0.149	2.66**	2
Whitethroat	0.158	5.75***	2	0.170	1.89	3
Yellowhammer	0.050	1.34	6	-	-	-
Yellow wagtail	0.028	1.59	10	-0.020	0.53	9
Species richness	0.180	3.89***	1	0.232	2.82**	2

	Region 2			Region 3		
	B	Z	Rank	B	Z	Rank
Bluethroat	0.059	0.50	12	0.163	2.77**	1
Lapwing	0.072	1.14	7	0.065	1.15	5
Linnet	0.188	2.28*	2	0.059	0.81	4
Meadow pipit			12	0.054	1.13	5
Pheasant	0.253	4.94***	2	0.097	2.31*	1
Quail	0.117	2.00*	3	0.108	1.73	5
Skylark	0.037	0.73	11	0.022	0.69	11
Whitethroat	0.316	6.16***	1	0.076	2.52*	3
Yellowhammer	0.081	0.32	10	0.088	2.66**	1
Yellow wagtail	0.028	0.94	9	0.042	1.45	4
Species richness	0.190	2.55*	5	0.314	3.93***	1

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: *$P < 0.05$, **$0.01 < P < 0.05$, ***$P < 0.001$.

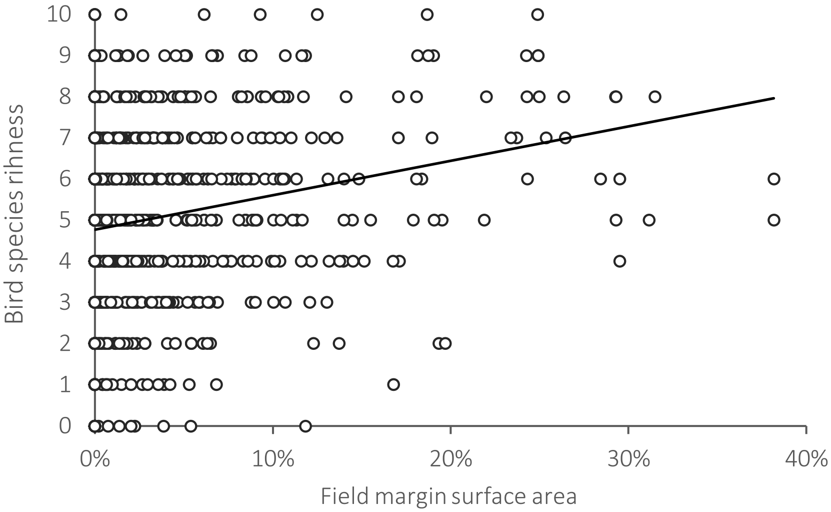


Figure 2. Relation between proportional field margin surface area and the number of study species observed within the 28.3 ha census circles ($P < 0.001$).

Table 4. Comparison of population growth rates and changes in bird species richness between census sites with and without field margins (year × field margin) over the period 2009 – 2013. Table lists F statistics with the degrees of freedom of the numerator and the denominator, respectively. For Yellowhammer, census points in region 1 were omitted because the species did not occur in this region.

	Year	Field margin	Year x Field margin
Bluethroat	$0.10_{1,1019}$	$6.38_{1,1019}^{*}$	$0.00_{1,1019}$
Lapwing	$19.85_{1,1019}^{***}$	$3.02_{1,1019}$	$1.83_{1,1019}$
Linnet	$0.70_{1,1019}$	$0.09_{1,1019}$	$1.56_{1,1019}$
Meadow pipit	$0.24_{1,1019}$	$7.96_{1,1019}^{**}$	$5.52_{1,1019}^{*}$
Pheasant	$0.58_{1,1019}$	$2.35_{1,1019}$	$0.17_{1,1019}$
Quail	$1.91_{1,1019}$	$1.50_{1,1019}$	$0.00_{1,1019}$
Skylark	$0.15_{1,1019}$	$6.01_{1,1019}^{*}$	$4.02_{1,1019}^{*}$
Whitethroat	$0.00_{1,1019}$	$6.66_{1,1019}^{*}$	$0.02_{1,1019}$
Yellowhammer	$6.93_{1,811}^{**}$	$0.38_{1,811}$	$0.70_{1,811}$
Yellow wagtail	$24.47_{1,1019}^{***}$	$6.26_{1,1019}^{*}$	$3.42_{1,1019}$
Species richness	$6.15_{1,1019}^{*}$	$16.39_{1,1019}^{***}$	$3.37_{1,1019}$

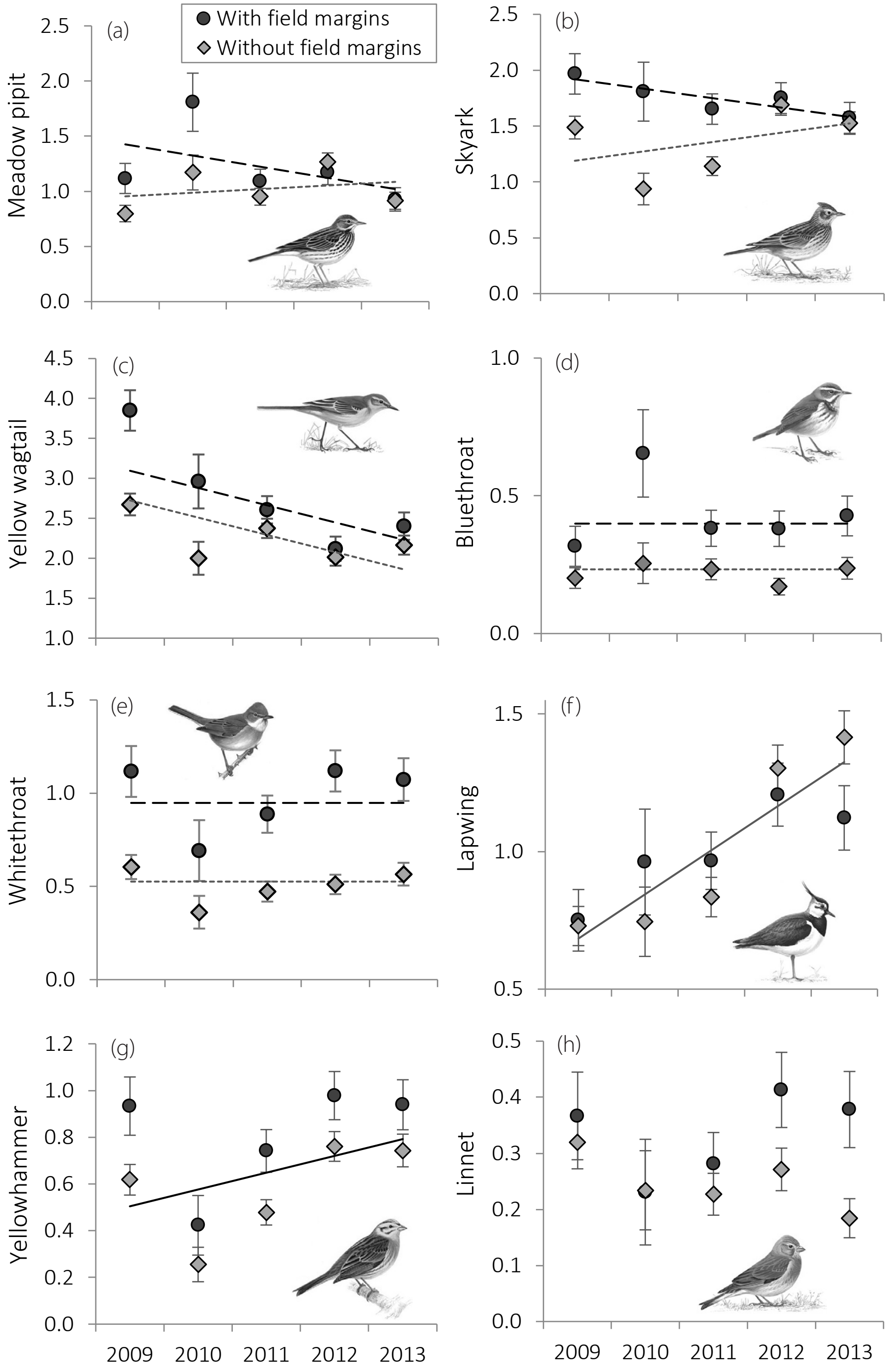
*$P < 0.05$, **$0.01 < P < 0.05$, ***$P < 0.001$

Temporal patterns

Population growth rates were calculated based on a smaller selection of census points that continuously contained field margins or no field margins between 2009 and 2013. Considering these points, the population densities of five species were significantly higher in areas with field margins than in control areas, which were Meadow pipit, Skylark, Yellow wagtail, Bluethroat and Whitethroat (Figures 3a-e; Table 4). Two species, Meadow Pipit and Skylark, showed different growth rates in areas with and without field margins (significant interaction term 'field margin × year', Table 4). In both cases the association was negative, i.e. the populations declined more in areas with field margins than in areas without (Figure 3a and b). Three species showed significant population changes over the 5-year period, a trend that was negative for Yellow wagtail and positive for Lapwing and Yellowhammer (Table 4; Figures 3 c, f and g). Linnet, Pheasant and Quail showed no significant population changes over time, nor any associations with field margin presence (Figures 3 h-j). Species richness was significantly higher on locations with field margins and increased with the same rate in both management and control areas (Figure 3 k).

Discussion

In the Netherlands, considerable weight of expectation is placed on field margins to support farmland bird populations, since field margins are the main management option for breeding birds in arable areas. It is therefore important that the effects of field margins are well monitored and their effectiveness is evaluated on a regular basis. This study is one of the first in the Netherlands to consider the relation between birds and field margins for multiple species over a large geographic area. The results show that field margins had a positive effect on bird densities for approximately half of the species-region combinations. Bird species richness was positively related to field margin surface area in all geographic regions, with model parameter estimates indicating that the richness of the ten study species in the census circle would increase by 0.2 - 0.3 with every 1 ha increase in field margin surface area (3.5% of the census circle surface area). The range of species showing a positive correlation between field margins and population density differed between the two analyses, which can be explained by their different character. The first analysis was based on the full sample and considered the associations of birds with field margin


With field margins
Without field margins
(a)
Meadow pipit
2.5
2.0
1.5
1.0
0.5
0.0
(b)
Skyark
2.5
2.0
1.5
1.0
0.5
0.0
(c)
Yellow wagtail
4.5
4.0
3.5
3.0
2.5
2.0
1.5
1.0
(d)
Bluethroat
1.0
0.5
0.0
(e)
Whitethroat
1.5
1.0
0.5
0.0
(f)
Lapwing
1.5
1.0
0.5
(g)
Yellowhammer
1.2
1.0
0.8
0.6
0.4
0.2
0.0
(h)
Linnet
0.5
0.4
0.3
0.2
0.1
0.0
2009
2010
2011
2012
2013

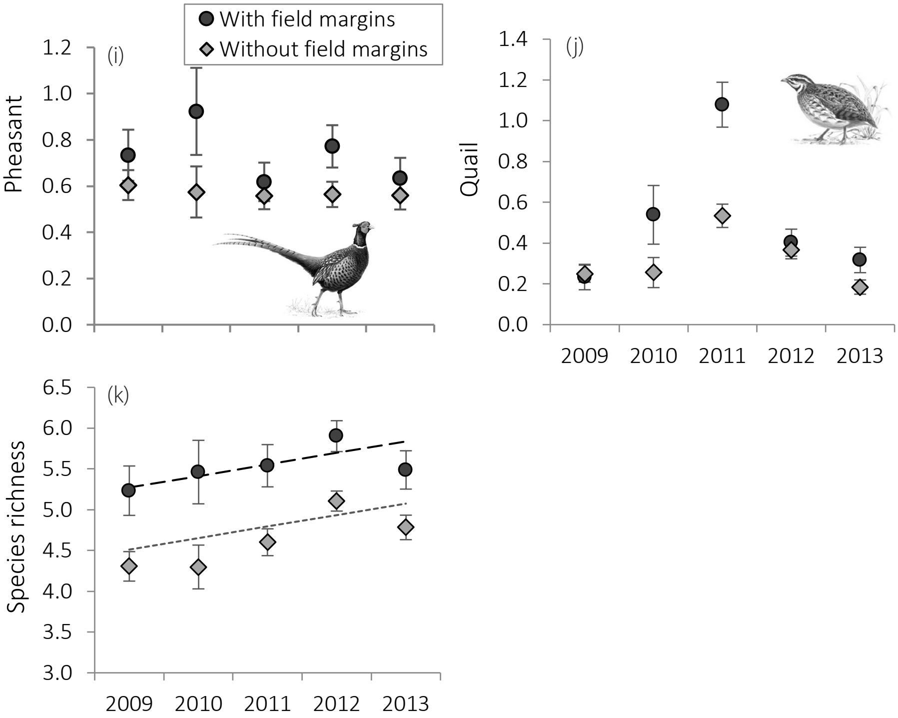


Figure 3. Mean density of Meadow pipit (a), Skylark (b), Yellow wagtail (c), Bluethroat (d), Whitethroat (e), Lapwing (f), Yellowhammer (g), Linnet (h), Pheasant (i), Quail (j) and mean species richness (k) per census point between 2009 and 2013. Points indicate average counts on locations with field margins (black dots) and without field margins (grey diamonds). Lines show model-estimated coefficients for significant variables, with black dashed lines representing trends for locations with field margins and dotted grey lines locations without field margins. Solid black lines indicate a general population growth rate over time without a significant difference between locations with and without field margins. When no lines are shown, population densities did not change significantly over time and did not differ between locations with and without field margins. Please note the differences in scales. Means are shown with standard errors. Illustrations by The Royal Society for the Protection of Birds (RSPB).

surface area, simultaneously taking into account the effects of other habitat types. The second analysis was based on a subset of sample points that continuously contained a field margin or no field margin, and took into account the effect of field margin presence instead of surface area, independent of the effects of other habitat types. The first analysis therefore provides the best information for determining habitat associations, while the second analysis enabled the study of population growth rates.

Despite the positive correlations between field margins and bird abundances, there was little evidence that field margins were positively affecting population growth rates. One species declined in abundance during the study period (Yellow wagtail, a long-distance migrant) and two species increased (Lapwing and Yellowhammer), but neither showed differences in growth rates between management and control areas. The only two species that did show different growth rates in management and control areas were Skylark and Meadow pipit, but for these species growth rates were negatively affected by field margin presence. Negative associations of population growth rates with field margins have also been reported for several species in the UK (Davey et al. 2010b, Baker et al. 2012). The negative response of the Skylark in this study seems to contrast earlier findings that Skylarks highly prefer field margins as a foraging habitat (Kuiper et al. 2013). Perhaps increased rates of nest predation in or near field margins contributed to the negative effect of field margins on population growth (Morris and Gilroy 2008). It is also possible that the negative correlation does not represent a causal effect of field margins on population growth, but that field margins correlated with other landscape or habitat variables that were responsible for the effect. This would be an unmeasured variable such as crop diversity, openness or mean field size, because field margins did not correlate strongly with any of the other habitat types considered in this study.

Since field margins did not seem to have a substantial positive effect on the population growth of the species, two reasons could explain the significantly higher bird abundances in management areas compared to control areas. First, it is possible that field margins were preferentially placed on farms or in areas with higher than average bird numbers (Kleijn and Sutherland 2003), in particular after 2008, when the establishment of new measures became restricted to 'core areas' (Provincie Groningen 2008). The delineation of the core areas was based on the densities of Montagu's harrier and Skylark (Provincie Groningen Afdeling Landelijk Gebied / Team Monitoring 2005), so it seems surprising that Skylark abundance did not show a clear positive relation with field margin surface area. Likely this is partially due to the fact that the densities of the two target species often were not correlated, so that Skylark densities were low in part of the core areas, while some areas with high Skylark densities were not included. Additionally, due to the large size of the core areas, Skylark densities were probably highly variable even within core areas. It is also possible that the effect of core areas was not yet visible during the study period, because contracts with farmers last six years and a substantial part of all field margins was still located outside the core areas (19% in 2011, Wiersma et al. 2014).

A second possible explanation for the differences in bird abundances between areas with and without field margins is a habitat selection effect. Breeding birds may preferentially select areas with field margins to establish their territory if they value field margins as a foraging or breeding habitat. The bird abundance graphs seem to point at such a habitat selection effect: in years of population increase, the increase is often stronger on locations with field margins than on locations without, for example for Bluethroat and Meadow pipit in 2010, Quail in 2011, Linnet in 2012, Pheasant in 2010 and 2012 and Whitethroat in 2011 and 2012 (see Figure 3). The fact that the population increase takes place in management as well as control areas suggests that the underlying reason is independent of agri-environmental management, for example a mild winter, favourable migratory conditions or good reproductive rates in the previous year. Yet the population increase is steeper in management areas, possibly indicating that a relatively large proportion of the increased population selects these areas for breeding. However, after such a peak in bird abundance, the populations mostly relapsed in the following year, which may indicate that the areas with field margins are not of such quality that the high bird densities can be maintained.

When studying the response of animals to landscape composition, the scale of research influences which relationships will be detected or missed (Schmidt et al. 2008, Pickett and Siriwardena 2011, Baker et al. 2012). In this research, habitat associations needed to be present within a maximum distance of 600m, the diameter of the census circle. When species interact with their environment at a larger or much smaller scale, correlations between field margins and bird numbers might not have been noticed. For example, the small foraging range of Meadow pipits (Douglas et al. 2008) might be the reason that so few habitat correlations were found for this species. Species' habitat associations often differ from one region to another, which can influence the effectiveness of conservation measures (Whittingham et al., 2007, Davey et al., 2010a). Also the results presented here show clear regional differences in the habitat associations of almost all bird species, including considerable variation in the associations with field margins. This suggests that the effectiveness of agri-environmental management in the province of Groningen can be improved when management plans take geographic variation into account. Davey et al. (2010a) give two options for addressing regional variation in scheme effectiveness: management actions can be concentrated in regions where effectiveness is greatest or options can be revised in regions where effects are not apparent. However, in order to make informed decisions, a better understanding of the regional variation is needed. In this respect it would be valuable to study how the effectiveness of field margins interacts with the presence of other habitat types. The value of field margins for birds may for example have varied regionally depending on the availability of suitable breeding habitat in the vicinity of field margins, or on the availability of other foraging habitat (Vickery et al. 2004). Identification of such relations will also help to improve the overall effectiveness of agri-environmental management

For some species and geographical regions, a large number of different models performed almost equally well. This does not necessarily imply that the habitat associations were weak or the model outcomes unreliable. In many cases, one or a few habitat variables were present in nearly all models, and turned out to be significant in the model-averaged estimates, while the effect of the other habitat types was interchangeable and caused the large number of equally well-fitting models. Considering the habitat associations of all species across regions, vertical structures were the habitat type affecting the largest number of species, mostly negatively. This suggests that field margins for most species are best located at a distance of several hundred metres from buildings and tree stands. Also autumn-sown cereals had a significant correlation with a large number of species, the relationship being negative for all species except Yellow wagtail and Quail, which use this crop for nesting. Ditches and dry ditches were influencing the densities of several species, mostly positively, such as Meadow pipit and Bluethroat that breed in these habitats.

Given the natural yearly fluctuations in population sizes that may obscure long-term trends, a period of five years might not be sufficient to detect clear relationships between bird population development and field margin uptake. It is therefore advisable to sustain the network of census points over the coming years, so that future evaluations can consider population growth rates over a longer time period. Field margins contracts last at least six years, but are often extended to twelve years. Field margins have been present in the area for more than 15 years and if they had a convincing positive influence on bird population development, at least some indications for this effect would have been expected (Davey et al. 2010b). The apparent lack of a clear effect on population growth rates can be explained in numerous ways, but additional research is needed to identify which potential explanations are correct. For some species, the vegetation composition, height or density of field margins might not be right to allow usage as a breeding or foraging habitat (Odderskær et al. 1997, Douglas et al. 2009). It is also possible that field margins in themselves met species' requirements, but that their value was negatively affected by incorrect placement or insufficient quantity (Davey et al. 2010b, Meichtry-Stier et al. 2014). A third possibility is that the quality and quantity of field margins was sufficient, but that field margins are simply not appropriate as the primary management option to sustain farmland birds in this arable area, because they do not address all factors that limit population growth (Vickery et al. 2004). Detailed studies that consider for example breeding biology, winter survival and foraging behaviour are needed to identify the population-limiting factors for each species, and based on this knowledge, it can be deduced which are the most appropriate measures to improve population trends (Roodbergen et al. 2012).

Acknowledgements

We would like to thank all professional and volunteer ornithologists who contributed to the collection of field data. We also sincerely thank all farmers who allowed field work to be carried out on their property. This work was partly funded by the Province of Groningen, the Ministry of Economic Affairs and the Foundation Chair in Nature Conservation on Farmland. Kees van Scharenburg (province of Groningen) and Leo Soldaat (CBS) have contributed significantly to the development of the MAS monitoring network in the Netherlands.

Appendix A. Habitat associations of the Bluethroat in the whole province of Groningen and in three regions within the province. Average results are given of the information-theoretic model selection based on Akaike information criterion (i) for all models with Δi < 2. When a variable was not included in any of the best models the cells are left empty. When the surface area of a habitat type was too low for analysis this is marked with a '-' n gives the number of census points counted over all years per geographic area (for bird numbers see Table 2).

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	0.014	2.02*	9	-	-	-	-	-	-	-	-	-
Potato	0.026	0.80	6	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	-0.008	0.39	7	-0.038	0.92	7			7
Cereals, autumn-sown	-0.019	1.62	7	-0.034	1.98*	6	0.029	1.05	8	-0.018	0.59	8
Cereals, spring-sown	-0.008	0.43	11			10	0.027	0.40	10	-0.043	1.75	5
Field margin	0.144	3.55***	3	0.116	2.20*	1	0.059	0.50	12	0.163	2.77**	1
Grassland	-0.038	2.48*	4	-0.05	2.49*	3	-0.059	1.68	2	-0.153	2.26	3
Maize	-0.019	0.90	10			11	-0.075	0.75	9			10
Rapeseed	0.147	5.98***	1	-	-	-	0.209	6.25***	1	-	-	-
Onion	-	-	-	-0.118	1.88	4	-	-	-	-	-	-
Vegetables	-	-	-	0.027	0.57	9	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-	-0.036	0.39	11	-	-	-
Hemp	-	-	-	-	-	-	-	-	-	-0.016	0.33	11
Dry ditch	0.733	1.12	8	3.050	2.19*	2	3.109	1.40	5			9
Road verge	0.167	0.82	12				0.844	1.27	6	0.257	1.39	6
Vertical structures	-0.123	2.19*	5	-0.142	1.05	8	-0.334	1.19	3	-0.153	2.26*	2
Wet ditch	1.692	5.14***	2	0.965	1.80	5	1.568	1.33	4	0.817	1.76	4

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $^*P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix B. Habitat associations of the Lapwing in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	0.019	2.01*	7	-	-	-	-	-	-	-	-	-
Potato	0.024	3.02**	3	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	0.010	0.92	9	0.030	1.63	3	0.042	3.21**	2
Cereals, autumn-sown	-0.029	3.76***	2	-0.01	3.68***	3	-0.032	3.02**	2	-0.012	0.66	9
Cereals, spring-sown	0.012	1.01	10			11	0.034	1.24	6			8
Field margin	0.077	2.80**	6	0.140	3.38***	2	0.072	1.14	7	0.065	1.15	5
Grassland	0.009	1.02	9	-0.010	0.91	10	0.026	1.48	4	0.032	1.38	4
Maize	0.032	2.89**	5	0.034	1.30	8	0.039	1.26	9	0.056	2.66**	3
Rapeseed	-0.026	1.32	8	-	-	-	-0.016	0.70	10	-	-	-
Onion	-	-	-	-0.078	2.03*	4	-	-	-	-	-	-
Vegetables	-	-	-	0.057	2.04*	5	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-	-0.058	1.24	5	-	-	-
Hemp	-	-	-	-	-	-	-	-	-			10
Dry ditch	-1.162	2.86**	4	1.997	1.80	6	-0.378	0.29	12	0.188	0.28	11
Road verge			12	-0.581	1.50	7	-0.394	1.02	8	0.208	1.18	6
Vertical structures	-0.190	5.29***	1	-0.430	3.78***	1	-0.592	3.56***	1	-0.121	2.41*	1
Wet ditch			11	-0.195	0.51	12	-0.385	0.61	11	-0.433	1.11	7

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix C. Habitat associations of the Linnet in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	-0.079	3.65***	2	-	-	-	-	-	-	-	-	-
Potato	-0.036	2.56*	5	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	-0.055	1.25	5	-0.040	1.23	4	-0.024	1.23	5
Cereals, autumn-sown	-0.063	4.28***	1	-0.067	1.99*	1	-0.013	0.81	5	-0.026	0.79	7
Cereals, spring-sown	-0.063	2.95**	3	-0.082	1.37	7	0.015	0.28	12	-0.056	1.95	1
Field margin	0.039	0.86	9	0.114	1.10	10	0.188	2.28*	2	0.059	0.81	4
Grassland	-0.050	3.14**	4	-0.040	0.82	9	0.014	0.80	7	-0.070	1.78	2
Maize	-0.040	1.72	6	-0.092	1.25	6			10	0.029	0.92	3
Rapeseed	0.027	0.88	8	-	-	-	0.093	2.92**	1	-	-	-
Onion	-	-	-	0.117	1.87	3	-	-	-	-	-	-
Vegetables	-	-	-	0.083	1.22	8	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-	0.020	0.42	11	-	-	-
Hemp	-	-	-	-	-	-	-	-	-			9
Dry ditch			11	1.448	0.62	11	-0.707	0.35	9	0.722	0.85	6
Road verge	0.343	1.46	7	1.754	2.59**	2	0.303	0.59	8			10
Vertical structures	-0.022	0.67	10	0.328	1.83	4	0.159	1.59	3			8
Wet ditch			12	-0.677	0.71	12	-0.630	0.70	6			11

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix D. Habitat associations of the Meadow pipit in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	-0.024	2.85*	5	-	-	-	-	-	-	-	-	-
Potato	-0.021	2.91**	4	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	-0.005	0.49	11	-0.011	0.93	7	-0.005	0.38	11
Cereals, autumn-sown	-0.009	1.61	8	0.003	0.36	6	-0.008	1.21	5	0.022	1.28	4
Cereals, spring-sown	-0.032	3.19**	3	-0.033	1.56	2	0.013	0.60	10	-0.016	0.98	7
Field margin	-0.020	0.83	9	0.019	0.49	8			12	0.054	1.13	5
Grassland	0.010	1.72	7			9	0.010	1.36	4	0.057	3.51***	2
Maize	-0.024	2.08*	6	-0.015	0.56	7	-0.029	1.06	6	0.021	1.02	6
Rapeseed	0.010	0.66	10	-	-	-	0.011	0.68	8	-	-	-
Onion	-	-	-	0.010	0.32	10	-	-	-	-	-	-
Vegetables	-	-	-	0.023	0.70	5	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-	-0.008	0.31	11	-	-	-
Hemp	-	-	-	-	-	-	-	-	-	0.017	0.58	10
Dry ditch			12	-0.693	0.73	4	1.554	2.23*	2	0.470	0.80	8
Road verge	-0.042	0.32	11	0.115	0.40	12	-0.174	0.72	9	-0.138	0.64	9
Vertical structures	-0.180	6.02***	1	-0.135	1.61	1	-0.326	4.00***	1	-0.116	2.83**	1
Wet ditch	0.743	5.13***	2	0.381	1.26	3	0.662	1.79	3	0.948	3.04**	3

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix E. Habitat associations of the Pheasant in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	-0.018	1.54	6	-	-	-	-	-	-	-	-	-
Potato	-0.014	1.60	7	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	-0.016	0.90	7	0.007	0.39	10	-0.013	2.04	4
Cereals, autumn-sown	-0.024	3.31***	3	-0.015	0.84	6	-0.016	1.47	4			8
Cereals, spring-sown			9	0.037	1.62	4	0.031	0.98	6	0.010	0.60	6
Field margin	0.103	4.17***	2	0.061	1.29	5	0.253	4.94***	2	0.097	2.31*	1
Grassland	-0.027	3.05**	4	-0.031	1.97*	1	0.012	0.99	7	-0.012	0.61	5
Maize			10	-0.017	0.44	8	-0.051	1.13	5	0.037	1.90	3
Rapeseed	0.021	1.00	8	-	-	-	0.057	2.44*	3	-	-	-
Onion	-	-	-			12	-	-	-	-	-	-
Vegetables	-	-	-	0.016	0.36	11	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-			11	-	-	-
Hemp	-	-	-	-	-	-	-	-	-	0.010	0.33	10
Dry ditch	1.459	4.57***	1	2.536	2.26*	2	4.912	6.23***	1	0.297	0.59	7
Road verge	-0.081	0.50	11	-0.733	1.61	3	-0.319	0.86	9	0.111	0.67	9
Vertical structures	0.048	2.75**	5			10			12	0.044	2.27*	2
Wet ditch	0.058	0.30	12	0.308	0.65	9	-0.570	0.95	8			11

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix F. Habitat associations of the Quail in the whole province of Groningen and in two regions within the province. Abundances in region 1 were too low for analysis. For further information see Appendix A.

	Province (n = 1769)			**Region 1**			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	-0.018	1.08	6				-	-	-	-	-	-
Potato	0.020	1.54	9				-	-	-	-	-	-
Beet & potato	-	-	-				-0.045	0.79	7	0.056	2.58**	3
Cereals, autumn-sown	0.028	2.54*	5				0.014	1.38	4	0.063	2.10*	4
Cereals, spring-sown	0.061	3.97***	2				-0.013	0.41	11	0.075	3.07**	2
Field margin	0.095	2.70**	4				0.117	2.00*	3	0.108	1.73	5
Grassland	0.026	2.11*	7				-0.006	0.47	8	0.013	0.34	6
Maize			10						10	0.016	0.40	7
Rapeseed	0.043	1.76	8				0.025	0.99	5	-	-	-
Onion	-	-	-				-	-	-	-	-	-
Vegetables	-	-	-				-	-	-	-	-	-
Lucerne	-	-	-				0.033	0.92	6	-	-	-
Hemp	-	-	-				-	-	-			8
Dry ditch			12						12	-0.366	0.43	9
Road verge	-0.074	0.33	11				-0.207	0.50	9	-0.112	0.32	10
Vertical structures	-0.322	4.60***	1				-0.331	2.34*	1	-0.297	2.70**	1
Wet ditch	-0.628	2.39*	3				-1.62	2.63**	2			11

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix G. Habitat associations of the Skylark in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	0.008	0.86	9	-	-	-	-	-	-	-	-	-
Potato	0.010	1.22	7	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	-0.025	1.51	4	0.054	2.38*	8	0.020	1.56	3
Cereals, autumn-sown	-0.016	3.33***	4	-0.014	0.88	5	0.057	2.79**	6	0.028	1.59	5
Cereals, spring-sown	0.019	2.38*	3			11	0.067	2.54*	7	0.023	1.59	4
Field margin	0.028	1.13	8	0.149	2.66**	2	0.037	0.73	11	0.022	0.69	11
Grassland	0.010	1.55	6	0.010	0.66	7	0.064	1.98*	2	0.015	0.76	8
Maize	0.017	1.75	5	-0.017	0.40	10	0.074	2.15*	5	0.021	1.06	7
Rapeseed	0.003	0.19	11	-	-	-	0.065	2.20*	4	-	-	-
Onion	-	-	-	-0.037	0.59	9	-	-	-	-	-	-
Vegetables	-	-	-	0.040	0.97	6	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-	0.092	2.41*	3	-	-	-
Hemp	-	-	-	-	-	-	-	-	-	-0.017	0.79	9
Dry ditch	0.274	0.84	10	3.82	2.43*	3	1.053	1.25	10	-0.802	2.20*	2
Road verge	0.087	0.68	12			12	-0.121	0.51	9	-0.064	0.56	10
Vertical structures	-0.167	6.22***	1	-1.018	4.66***	1	-0.395	4.08***	1	-0.130	4.30***	1
Wet ditch	-0.636	3.80***	2	-0.382	0.69	8	0.178	0.46	12	-0.193	0.96	6

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix H. Habitat associations of the Whitethroat in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	-0.029	2.18*	7	-	-	-	-	-	-	-	-	-
Potato	0.017	1.52	0	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	-0.008	0.31	6			8	-0.035	3.34***	7
Cereals, autumn-sown	-0.058	5.05***	3	0.018	0.76	7	-0.033	2.48*	4	-0.043	2.44*	10
Cereals, spring-sown	-0.019	1.64	10			12	-0.020	0.45	9	-0.061	4.24***	2
Field margin	0.158	5.75***	2	0.170	1.89	3	0.316	6.16***	1	0.076	2.52*	3
Grassland	-0.046	3.60***	4	-0.029	1.01	4	-0.011	0.58	7	-0.085	4.51***	1
Maize	-0.027	1.88	8	-0.028	0.42	9	-0.170	2.54*	2	-0.049	2.74**	8
Rapeseed	0.039	1.76	9	-	-	-	0.074	3.09**	6	-	-	-
Onion	-	-	-	0.032	0.49	10	-	-	-	-	-	-
Vegetables	-	-	-			11	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-	0.095	3.12**	5	-	-	-
Hemp	-	-	-	-	-	-	-	-	-	-0.068	2.61*	6
Dry ditch	2.133	6.25***	1	4.801	2.05*	1	1.095	0.90	10	0.805	2.08*	5
Road verge	0.329	2.41*	5	1.556	2.16*	2			12	0.086	0.73	11
Vertical structures	0.042	2.19*	6	0.136	0.58	8	0.209	3.09**	3			9
Wet ditch	-0.148	0.68	11	0.995	1.01	5			11	0.481	2.10*	4

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix I. Habitat associations of the Yellowhammer in the whole province of Groningen and in two regions within the province. Abundances in region 1 were too low for analysis. For further information see Appendix A.

	Province (n = 1769)			**Region 1**			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	-0.012	1.15	9				-	-	-	-	-	-
Potato	0.009	1.19	8				-	-	-	-	-	-
Beet & potato	-	-	-				0.051	1.17	5	-0.006	0.32	7
Cereals, autumn-sown	-0.125	11.7***	1				-0.046	1.40	3	-0.030	1.50	5
Cereals, spring-sown	0.008	0.76	11				0.047	0.52	8	-0.026	1.57	3
Field margin	0.050	1.34	6				0.081	0.32	10	0.088	2.66**	1
Grassland	-0.066	6.26***	3				-0.015	0.31	7	-0.027	1.39	9
Maize	0.005	0.46	10				-0.128	1.07	6	0.029	1.97*	6
Rapeseed	-0.042	1.20	7						11	-	-	-
Onion	-	-	-				-	-	-	-	-	-
Vegetables	-	-	-				-	-	-	-	-	-
Lucerne	-	-	-						12	-	-	-
Hemp	-	-	-				-	-	-	0.042	2.05*	4
Dry ditch	3.291	7.81***	2				6.865	2.44*	1	0.460	1.28	8
Road verge	0.289	1.58	5				1.317	1.26	4	0.074	0.64	10
Vertical structures	0.087	4.17***	4				0.369	2.06*	2	0.043	2.63**	2
Wet ditch			12				1.168	0.56	9			11

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix J. Habitat associations of the Yellow wagtail in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	0.039	5.62***	5	-	-	-	-	-	-	-	-	-
Potato	0.041	6.87***	3	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-	-0.011	1.02	6	0.038	4.29***	4	0.008	0.95	7
Cereals, autumn-sown	0.052	9.15***	2	0.017	1.93	5	0.052	8.09***	1	0.026	2.23*	3
Cereals, spring-sown	0.065	9.16***	1	0.013	0.82	10	0.038	2.48*	5	0.033	3.59***	1
Field margin	0.028	1.59	10	-0.020	0.53	9	0.028	0.94	9	0.042	1.45	4
Grassland	-0.008	1.03	11	-0.056	4.77***	1	-0.007	0.59	10			10
Maize	0.039	4.61***	7	-0.015	0.62	7	0.022	1.10	8	-0.005	0.34	11
Rapeseed	0.057	5.09***	4	-	-	-	0.052	4.25***	3	-	-	-
Onion	-	-	-			12	-	-	-	-	-	-
Vegetables	-	-	-	0.025	1.00	8	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-	0.024	1.25	7	-	-	-
Hemp	-	-	-	-	-	-	-	-	-	0.023	1.20	5
Dry ditch	-0.525	2.16*	8	-2.556	2.97**	2	-0.316	0.51	11	-0.411	1.25	6
Road verge	0.057	0.64	12	0.204	0.82	11			12	-0.117	0.93	9
Vertical structures	-0.086	4.21***	6	-0.196	2.35*	3	-0.181	3.44***	2	-0.087	3.78***	2
Wet ditch	-0.227	1.84	9	-0.597	1.89	4	-0.553	2.13*	6	0.193	1.06	8

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Appendix K. Correlations between bird species richness and several habitat types in the whole province of Groningen and in three regions within the province. For further information see Appendix A.

	Province (n = 1769)			**Region 1** (n = 374)			**Region 2** (n = 590)			**Region 3** (n = 393)		
	B	Z	Rank	B	Z	Rank	B	Z	Rank	B	Z	Rank
Beet	0.038	3.19**	12	-	-	-	-	-	-	-	-	-
Potato	0.066	7.82***	8	-	-	-	-	-	-	-	-	-
Beet & potato	-	-	-			12			9			8
Cereals, autumn-sown	-0.057	7.91***	4			11	-0.031	2.99**	7			9
Cereals, spring-sown	0.055	4.34***	10			9			10			11
Field margin	0.180	3.89***	1	0.232	2.82**	2	0.190	2.55*	5	0.314	3.93***	1
Grassland	-0.048	5.43***	6			10			12			10
Maize	0.059	3.72***	11			8			11			6
Rapeseed	0.100	3.26**	3	-	-	-	0.138	5.29***	1	-	-	-
Onion	-	-	-			7	-	-	-	-	-	-
Vegetables	-	-	-			6	-	-	-	-	-	-
Lucerne	-	-	-	-	-	-			8	-	-	-
Hemp	-	-	-	-	-	-	-	-	-			7
Dry ditch	1.809	3.22**	2	5.203	2.63**	1	3.942	2.74**	2	0.184	0.21	3
Road verge	0.329	1.46	9	0.116	0.19	5	0.477	1.08	6			5
Vertical structures	-0.109	3.47***	5	-0.422	2.45*	3	-0.267	2.70**	3	-0.103	2.86**	2
Wet ditch	0.558	1.89	7	0.074	0.11	4	-0.880	1.81	4	0.309	0.61	4

B = model-averaged coefficient, Z = model-averaged Z-value. Asterisks show the *P*-values from the likelihood-ratio-test: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$. Rank = relative variable importance based on the sum of the Akaike weights over all models including the explanatory variable.

Hulde aan de leeuwerik
Die dwars tegen de feiten in
Gelooft en hoopt en daar van zingt

Die daarmee onze oren boeit
En daarmee onze harten troost

Ik weet dat liefde echt bestaat
Levend en onvergankelijk
Hulde aan de leeuwerik

naar J. de Corte (Ik ben je reisgenoot, 1994)

Chapter 3

Field margins as foraging habitat for Skylarks (*Alauda arvensis*) in the breeding season

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Abstract

Agri-environment schemes have been established in many European countries to counteract the ongoing decline of farmland birds. In this study, the selection of foraging habitat by breeding Skylarks was examined in relation to agri-environmental management on Dutch farmland. Field margin use was quantified and, based on the observed flight distances, the appropriateness of the current spatial arrangement of field margins in the study landscape was evaluated. Skylarks preferred field margins for foraging over all other habitat types relative to their surface area within the territories. The visiting rate of field margins decreased with increasing distance to the nest, and especially dropped markedly when the distance between the nest and a field margin exceeded 100 m. Analysis of the current spatial arrangement of field margins in the landscape suggested that the area of Skylark breeding habitat within 100 m of a field margin could be increased by 46%. This was due to the placement of field margins alongside unsuitable breeding habitat and to the positioning of field margins at short distances from each other. The efficiency of agri-environmental management for Skylarks can likely be improved by a more careful spatial arrangement of field margins in the landscape.

Introduction

Over the past two decades, a wide variety of agri-environmental measures has been designed and implemented to counteract biodiversity loss in agricultural areas. One target group for these measures has been farmland birds, i.e. bird species that rely on agricultural land for at least part of their reproductive cycle. Although conservation efforts have increased considerably since the 1970s, biodiversity threats have also increased (Kleijn et al. 2011), and the effectiveness of agri-environmental management has been both variable and unpredictable (Kleijn et al. 2006). As a net result, Western Europe still faces declining populations of many farmland bird species, including the Skylark Alauda arvensis (Gregory et al. 2004; Wretenberg et al. 2006). In the Netherlands, the Skylark declined by 96% since 1960 (Sovon 2012). More recently the negative trend continued, with yearly declines of 1.8% in the Netherlands (NEM 2013) and 1.0% in Europe (EBCC, 2013) between 2000 and 2010.

Two factors have been identified as key drivers of declining farmland bird populations: reduced food availability and a paucity of safe nesting sites on agricultural land (Butler et al. 2007). Low food availability in the direct surroundings of the nest results in poorer nestling condition (Brickle et al. 2000; Hart et al. 2006), which in turn may negatively affect the chance that a bird will reach the reproductive stage (Magrath 1991). Food availability can likely be improved by the establishment of arable field margins, a widely applied agri-environment scheme in many European countries, including the Netherlands (Noordijk et al. 2010), the United Kingdom (Vickery et al. 2009), Switzerland (Jeanneret et al. 2003) and France (Cordeau et al. 2012). Field margins are relatively rich in arthropods and seeds, suggesting a high potential value as foraging habitat for farmland birds (Vickery et al. 2002; McCracken and Tallowin 2004; Vickery et al. 2009). Surprisingly, there has been little effort to study the actual utilisation of field margins by farmland birds, even though such knowledge is essential for the evaluation and improvement of field margins (Perkins et al. 2002; Douglas et al. 2009).

Existing studies of bird foraging behaviour in response to agri-environmental measures mostly focus on the relationship between habitat utilisation and the vegetation characteristics that result from local management, such as cutting regime (Odderskær et al. 1997; Perkins et al. 2002; Douglas et al. 2009; Smith et al. 2009). However, the effectiveness of agri-environment schemes also depends on the spatial arrangement of these measures in the landscape and on the overall quality of the landscape in which they are situated (Steffan-Dewenter et al. 2002; Melman et al. 2008; Concepción et al. 2012; Henderson et al. 2012).

Here, we present the results of a study considering the utilisation of field margins by breeding Skylarks in the Netherlands. The aim of the study was three-fold. First, we quantified to what extent Skylarks use field margins as a foraging habitat when breeding on intensively managed farmland. Second, we studied how the distance from the nest to a field margin affected the use of field margins as a foraging habitat. Third, we explored whether the current spatial configuration of field margins in the research area can be improved for foraging Skylarks, in order to increase the efficiency of agri-environmental management.

Methods

Field work was conducted in the municipality Oldambt in the northeast of the Netherlands (N53°11.585, E007°7.798) from April through July in 2007, 2008 and 2011. The research area (ca. 100 km2) is situated on marine clay, and agriculture is the main land use. The predominant crops were winter wheat (covering 56% of all agricultural land in 2011) and permanent grassland (23%); other crops included sugar beet, lucerne, rape seed and maize (3-5% each). In 2011, the surface area of field margins was 3% of the agricultural land, reaching 10% in the central part of the research area. Generally, field margins were 12 m wide and 500-1000 m long. Regulations required that 20-70% of a field margin was cut twice-annually; once between 1 March and 15 April and once between 15 July and 15 September.

Bird observations

Skylark nests were located by searching for birds that showed signs of breeding behaviour or performed provisioning flights. The foraging behaviour of Skylark parents was studied from April through July in the years 2007 (8 nests), 2008 (15 nests) and 2011 (50 nests). In 2007 and 2008, each nest was observed for 1 h. In 2011, the nests were observed twice for 1 h on two different days (except for eight nests that were lost due to agricultural practices or predation before the second observation). Observations were conducted from 6:00 to 17:00 h Dutch summer time, with none occurring in heavy rain or during the warmest hours of the day when provisioning activity was low. The destinations of the foraging flights of both parents were determined using 10x binoculars and recorded on a map by an observer that was concealed in a vehicle or tent. When possible, the two observations of the same nest were conducted from different positions in order to minimize the influence of the observer on foraging habitat selection. Subsequent to the observation, the foraging locations were visited in the field and coordinates taken using a handheld GPS (in 2007 and 2008) or the foraging locations were directly copied from the field map into ArcGIS 10.1 (ESRI, Redlands, California; in 2011). Skylarks were sometimes observed to visit several locations before returning to the nest. When this occurred, the visited locations were regarded as separate foraging sites if they were located in different habitat types or were separated by at least 50 m. Foraging distances were calculated as the shortest distance between the nest and the foraging locations. The destination of 4% of all flights could not be determined or were ambiguous, these flights were excluded from the analyses. The age of the nestlings ranged from 1 - 10 days at the time of observation (estimates based on weight and the lengths of wings, feathers and tarsi).

Invertebrate sampling

Invertebrates were collected by vacuum sampling using a modified leaf vacuum (McCulloch MAC GBV 345) with a 12-cm diameter suction tube in 2011. Two fields each of winter wheat, lucerne and permanent grassland, two road verges and five field margins were sampled (13 sites in total). The sites were sampled six times during the breeding season, around the 10th and 25th of the months May, June and July. Sampling was conducted in sunny and dry weather conditions only. Each sample consisted of five subsamples of 15-s vacuum sessions within a bottomless circular frame (50 cm diameter), thus sampling a total area of 0.982 m^2 per sample. Invertebrates were identified to the order level and allocated to three size classes (3-5, 6-8 and >8 mm). Only invertebrates that are part of the Skylark diet -individuals larger than 5 mm in the taxa Arachnida, Coleoptera, Diptera, Lepidoptera, Orthoptera, Hemiptera and Hymenoptera, including adults and larvae- were included in the analysis (Holland et al. 2006; Smith et al. 2009). The choice of invertebrate sampling technique determines to a large extent the taxa and sizes of invertebrates that will be captured (Doxon et al. 2011). Vacuum sampling was considered most appropriate because this method mainly captures invertebrates from the ground and the lower parts of plants (Doxon et al. 2011), where Skylarks search for prey (Donald 2004). Additionally, vacuum sampling allows density calculations and does not overestimate the availability of nocturnal or very active invertebrate species.

Landscape calculations

Landscape composition was calculated using ArcGIS 10.1. Land use maps of the Ministry of Economic Affairs of the years 2007, 2008 and 2011 were used to calculate the surface areas of crops and field margins, supplemented with a national topography map (Basis Registratie Topografie top10 vector map; Kadaster, 2009, 2011) for primary land use types. The 2009 topography map was used as a substitute for the years 2007 and 2008, as no maps were made in those years. In this study, road verges and ditch banks (1 – 3 m wide grassy strips adjacent to waterways such as ditches and canals) were pooled into one habitat type termed verges, because they often bordered on each other and had highly similar vegetation, making it impossible to determine the boundary between them.

To compare habitat use with availability within the home range (third-order habitat selection, Johnson, 1980), the surface area of available habitat types was calculated within each Skylark 'territory', which was defined as a circular area around the nest with a radius equal to the 95th percentile of the lengths of all recorded foraging flights in all years (272 m). Although this might not reflect the true size and shape of each territory, the method provides a good estimate of all habitat types within the reach of a Skylark breeding pair. To correct for observed distance dependency in the selection of foraging habitats within the territory, the surface area of the habitat types was calculated within four concentric rings, the outer borders of which were set at distances from the nest equal to the 24^{th}, $48^{th,}$ 71^{st} and 95^{th} percentiles of all mapped foraging flights in all years (37, 76, 117 and 272 m, respectively). Thus, each ring represented an area to which one quarter of all foraging flights were directed. The surface areas of habitat types and crops were determined for each ring and averaged with equal weighting to rings to obtain the weighted surface area within a territory.

To evaluate the spatial configuration of field margins in the landscape, a continuous research area was defined by creating a circle with a radius of 2 km around all 80 Skylark nests that were found in 2011 and merging these circles into one area. Based on the distances that the Skylarks flew to forage in field margins (see Section 3.2), all land within 100 m of a field margin was designated as potentially suitable breeding ground (i.e. land from where a breeding Skylark pair would have at least one field margin within reach for foraging). The proportion of the potentially suitable breeding ground that was covered by roads, buildings, forest, or water (unsuitable for breeding) was calculated as well as the overlap of potentially suitable breeding ground around different field margins.

Statistical analyses

The number of foraging flights to different habitats was converted to proportional usage per nest by dividing the number of flights to each habitat type by the total number of flights performed by the birds of that nest. To test whether habitat use differed from random and to rank habitats, compositional analysis was conducted in R 2.15.2 (R Development Core Team 2013) using the compana function in the adehabitat package (Aebischer et al. 1993; Calenge 2006). Analysed habitat types included the five habitat types that were present in most territories (winter wheat, lucerne, grassland, field margins and verges) and a category 'other' where all other habitat types were pooled into. Randomization tests with 10,000 repetitions were used for both the tests of habitat selection and ranking, because not all habitat types were available in each territory.

All other statistical analyses were performed using SPSS 19 (IBM, Armonk, New York). To determine whether field margin use changed over the season, a linear regression analysis was performed with percentage field margin use per nest as the dependent factor (n = 44 nests with a field margin availability >1%) and the day of observation as the independent factor. The foraging distances in the three study years were compared using a General Linear Model and pairwise comparisons with Bonferroni correction, with log-transformed foraging distances to achieve normality.

To test whether field margin use was affected by the distance of the margin to the nest, a logit Binary Logistic Generalized Estimated Equations analysis (Zeger and Liang 1986) was performed. This method models a general logistic regression, but allows for the analysis of dichotomous outcomes that are obtained from correlated observations. Our data consisted of multiple observations of field margin use by birds from the same nest, since the majority of territories that contained field margins had more than two. Thus, observations of field margin use were correlated at the level of nest, and nest was entered as subject variable with an exchangeable working correlation matrix. Binary margin use was entered as dependent variable (used or not used, n = 142 field margins) and the distance from the nest to a margin was entered as covariate.

Seasonal differences in arthropod abundance and differences between habitat types were analysed using a Linear Mixed Model. The number of prey items was square root transformed in order to achieve normality, and entered as the dependent variable. Sampling site was entered as the subject and random factor, and catch round as the repeated factor. Habitat type and catch round were added to the model as fixed factors. Observations were assumed to have an uncorrelated covariance structure.

Results

The foraging flights of Skylarks that provisioned nestlings were observed for 73 nests, and in total 1363 foraging flights to known destinations were recorded (101 in 2007, 129 in 2008 and 1133 in 2011). The mean number (±SE) of foraging flights per hour of both parents was 12.2 ± 0.57 per nest, with a range of 4 - 25. The compositional analysis indicated that foraging habitat use within the territories was significantly non-random (Wilks' $\Lambda = 0.306$, *df* 5, $P < 0.001$; Figure 1). The ranking order from most to least selected was field margins > lucerne > verges > grassland > other > winter wheat. Field margins were significantly selected over all other habitats while winter wheat was strongly avoided (*P*-values ranging from <0.05 to <0.001, Table 1). The differences between the intermediately selected habitats were only significant for the use of lucerne and verges relative to the category other (Table 1).

The relative use of field margins did not change over the breeding season ($r^2 = 0.014$, $P = 0.43$). There were significant differences in foraging flight distances between years ($F_{2,1389} = 12.4$, $P < 0.001$). The distances flown in 2008 differed from those in 2011 (average 129 and 100 m, respectively; $P < 0.001$), whilst the year 2007 did not differ from the other two years (average 108 m). The mean distance of all foraging flights was 104 m.

Table 1. Log-ratio differences (numerator habitat in rows, denominator in columns) and ranking of foraging habitats.

	Wheat	Other	Grassland	Verges	Lucerne	Field margin	Rank
Wheat	0.00						0
Other	1.85*	0.00					1
Grassland	3.54**	2.09	0.00				2
Verges	4.61***	2.76**	0.34	0.00			3
Lucerne	5.72***	4.79***	1.79	1.68	0.00		4
Field margin	7.94***	6.77***	4.54**	4.28***	3.69*	0.00	5

**P* < 0.05, ***P* < 0.01, ****P* < 0.001.

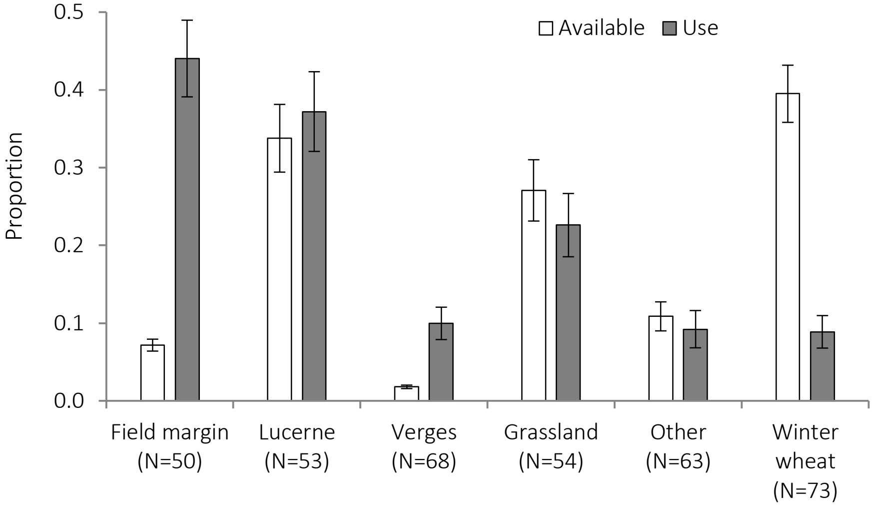

Figure 1. Mean relative availability of six habitat types within Skylark territories (white bars) and mean relative usage of these habitat types (grey bars) by 73 Skylark pairs provisioning young (± SE). Sample sizes under the bars indicate the number of territories where the specific habitat was present.

Invertebrate availability

Invertebrate prey availability differed significantly between the five habitat types that were sampled ($F_{4,8} = 7.1$, *df* 4; 8, $P < 0.01$) and between catch rounds ($F_{5,8} = 6.5$, *df* = 5; 8, $P < 0.05$). Also the interaction between these two variables was significant ($F_{20,8} = 3.5$, *df* 20; 8, $P < 0.05$), indicating that the differences in prey availability between habitats varied over time (Figure 2). Prey availability peaked in field margins and verges in June, but stayed at approximately the same low level in the three crops. Averaged over all sampling rounds, field margins and verges contained approximately 3.5 times as many prey items per m^2 as the average of winter wheat, grassland and lucerne.

Spatial configuration of field margins

The use of a field margin decreased with increasing distance to the nest (Wald $X^2 = 44.5$, $P < 0.001$). Especially when the distance between the nest and a margin was larger than 100 m, the visiting rate dropped markedly (Figure 3a). Of the 54 field margins that were located within 100 m from a nest, 41 (76%) had been visited at least once. Of the 89 margins located further than 100 m from a nest (but within 272 m, the 95th percentile of all recorded foraging flights), only 11 (12%) had been visited. Even when the nearest field margin was more than 100 m away from the nest, only 4 of 21 margins (19%) were visited. In the model that resulted from the Generalized Estimated Equations, the chance of a Skylark pair visiting a field margin was less than 50% at distances larger than 100 m (Figure 3b).

When all land within 100 m of a field margin was defined as suitable breeding ground, the potential nesting area for Skylarks in 2011 was 2284 ha. Of this potential nesting area, only 1422 ha (62%) had been realised, because margins were located so close to each other that the potential nesting areas around different field margins overlapped. Of this realised area, approximately 13% (187 ha) was covered by roads, water, forest or farms and therefore unsuitable as a nesting habitat for Skylarks. The total nesting area for Skylarks within the research area thus was 1235 ha, which is 54% of the potential nesting area that could have been realised with the same length of field margins.

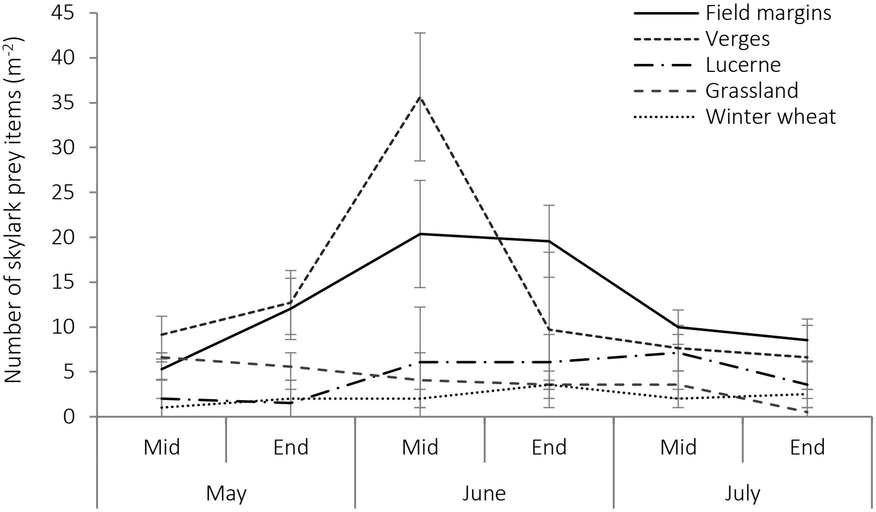

Figure 2. Mean availability of invertebrate prey for Skylarks in five different habitat types during the breeding season (±SE).

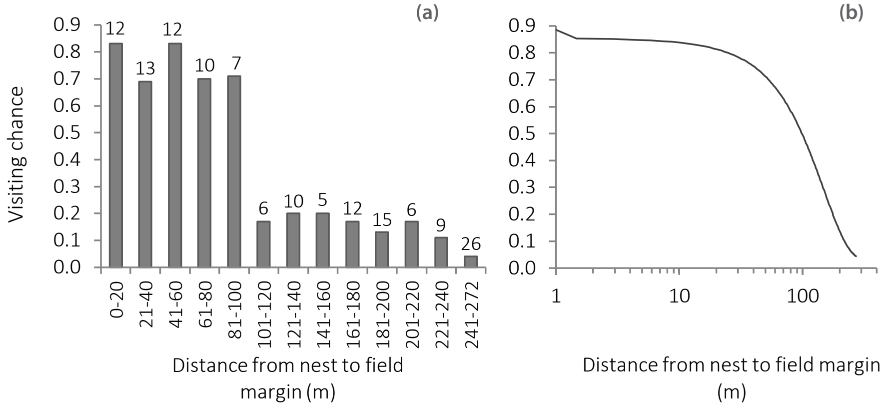

Figure 3. Relationship between the distance from the nest to a field margin and the probability that the margin was visited at least once by foraging Skylarks. (a) Observational data on 143 field margins, visited by Skylark parents of 49 nests. Numbers above bars indicate the number of field margins within the category. (b) Visiting chance modeled by Binary Logistic Generalized Estimating Equations. The predicted visiting chance was described by 1 / (1 + e(-(1.81 – 0.018 * D))) where D is the distance from the nest to the field margin.

Discussion

Several earlier studies have shown that Skylarks breeding on farmland prefer certain crops for foraging and avoid others (Davis 1967; Odderskær et al. 1997). A better insight in the use of field margins by Skylarks and other bird species can provide clues on how to improve the ecological effectiveness of this agri-environment scheme (Douglas et al. 2009). The present study shows that Skylarks that were providing for nestlings preferred field margins over all other habitat types. The foraging habitat preferences matched to a large extent the availability of invertebrate prey. Together with verges, field margins supported the highest prey densities. Lucerne, which contained most prey items of three sampled crops, was ranked as the second most preferred foraging habitat. Winter wheat had the lowest prey availability throughout the breeding season and was strongly avoided as foraging habitat.

The visiting rate of field margins was stable throughout the breeding season, as opposed to the decreasing usage of field margins by the Yellowhammer *Emberiza citrinella* in the UK (Douglas et al. 2009). This might be an indication that the current regulations, which require the biannual cutting of 20-70% of the field margin, are effective to maintain a good accessibility of field margins for Skylarks throughout the entire breeding season. An important factor influencing field margin use was the distance between the nest and a field margin. The chance that a margin was visited was approximately 70-80% for distances up to 100 m, but less than 20% for larger distances. Apparently in most cases it was not profitable to fly more than 100 m to forage in a field margin. Aside from the physiological abilities of the study species, this distance probably depends on the food availability in the field margin as well as in the surrounding landscape.

It is clear that field margins are an important and highly preferred foraging habitat for birds breeding in intensively managed agricultural areas. Our findings are in agreement with studies of other farmland passerines such as *E. citrinella* and the Corn bunting *E. calandra* (Brickle et al. 2000; Perkins et al. 2002; Douglas et al. 2009). The low availability of invertebrates and seeds on present-day farmland is thought to be a key factor in the decline of farmland bird populations (Boatman et al. 2004; Holland et al. 2012), and the results of the present and other foraging studies suggest that the establishment of field margins can be a valuable instrument for increasing the food availability in agricultural landscapes.

The effectiveness of field margins and other agri-environment schemes can likely be improved by considering the quality of the landscape in which they are positioned, as well as by optimizing the spatial configuration of these measures. For example, the quantity of (semi)natural habitat in the landscape partly determines the added value of agri-environment schemes, which are expected to be most effective at intermediate levels of landscape complexity (Tscharntke et al. 2005; Kleijn and van Langevelde 2006; Concepción et al. 2008; 2012). Also, the effectiveness of agri-environment schemes may be negatively affected when they are located in landscapes with poor environmental conditions (Melman et al. 2008). Since such conditions (e.g. hydrology, landscape openness, dispersal barriers) mostly cannot be managed at the field scale, a landscape scale approach seems unavoidable to meet conservation aims (Kleijn et al. 2004).

In contrast to the substantial interest in the effects of landscape on the effectiveness of agri-environment schemes, relatively little research has focused on the effects of the spatial arrangement of such schemes. One large-scale experiment has considered the effects of the placement of winter food resource patches on exploitation by birds (Siriwardena et al. 2006; Siriwardena 2010), while more recently the effect of the arrangement of un-cropped patches on bird abundance was examined (Henderson et al. 2012). The results of such studies can help to increase the efficiency of conservation efforts and reduce costs. The analysis of the field margin arrangement in our research area showed that the area of suitable breeding ground from where Skylarks have access to field margins could potentially be almost doubled when margins would be placed at larger spatial intervals and at locations where suitable breeding habitat is present in the direct proximity.

A problematic aspect of this analysis, however, is that it is largely unknown how the presence of one or more field margins at various distances from the nest (i.e. margin density) affects bird reproductive success. Depending on the food availability in field margins and the surrounding landscape, the presence of one margin in the territory of a Skylark pair might not be sufficient to raise their brood, and clustering would be essential to ensure that each territory contains multiple field margins. On the other hand, as illustrated by the results of this study, the positioning of field margins at small spatial intervals will reduce the total area of breeding habitat directly surrounding them due to overlap, thereby limiting the potential number of birds that can breed in the proximity of field margins.

Acknowledgements

The authors wish to thank all the farmers who kindly allowed us to carry out this research on their properties. The observations from 2007 and 2008 were collected by Sovon, the Dutch Centre for Field Ornithology. Bart Nolet and Andrea Koelzsch gave advice about the landscape calculations. Raymond Klaassen, Curtis Barrett and two anonymous reviewers provided valuable comments and suggestions to improve the paper. This research was partly funded by the Foundation Chair in Nature Conservation on Farmland, the province Groningen and the Prins Bernhard Cultuurfonds (Paul van Hoorn Fund, Robert Persman Fund, Bruinvis Meijer Fund, Barbara Eveline Keuning Fund).

He rises and begins to round,
He drops the silver chain of sound
Of many links without a break,
In chirrup, whistle, slur and shake

For singing till his heaven fills,
'T is love of earth that he instills,
And ever winging up and up,
Our valley is his golden cup,

And he the wine which overflows
To lift us with him as he goes:
The woods and brooks, the sheep and kine
He is, the hills, the human line,

The meadows green, the fallows brown,
The dreams of labour in the town;
He sings the sap, the quicken'd veins;
The wedding song of sun and rains

And you shall hear the herb and tree,
The better heart of men shall see,
Shall feel celestially, as long
As you crave nothing, save the song.

G. Meredith (The Lark Ascending, 1895)

Chapter 4

Do field margins enrich the diet of the Skylark *Alauda arvensis* on intensive farmland?

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Abstract

To help restore food availability for birds, arable field margins (extensively managed strips of land sown with grasses and forbs) have been established on European farmland. In this study we describe the effect of field margins on the diet of Eurasian Skylark nestlings and adults living on intensively managed Dutch farmland. We tested the hypotheses that field margins offer a higher diversity of invertebrate prey than intensively managed crops, and that the diet of nestlings receiving food from field margins will therefore be more diverse than that of other nestlings. Field margins had a greater variety of invertebrate prey groups to offer than the intensively managed crops. Coleoptera were the most frequently and most abundantly eaten prey group by both adults and nestlings. Together, Coleoptera, Diptera, Lepidoptera, Hymenoptera and Araneae accounted for 91% of the nestling diet. Nestlings ate larger prey items and a larger proportion of larvae than adults. Almost 75% of both adults and nestlings consumed plant material, perhaps indicating a scarcity of invertebrate resources. When provided with food from field margins, the mean number of invertebrate orders in the nestling diet increased significantly from 4.7 to 5.5 and the number of families from 4.2 to 5.8 per sample. Thus, birds that foraged in field margins could indeed provide their young with more invertebrate prey groups than birds only foraging in crops and grassland.

Introduction

The Europe-wide decline of farmland bird populations during the last quarter of the 20th century can to a large degree be linked to the intensification and industrialisation of agriculture (e.g. Chamberlain et al. 2000, Donald et al. 2001b, Benton et al. 2003, Newton 2004, Stoate et al. 2009, Geiger et al. 2010). Major agricultural changes include increased agro-chemical inputs, land consolidation and the associated removal of natural landscape elements, improved drainage, the conversion of species-rich meadows to high-input grassland, a switch from spring to autumn sown cereals and reduced crop diversity at the landscape level. These changes have resulted in a loss of foraging habitat for farmland birds, as well as an overall reduction in the availability of invertebrate and plant food in the agricultural landscape (Wilson et al. 1999, Taylor et al. 2006, Butler et al. 2007, Siriwardena et al. 2008). To counteract the negative effects of agricultural change on food availability, agri-environmental measures such as field margins, set-asides and winter food patches have been established to restore resources (Vickery et al. 2002, Siriwardena et al. 2008, Vickery et al. 2009). Various bird species prefer these semi-natural elements for foraging over cropped land, demonstrating their value as foraging habitat (Perkins et al. 2002, Siriwardena et al. 2007, Kuiper et al. 2013).

Presumably, the attractiveness of semi-natural habitat to birds is largely explained by higher food abundance (Vickery et al. 2002). However, food diversity or the availability of particular food items may also be a factor. Animals forage to regulate the intake of multiple nutrients, rather than solely maximising their energy intake (Simpson et al. 2004). To ensure the provisioning of all necessary nutrients, passerines feed their young a range of different prey groups (Tinbergen 1980, Krebs 1984). In particular during the developmental stage, the diet quality of birds can have profound effects on their growth, immune functioning and overall health that can extend into the adult stage (Boag 1987, Birkhead et al. 1999). Nutritional deficiencies can occur when prey items are absent that provide essential nutrients or amino acids, leading to reduced growth rates and later fledging (Johnston 1993, Graveland 1996, Ramsay and Houston 2003, Sillanpää et al. 2010).

The decrease in the overall diversity of plants and invertebrates in agricultural areas (Wilson et al. 1999, Vickery et al. 2001, De Snoo et al. 2012b) is likely to be reflected in the diet of farmland birds. The establishment of agri-environment schemes that increase the area of un-cropped land may help to offer birds a wider variety of prey taxa in impoverished agricultural landscapes.

In this paper we study the effect of extensively managed field margins on the diet of the Eurasian Skylark *Alauda arvensis*, a bird species that has been severely declining in most Western European countries (EBCC 2013). It has been shown previously that the body condition of Skylark nestlings is negatively affected when they are provided a less diverse diet (Donald et al. 2001c). Changes in nestling diet composition, imposed by experimentally handicapping provisioning parents, contributed to lower immune functioning and reduced long-term survival of Skylark nestlings (Hegemann et al. 2012, 2013). Although scarcity of safe nesting habitat in agricultural landscapes has been identified as a major bottleneck for this species (Wilson et al. 1997, Chamberlain et al. 1999, Chamberlain and Vickery 2000, Kragten et al. 2008b), reduced food availability and diversity may have contributed to population declines (Donald et al. 2001c, Geiger et al. 2014, Hallmann et al. 2014).

This paper has three objectives: (1) to compare the taxon richness of invertebrate prey groups in field margins with common crops, pasture and road verges, (2) to describe the diet of nestling and adult Skylarks on intensively managed farmland during the breeding season and (3) to assess whether field margins as a supplementary foraging habitat affects the diversity and composition of the nestling diet. We hypothesise that field margins contain a wider range of prey groups than crops and pasture. Consequently, the diet of nestlings receiving food from field margins is expected to be more diverse than the diet of nestlings of which the parents have no access to field margins.

Methods

The study was carried out from April to August 2011 and 2012 in the Province of Groningen in the northeast of The Netherlands. The research area of approximately 970 ha was situated on marine clay and agriculture was the main land use. The predominant crops were winter wheat (±50%), silage grassland (±25%), maize (±8%), lucerne (±5%), sugar beet (±5%) and rapeseed (±3%). In this province, field margins are one of two possible agri-environmental prescriptions for breeding birds on arable land, the other being set-aside. Field margins account for 92% of the total area of field margins and set-aside together (Wiersma et al. 2014). The surface area of field margins was approximately 5% of the cropped land in both years. Field margins generally were 12 m wide and 500–1000 m long, sown with a mixture of grasses, forbs and cereals. The age of the field margins ranged between one and twelve years. Regulations required that 20–70% of the field margin surface was cut twice-annually to keep the vegetation open; once between 1 March and 15 April and once between 15 July and 15 September.

Invertebrate sampling

Invertebrates were sampled in 2011 and 2012 to compare prey taxon richness between field margins, crops, grassland and verges (strips of grassy vegetation along roads and ditches) using a modified leaf vacuum (McCulloch MAC GBV 345) with a 12-cm diameter suction tube. Sampled crops were winter wheat (intensively managed), lucerne (cut two or three times per year followed by manure application, no pesticide use) and grassland (high-input silage fields cut five times per year). Each suction sample consisted of five subsamples of 15-second vacuum sessions within a bottomless circular frame (50 cm diameter), thus sampling a total area of 0.982 m^2 per sample. Five field margins were sampled in both years. Two verges were sampled in 2011 and four in 2012. Of each crop type (grassland, lucerne and wheat) two fields were sampled in 2011 and five in 2012. Each margin, verge and field was sampled five times throughout the breeding season, from mid-May through mid-July. Sampling was conducted in sunny and dry weather conditions only. Invertebrate numbers were converted to dry biomass by applying the length-biomass relationships given in Hawkins et al. (1997, Stylommatophora), Ganihar (1997, Isopoda) and Sage (1982, all other taxa).

Diet

Skylark nests were located as part of a study monitoring reproductive success and the effect of field margins on breeding and foraging. Foraging habitat use by parental birds was recorded during two one-hour observations on two separate days, performed from a hide using binoculars (see Kuiper et al. 2013 for detailed methods). 95 faecal droppings were collected from 50 broods in 2011 and 16 broods in 2012, with nestlings aged between 5 and 8 days. Samples were collected between 26 April and 6 August, with 70% of the samples being collected in June and July. Nestlings usually defecated when they were handled for weighing and ringing, after which faecal samples were stored in vials with sodium chloride for preservation. Mostly two but sometimes one or three faecal droppings were collected per brood. Samples from nine adult birds were collected when they were caught in mist nets that were placed over the nest for the purpose of placing radio tags for a different study (Ottens et al. 2013).

For examination, the faeces were soaked in water for 30 min and analysed under a binocular microscope at 20× magnification using a standard method (Ralph et al. 1985, Flinks and Pfeifer 1987). Prey fragments were identified to class, order and where possible to family, genus or species level. Field guides, taxonomic keys and reference material were used to aid identification. Because of uncertainties in taxonomy or identification, the subclass Acarina and clade Stylommatophora were used as taxonomic entities equivalent to order, and the superfamily Aphidoidea and suborders Heteroptera and Auchenorrhyncha were used as equivalents to family. Based on the animal remains, the minimum number of individuals per taxon was assessed. Invertebrate length was estimated using a reference collection and information from the literature (Calver and Wooller 1982, Ralph et al. 1985, Flinks and Pfeifer 1987). Diet diversity was calculated as the total number of unique invertebrate taxa present per dropping. The number of prey taxa was used as a measure of diversity rather than a diversity index that incorporates evenness, because studies on this subject indicate that equal amounts of each prey taxon are not necessary to balance nutrient intake (Westoby 1978, Tinbergen 1980, Simpson et al. 2004).

The method of faecal analysis to study the diet of birds causes less disturbance than invasive methods such as neck-collars and allows for a better determination of food items than observation by telescope or camera. Concerns have been raised about the differential digestion of prey items, which could yield inexact estimations of the proportions of different prey groups (Moreby & Stoate 2000), but in a comparative study with Skylark nestlings, no differences in diet composition were detected between faecal analysis and applying neck collars, possibly because the passage of food through the gut is relatively quick in Skylark nestlings (Poulsen 1995).

Data analyses

Differences in invertebrate diversity between habitat types were analysed using a Generalised Linear Mixed Model with unstructured covariance structure. The number of taxa identified after suction sampling was entered as the dependent variable with Poisson distribution and identity link (taxa included Araneae, Auchenorrhyncha, Chilopoda, Coleoptera, Diplopoda, Diptera, Heteroptera, Hymenoptera, Isopoda, Lepidoptera imagoes, Lepidoptera and Symphyta larvae, Opiliones, Orthoptera and Stylommatophora). Sampling site was entered as subject and catch round as the repeated factor, so that each catch round in the same margin or field was considered a repeated observation. Habitat type and catch round were added to the model as fixed factors and the interaction between habitat type and catch round was entered to detect whether differences in prey diversity changed over time. To account for possible differences between years, year was added as a random factor. When differences were significant, pairwise post-hoc tests were conducted with Bonferroni-correction.

To characterise the diet in more detail, the length of consumed invertebrate prey items was compared between nestlings and adults using a General Linear Mixed Model. The length of the prey items was log-transformed to achieve normality of residuals and entered as the dependent variable. Nest and adult bird identity were entered as subject, so that each prey item eaten by the same brood or adult bird was regarded as a repeated observation. The life stage of the subjects (nestling or adult) was entered as explanatory factor. Year was added as a factor to control for possible differences in prey size between years.

To assess the effect of the foraging in field margins by the parental birds on the diversity of the nestling diet, Generalised Linear Mixed Models were used. The number of invertebrate orders or families in the diet per dropping was entered as the dependent variable with Poisson distribution and identity link. Nest identity was entered as subject and dropping as the repeated factor, so that each dropping collected from the same brood was considered a repeated observation. The use of field margins as a foraging habitat by the parents during the foraging observations was entered as a factor. To test for possible changes in diet diversity over the course of the breeding season, sampling date was added as a covariate. Sampling date was also tested in a quadratic relationship with diet diversity, but this did not provide a better fit to the data and only the linear term was used in the final models. Year was added as a random factor to control for possible differences in prey diversity between years. Only nests where foraging observations had been conducted were included in this analysis (53 nests, of which 20 had been fed from field margins). Chi-square tests of independence were used to test whether the frequency of occurrence of invertebrate orders and families in the diet differed between nestlings fed from field margins and those not fed from field margins. The Benjamini–Hochberg correction was applied to reduce the chance of false positives when performing multiple tests (Benjamini and Hochberg 1995, Waite and Campbell 2006).

All statistical analyses were performed with SPSS v.21 (IBM, Armonk, New York). Means are given with standard errors.

Results

Available prey

Summed over all habitat types, Diptera (true flies), Coleoptera (beetles) and Araneae (spiders) were the most abundant prey groups sampled by suction sampling (Figure 1). Also Isopoda (woodlice), Stylommatophora (snails and slugs), Auchenorrhyncha (cicadas) and Heteroptera (bugs) were relatively common. Opiliones (harvestmen), Lepidoptera (moths and butterflies), Hymenoptera (ants and sawflies) and Orthoptera (grasshoppers and crickets) were found in small quantities.

The taxon richness of invertebrate prey differed significantly between the sampled habitat types ($F_{4,32} = 25.7$, $P < 0.001$) and between the five catch rounds ($F_{4,32} = 9.3$, $P < 0.001$). The differences between habitat types changed over time (interaction between habitat type and catch round: $F_{16,32} = 1.9$, $P < 0.05$): field margins contained more taxa than winter wheat throughout the entire sampling period, more than grassland during both catch rounds in June, and more than lucerne in the end of June. There were no differences between field margins and road verges. Averaged over the whole sampling period, the mean number of taxa was 5.4 (± 0.3) in field margins, 6.0 (± 0.4) in road verges, 3.9 (± 0.3) in lucerne, 2.9 (± 0.3) in grassland and 2.1 (± 0.2) in winter wheat.

All invertebrate taxa, with the exception of Diptera and larvae of Diptera and Coleoptera, were found in higher quantities in field margins and verges than in grassland, lucerne and winter wheat (Figure 1). Certain taxa were found almost exclusively in field margins and verges, such as Isopoda, Orthoptera, Hymenoptera, Stylommatophora, Heteroptera, Auchenorrhyncha and Opiliones.

Diet composition

In the diet of 66 broods, 1619 invertebrate prey items were recognised, of which 1611 could be identified to at least order level (see Appendix A for a detailed overview). In the faeces of nine adult birds, remains of 68 prey items were found that could all be identified to at least order level (Appendix B). Some prey orders, including Stylommatophora, Isopoda and Lepidoptera, could never be identified to family level and are thus underrepresented in analyses of family diversity.

Coleoptera were the most important prey group for nestlings as well as adult birds. 94% of all broods and 100% of all adults had eaten Coleoptera (Figure 2) and this group accounted for 44% and 53% of the total number of invertebrate prey items eaten by nestlings and adults, respectively (Figure 3). Eleven families

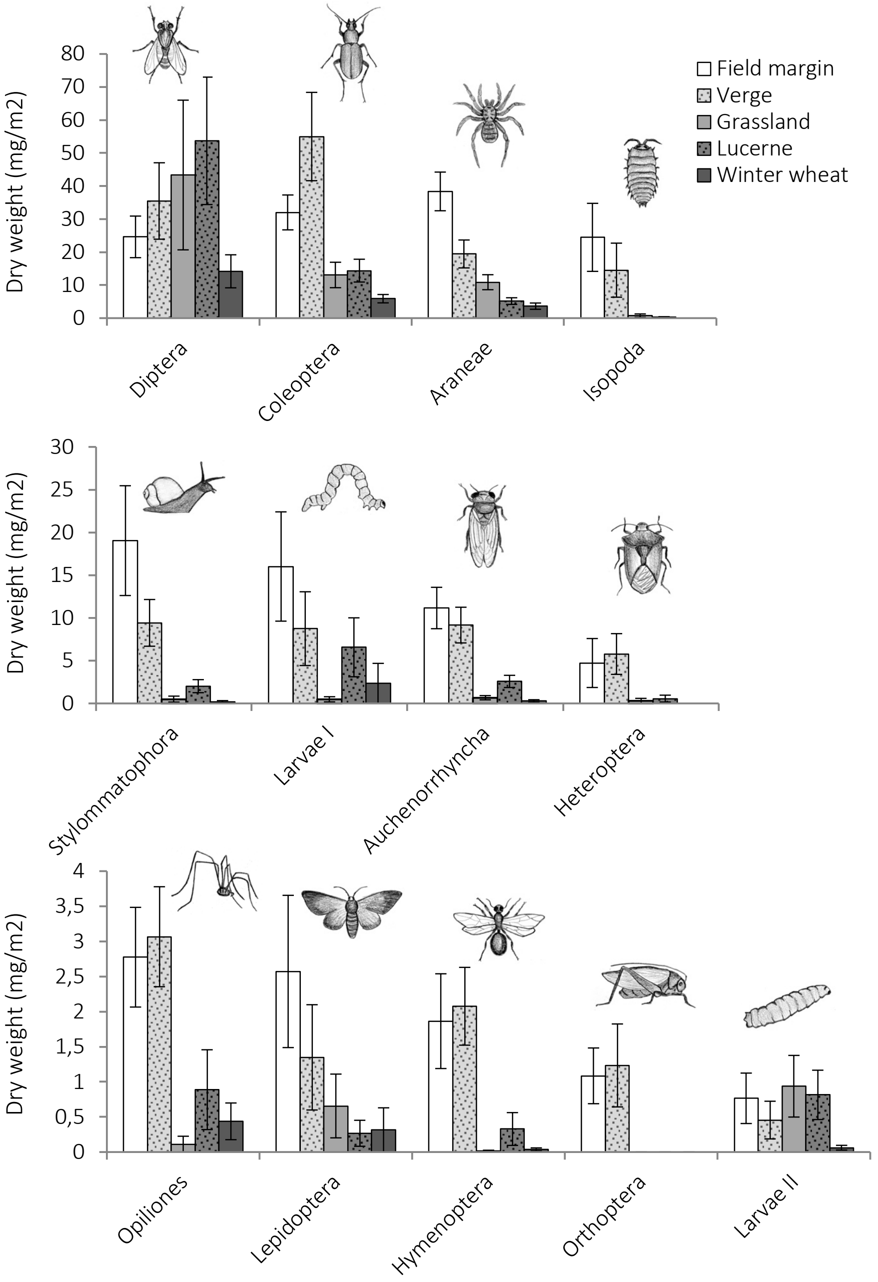

Figure 1. Biomass contributions of invertebrate groups in five habitat types, averaged over the breeding seasons of 2011 and 2012 (± SE). Note the variable scale of the y-axes. Larvae I include Lepidoptera and Symphyta larvae, Larvae II include Diptera and Coleoptera larvae.

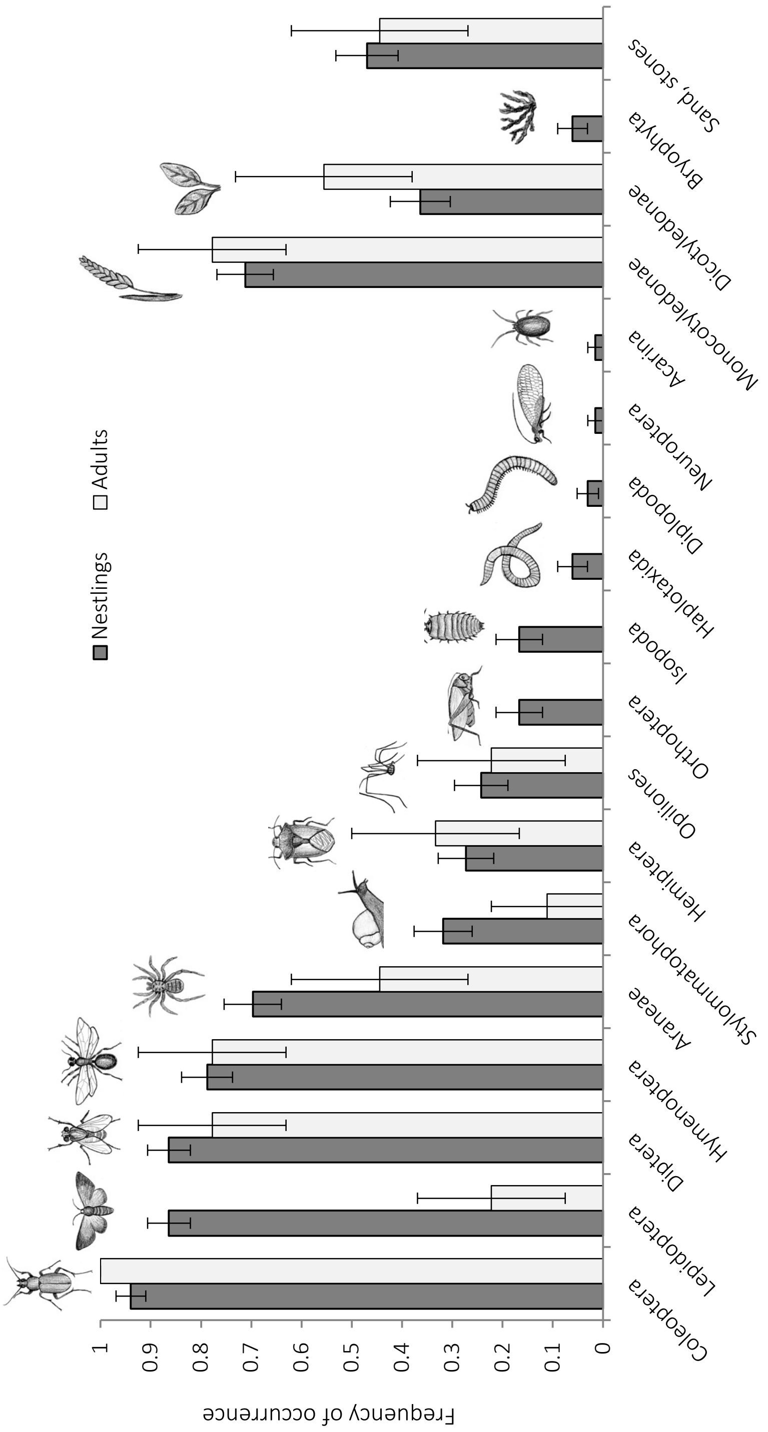

Figure 2. Frequency of occurrence of invertebrate and plant groups in the diet of 66 Skylark broods and nine adults (± SE).

of Coleoptera were identified in the diet of nestlings, of which Carabidae (62%), Elateridae (14%), Curculionidae (7%) and Byrrhidae (6%) were the most numerous (Appendix A). One quarter of the Coleoptera eaten by nestlings were larvae, while adults ate imagoes only (Figure 3).

Lepidoptera, Diptera, Hymenoptera and Araneae each formed between 7–15% of the diet of nestlings and occurred in the diet of 70–86% of all broods. Adults ate fewer Lepidoptera than nestlings and only took imagoes, while nestlings received a large proportion of larvae (64%). Of the Diptera that could be identified, Tipulidae were the most abundant family (95%). Within the Hymenoptera, the Symphyta were by far the most frequently eaten family (90%), mainly pupae (60%) and larvae (33%). Within the Araneae, the families Lycosidae (75%), Linyphiidae (13%) and Salticidae (10%) were the most numerous. Minor prey groups for nestlings were Stylommatophora, Hemiptera, Opiliones, Orthoptera and Isopoda, which were eaten by 17–32% of all broods but comprised only 1–2% of the total number of prey items. Oligochaeta, Diplopoda, Neuroptera and Acarina occurred in the nestling diet sporadically. The last six groups were not found in the diet of adults.

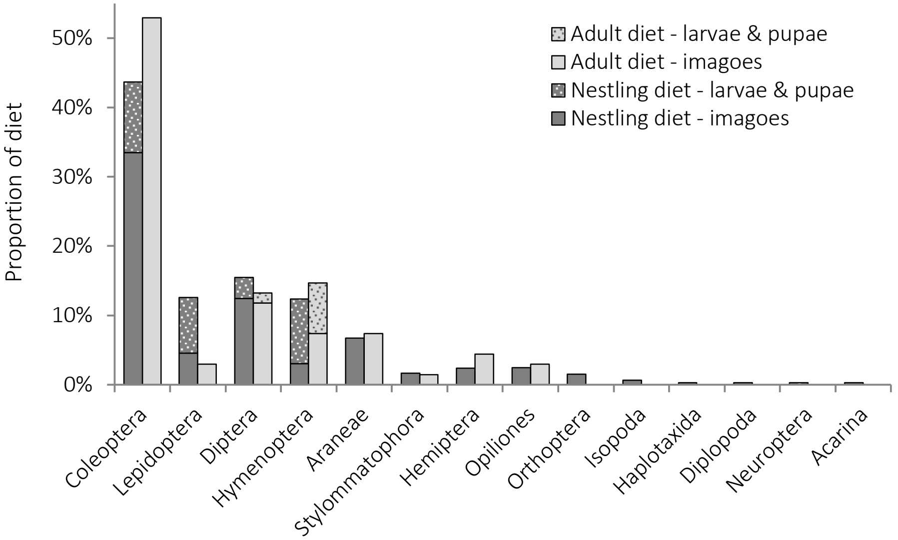

Figure 3. Proportions of invertebrate prey groups in the diet of 6Skylark nestlings and adults, based on prey numbers.

Nestlings ate significantly larger invertebrates than adults $F_{1,1673} = 42.9$, $P < 0.001$). The size of nestling prey ranged between 0.3 and 50 mm, with a mean of 10.7 ± 0.2 mm. The mean prey size of adult birds was 6.1 ± 0.5 mm, ranging between 1 and 16 mm. There were no differences in prey sizes between years ($F_{1,1673} = 2.6$, $P = 0.10$).

Both nestlings and adults consumed plant material (Figure 3), the vast majority being seeds and occasionally stems, leaves and inflorescences of *Triticum* and *Secale* (Appendices C and D). Adult birds also ate other Poaceae, such as *Setaria* and *Poa annua*. Nestlings were fed a range of Dicotyledonae, including seeds of *Taraxacum officinale* (Asteraceae), *Capsella bursa-pastoris* (Brassicaceae) and *Lamium amplexicaule* (Lamiaceae). Also remains of Euphorbiaceae, Caryophyllaceae, Geraniaceae, Plantaginaceae, Polygonaceae and Violaceae were found in the diet. Adults ate seeds of Asteraceae and Polygonaceae and leaves from unidentified Dicotyledonae. Both nestlings (47%) and adults (44%) had small stones (mean length 1.3 ± 0.11 mm, predominantly gastroliths) and sand in their faeces. Two nestlings had eaten pieces of charcoal.

Diet diversity and effect of field margins

The mean number of invertebrate orders and families in the diet was significantly larger for nestlings that were fed from field margins than for other nestlings (orders: $F_{1,78} = 6.6$, $P < 0.05$; families: $F_{1,78} = 8.8$, $P < 0.01$; Figure 4). The diversity of invertebrate families in the diet decreased significantly over the course of the breeding season ($F_{1,78} = 9.1$, $P < 0.01$), while the diversity of invertebrate orders remained stable ($F_{1,78} = 0.2$, $P = 0.7$).

When comparing the frequency of occurrence of invertebrate taxa in the diet (Figures 5 and 6), the diet of broods that received food from field margins contained higher frequencies of the order Opiliones ($X^2 = 4.2$, $P = 0.042$), the Dipteran family Tipulidae ($X^2 = 8.3$, $P = 0.004$) and the Coleopteran families Elateridae ($X^2 = 6.3$, $P = 0.012$), Byrrhidae ($X^2 = 6.1$, $P = 0.013$) and Curculionidae ($X^2 = 4.1$, $P = 0.044$), but the differences did not remain significant after applying the Benjamini–Hochberg correction for multiple testing.

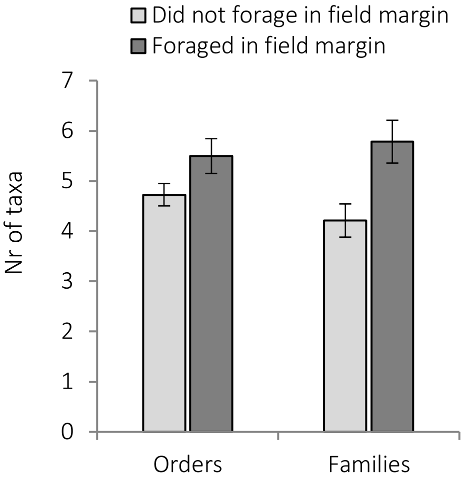

Figure 4. Mean number of invertebrate orders and families in the diet of Skylark nestlings of which the parents did or did not forage in field margins (± SE).

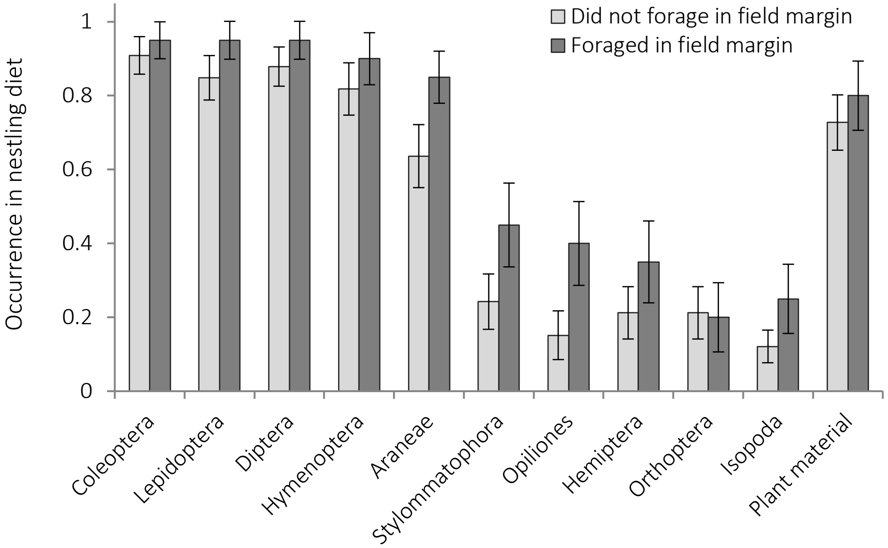

Figure 5. Frequency of occurrence of invertebrate orders in the diet of Skylark nestlings of which the parents did or did not forage in field margins (± SE).

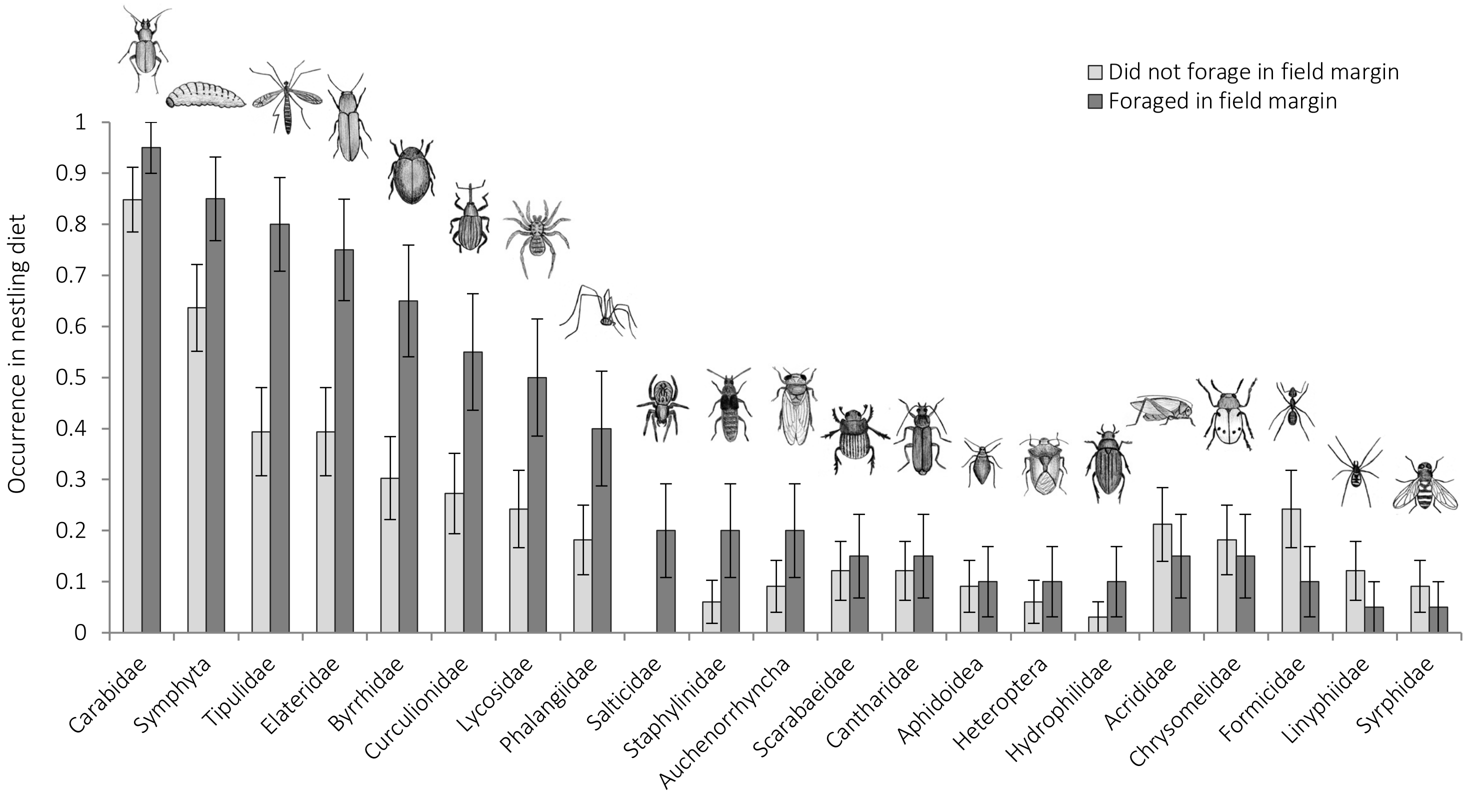

Figure 6. Frequency of occurrence of invertebrate families in the diet of Skylark nestlings of which the parents did or did not forage in field margins (± SE).

Discussion

The diet composition of Eurasian Skylarks in the north of The Netherlands appeared to be broadly comparable with other parts of Europe in terms of the range of prey groups eaten, although differences exist in the relative abundances of groups (Jenny 1990a, Poulsen and Aebischer 1995, Donald et al. 2001c, Smith et al. 2009). Coleoptera were the most numerous prey item, which is similar to some earlier studies (Donald et al. 2001c, Smith et al. 2009), although very low proportions of Coleoptera have been found elsewhere (Jenny 1990a, Poulsen and Aebischer 1995). A comparison of diet composition and prey availability by Jenny (1990) indicated that Coleoptera were actively avoided, leading to the hypothesis that this prey group is less preferential because of their longer handling time and the slower digestion of hard body parts. Our findings partly contradict this hypothesis, because the consumption of Coleoptera in our study site seemed to be larger than would be expected based on Coleoptera abundance in the invertebrate samples. It is interesting to note, however, that a considerable proportion of the Coleoptera provided to the nestlings were larvae, which do not require the removal of elytra, so that their handling time is reduced compared to imagoes (Poulsen and Aebischer 1995). Additionally, Coleoptera larvae may be preferred because the consumption of insect larvae in general has been shown to improve the body condition of Skylark nestlings (Donald et al. 2001c).

Compared to other studies (Weibel 1999, Holland et al. 2006, Smith et al. 2009), the amount of plant material in the nestling diet was relatively large: 79% of all broods had eaten plant material and the number of plant items accounted for 18% of the total amount of food items. This could be an indication that the availability of invertebrates was insufficient. On the other hand, foraging in invertebrate-rich field margins did not decrease the abundance of plant material in the diet, so plants could also have been taken to supply certain nutrients. Skylark nestlings ate only low quantities of less preferential prey groups such as aphids and ants, that have been associated with parasitic infections and reduced growth and survival in chicks of Grey Partridge *Perdix perdix* (Borg and Toft 2000, Browne et al. 2006).

Although our sample size for adult Skylarks was small, the diet of nestling and adult Skylarks seemed to differ in two respects. First, nestlings ate a larger proportion of insects in the larval or pupal stage than adults, mainly of the taxa Coleoptera, Lepidoptera and Hymenoptera. Probably parents reserved insect larvae for their offspring, because this type of food is easily digested and increases the condition of nestlings (Flinks and Pfeifer 1988, Donald et al. 2001c). Larvae may also be fed to nestlings to supply them with sufficient water (Beintema et al. 1991). Second, the size of the prey items eaten by adults was much smaller than for nestlings, which could reflect a predation avoidance strategy. Reserving larger prey items for the nestlings increases the food load that can be brought to the nest per provisioning trip, thereby reducing the number of parental visits to the nest and diminishing the chance that the nest is discovered by predators (Skutch 1949, Martin et al. 2000). A number of prey groups was eaten sporadically by nestlings while they were not found in the adult diet, but this was probably due to the much smaller adult sampling size.

We found that field margins contained a larger range of prey groups than regular crops and intensively managed grassland, which is in accordance with previous studies (Hassall et al. 1992, Frank 1997, 1999, Denys and Tscharntke 2002). The diversity of prey groups in field margins was generally comparable to road and ditch verges, which are semi-natural habitat elements with a more permanent character. Foraging in field margins by Skylark parents significantly increased the number of invertebrate taxa in the nestling diet, both at order and family level. Comparisons of the frequency of occurrence of the taxa in the diet indicated that the improved diversity was due to small but consistent increases in the frequencies of nearly all taxa, rather than specific taxa being unique for a diet collected in field margins. Contradictory to our results, an earlier study found a lower number of invertebrate orders in the diet of nestlings that were brought up in a territory containing wildflower strips than in territories without such strips (Weibel 1999). It is possible that in this area, certain prey groups were present in wildflower strips that were so profitable that other taxa were taken less frequently. But also the accessibility of these strips may have played a role, because not all prey groups may have been within reach for Skylarks when the vegetation was dense or tall (Odderskær et al. 1997).

Considering the declined invertebrate diversity on farmland (Wilson et al. 1999) and the importance of diet composition and diversity for the health and growth of birds (Westoby 1978, Boag 1987, Johnston 1993, Borg and Toft 2000, Donald et al. 2001c, Ramsay and Houston 2003), the connection between these subjects and its role in the ongoing farmland bird declines is in clear need of further research. This study shows that field margins can supply invertebrate groups that are low in abundance in regular crops and intensively managed grassland and that Skylark parents that forage in field margins can provide their young with a more diverse diet. Further study is required to establish whether the increase in diet diversity implies that field margins also deliver a nutritionally more complete diet, and whether a more diverse diet will ultimately lead to improved growth and health of Skylark nestlings.

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Appendix A. Abundance and proportion of invertebrate taxa in the faeces of 66 Skylark broods aged 5–8 days, with estimated length and developmental stage.

Class Order Family	Abundance and proportion[a]			Mean length In mm (±SD)	% larvae and pupae
Arachnida	150 (9.3%)			6.5 (2.8)	
Acarina		1 (0.1%)		0.3 (–)	
Araneae		109 (6.8%)		7.0 (3.1)	
Linyphiidae			6 (0.7%)	2.2 (0.4)	
Lycosidae			36 (4.5%)	9.0 (1.40)	
Salticidae			5 (0.6%)	5.0 (0.0)	
Tetragnathidae			1 (0.1%)	–	
Opiliones		40 (2.5%)		5.4 (1.2)	
Phalangiidae			40 (5.0%)	5.4 (1.2)	
Diplopoda	2 (2.5%)			14.0 (8.5)	
Gastropoda	27 (1.7%)			4.6 (1.7)	
Stylommatophora		27 (1.7%)		4.6 (1.7)	
Insecta	1424 (88.0%)			11.1 (–)	
Coleoptera		705 (44%)		9.3 (3.4)	23
Byrrhidae			30 (3.7%)	7.3 (0.6)	
Cantharidae			16 (2.0%)	8.3 (2.7)	
Carabidae			322 (40.1%)	11.7 (3.0)	
Chrysomelidae			18 (2.2%)	5.2 (1.2)	
Coccinellidae			1 (0.1%)	5.1 (–)	
Curculionidae			37 (4.6%)	5.1 (1.2)	
Elateridae			74 (9.2%)	7.3 (1.0)	
Hydrophilidae			4 (0.5%)	4.3 (0.9)	
Scarabaeidae			9 (1.1%)	9.4 (3.4)	
Silphidae			2 (0.2%)	15.0 (0.0)	
Staphylinidae			6 (0.7%)	6.3 (1.9)	17
Diptera		250 (15.6%)		7.1 (4.1)	19
Scatophagidae			1 (0.1%)	7.0(–)	
Stratiomyidae			1 (0.1%)	11 (–)	
Syrphidae			4 (0.5%)	8.8 (1.5)	
Tipulidae			111 (13.8%)	15.7 (0.9)	
Hemiptera		39 (2.4%)		3.2 (2.0)	
Aphidoidea			21 (2.6%)	2.0 (0.0)	
Heteroptera			13 (1.6%)	6.5 (2.4)	
Auchenorrhyncha			4 (0.5%)	3.5 (1.3)	
Pentatomidae			1 (0.1%)	9.0 (–)	

Appendix A. *Continued*

Class Order Family	Abundance and proportion[a]			Mean length In mm (±SD)	% larvae and pupae
Hymenoptera		200 (12.5%)		5.3 (1.6)	76
Cynipoidae			1 (0.1%)	1.0 (–)	
Formicidae			17 (2.1%)	4.7 (1.4)	
Ichneumonidae			1 (0.1%)	6.0 (–)	
Symphyta			163 (20.3%)	12.8 (6.9)	93
Lepidoptera		203 (12.6%)		18.8 (7.0)	64
Orthoptera		24 (1.5%)		12.2 (3.0)	
Acrididae			20 (2.5%)	12.9 (2.7)	
Neuroptera		1 (0.1%)		8.0 (–)	100
Chrysopidae			1 (0.1%)	8.0 (–)	100
Malacostraca	11 (0.7%)			12.0 (6.9)	
Isopoda		11 (0.7%)		10.2 (0.0)	
Clitellata (Oligochaeta)	4 (0.2%)			50.0 (0.0)	
Haplotaxida		1 (0.1%)		50.0 (0.0)	
Lumbricidae			1 (0.1%)	50.0 (0.0)	
Total nr identified	*1618*	*1611*	*968*		

[a] Proportion of group relative to the total number of specimens identified to that taxonomic level.

Appendix B. Abundance and proportion of invertebrate taxa in the faeces of nine adult Skylarks with estimated length and developmental stage.

Class Order Family	Abundance and proportion[a]			Mean length in mm (±SD)	% larvae and pupae
Arachnida	7 (10.3%)			3.7 (2.4)	
Araneae		5 (7.4%)		3.2 (2.7)	
Linyphiidae			2 (3.7%)	2.0 (0)	
Lycosidae			1 (1.9%)	8.0 (–)	
Opiliones		2 (2.9%)		5.0 (0)	
Phalangiidae			2 (3.7%)	5.0 (0)	
Gastropoda	1 (1.5%)			3.0 (–)	
Stylommatophora		1 (1.5%)		3.0 (–)	
Insecta	60 (88.2%)			6.2 (3.6)	
Coleoptera		36 (52.9%)		5.7 (2.8)	
Byrrhidae			1 (1.9%)	7.5 (–)	
Carabidae			8 (14.8%)	8.1 (3.9)	
Chrysomelidae			3 (5.6%)	4.5 (0)	
Curculionidae			14 (25.9%)	4.4. (1.2)	
Elateridae			5 (9.3%)	6.4 (0.9)	
Hydrophilidae			2 (3.7%)	3.5 (0)	
Scarabaeidae			2 (3.7%)	9.0 (4.2)	
Diptera		9 (13.2%)		8.4 (5.7)	11
Tipulidae			3 (5.6%)	16.0 (0)	
Hemiptera		3 (4.4%)		4.7 (0.6)	
Heteroptera			3 (5.6%)	4.7 (0.6)	
Hymenoptera		10 (14.7%)		4.8 (2.3)	50
Cynipidae			2 (3.7%)	1.5 (0.7)	
Formicidae			1 (1.9%)	4.5 (–)	
Symphyta			5 (9.3%)	6.2 (1.8)	
Lepidoptera		2 (2.9%)		12.5 (3.5)	
Total nr identified	*68*	*68*	*54*		

[a] Proportion of group relative to the total number of specimens identified to that taxonomic level

Appendix C. Abundance and proportion of plant taxa in the faeces of 66 Skylark broods, aged 5–8 days.

Class Order Family Genus/species	Abundance and proportion[a]			
Bryophyta	4 (1.1%)			
Dicotyledonae	61 (17.2%)			
Asterales		6 (1.8%)		
Asteraceae			6 (1.8%)	
Taraxacum officinale				6 (2.0%)
Brassicales		18 (5.5%)		
Brassicaceae			18 (5.5%)	
Capsella pursa-pastoris				16 (5.4%)
Thlaspi arvense				1 (0.3%)
Caryophyllales		5 (1.5%)		
Caryophyllaceae			1 (0.3%)	
Stellaria media				1 (0.3%)
Polygonaceae			1 (0.3%)	
Geraniales		1 (0.3%)		
Geraniaceae			1 (0.3%)	
Geranium sp.				1 (0.3%)
Lamiales		9 (2.7%)		
Lamiaceae			7 (2.1%)	
Galeopsis sp.				1 (0.3%)
Lamium amplexicaule				6 (2.0%)
Plantaginaceae			2 (0.6%)	
Plantago sp.				2 (0.7%)
Malpighiales		2 (0.6%)		
Euphorbiaceae			1 (0.3%)	
Euphorbia sp.				1 (0.3%)
Violaceae			1 (0.3%)	
Viola sp.				1 (0.3%)
Monocotyledonae	289 (81.6%)			
Poales		288 (87.5%)		
Poaceae			288 (87.5%)	
Poa annua				1 (0.3%)
Secale/Triticum var.				256 (87.1%)
Setaria sp.				1 (0.3%)
Total nr identified	*354*	*329*	*329*	*294*

[a] Proportion of group relative to the total number of specimens identified to that taxonomic level.

Appendix D. Abundance and proportion of plant taxa in the faeces of nine adult Skylarks.

Class Order Family Genus/species	Abundance and proportion[a]			
Dicotyledonae	8 (32%)			
Asterales		2 (9.5%)		
Asteraceae			2 (9.5%)	
Caryophyllales		2 (9.5%)		
Polygonaceae			2 (9.5%)	
Monocotyledonae	17 (68%)			
Poales		17 (81%)		
Poaceae			17 (81%)	
Poa annua				5 (33%)
Secale/Triticum var.				5 (33%)
Setaria sp.				5 (33%)
Total nr identified	*25*	*21*	*21*	*15*

[a] Proportion of group relative to the total number of specimens identified to that taxonomic level.

Groots is het liedje niet
maar het geluid, het kleine vliegbeeld
de vleugels wijd gespreid om meer nog
van de warmte te ontvangen
de warmte opstijgend boven het koren
en daar een deel van zijn
deel zijn, deel hebben aan
uitstijgend zingend boven het warme land
zo houden van leven is leven
en weten van leven

D. Hillenius (Verzamelde gedichten, 1991)

Chapter 5

Effects of breeding habitat and agri-environmental management on the breeding performance of Skylarks (*Alauda arvensis*) on intensive farmland

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Abstract

Agricultural intensification has caused a number of farmland bird species to decline rapidly over the past decades, including the Skylark *Alauda arvensis*. Field margin management has been proposed as a way to increase food availability and enhance bird populations. In this study, we assessed the effect of arable field margins on the reproductive success of Skylarks breeding on intensively managed farmland in the Netherlands. The effect of field margins was studied at the level of individual nests, comparing territories with and without field margins. Neither clutch size, nest survival nor nestling body weight was improved by field margin availability, irrespective of breeding crop. However, breeding crop itself significantly affected nest survival and nestling body weight. Nestling weight was lowest in cereals, corresponding with the low prey densities in this crop. Nest survival was lowest in grassland due to frequent silage cutting, which was the main cause of nest loss. Predation rates did not differ between crops and were not affected by field margin proximity. Reproductive success was highest in lucerne, a crop that combines the advantages of larger cutting intervals, a suitable vegetation height for breeding throughout the breeding season and relatively high arthropod abundance. We conclude that field margins alone are not sufficient to maintain a Skylark population in this intensively farmed area. The presumably more subtle effects of increased food availability cannot compensate for the high nest failure rates resulting from agricultural operations and predation. In this and similar areas, the provisioning of safe nesting habitat throughout the breeding season is essential to improve breeding performance. Our research suggests this can be achieved by reducing the frequency of silage cuts on grassland and by increasing the surface area of lucerne.

Introduction

Agricultural intensification has been identified as the major driver behind the decline of farmland bird populations in western Europe (Donald et al. 2001b, Robinson and Sutherland 2002, Stoate et al. 2009). To counteract the negative effects of agricultural intensification on biodiversity and ecosystem services, the European Union introduced the possibility for farmers to voluntarily participate in agri-environment schemes, compensating them for income losses. In arable areas, agri-environment schemes often focus on increasing the area of un-cropped land, for example in the form of sown field margins or patches of winter food for birds (Vickery et al. 2002, Siriwardena et al. 2006). Many animal species living in agricultural areas depend on the presence of un-cropped land, including a range of arthropods (Duelli and Obrist 2003, Tscharntke et al. 2005) and birds (Henderson et al. 2012). Un-cropped land may function as breeding and foraging habitat (Carreck and Williams 2002, Fuller et al. 2004), dispersal corridor (Červinka et al. 2013, Van Dijk et al. 2013) or refugium (Geiger et al. 2009).

Evaluating the effectiveness of agri-environment schemes for farmland birds can be difficult. A number of studies compared bird abundances on different farms or in different regions, the so-called space-for-time substitution (Smith et al. 2010). However, when agri-environmental measures were preferentially established in landscapes or at farms that had higher bird abundances beforehand, a comparison of areas with and without agri-environmental measures is unavoidably biased (Kleijn and Sutherland 2003). Another difficulty is that changes in abundance do not necessarily correlate with changes in reproductive success or survival. Increased bird abundance in areas with agri-environmental management can for example be the result of a mere relocation of birds instead of increased reproduction, turning the area into a potential sink rather than a source (Geertsma et al. 2000). It is therefore essential to complement studies on bird abundances or changes therein with studies that investigate the direct effects of management on demographic processes (Henderson et al. 2012).

In this paper we assess the effect of agri-environmental management on individual-level reproductive performance of a rapidly declining farmland bird, the Eurasian Skylark *Alauda arvensis*. Populations of this species have been declining in most western European countries (EBCC 2013), including a 96% decrease in the Netherlands since 1960 (Sovon 2012). The decline of the Skylark has been linked to changes in agricultural land-use and decreased habitat diversity at the farm and landscape scale, that have reduced the number of breeding attempts that Skylark pairs undertake per year (Wilson et al. 1997, Chamberlain et al. 1999, Chamberlain and Vickery 2000, Geiger et al. 2010, Guerrero et al. 2012). Additionally, the availability of food resources during the breeding season has decreased due to increased agrochemical inputs and the loss of semi-natural habitat elements (Wilson et al. 1999, Chamberlain et al. 2000).

The problem of insufficient food availability can potentially be solved by the establishment of field margins (Vickery et al. 2002, 2009). Field margins are extensively managed strips of land, sown with forbs and grasses, that have in different forms been established in a range of countries, including the United Kingdom (Vickery et al. 2009), Switzerland (Zollinger et al. 2013), Germany (Denys and Tscharntke 2002), France (Cordeau et al. 2012) and the Netherlands (Noordijk et al. 2010). Field margins generally contain higher densities of arthropods than agricultural land and they are highly preferred as foraging habitat by Skylarks and other farmland passerines (Perkins et al. 2002, Kuiper et al. 2013). In the United Kingdom, the abundance of Skylarks was positively correlated with the area of un-cropped land on a farm, especially with un-cropped patches that have a large perimeter-to-area ratio (Henderson et al. 2012). The combined results from these studies suggest that Skylarks benefit from linearly structured agri-environmental schemes such as field margins and respond by increasing their density in areas where this habitat is more available. Yet, it is unknown whether increased abundance indeed reflects improved Skylark breeding performance.

The aim of this study was to examine whether field margins have a positive impact on the reproduction of Skylarks. The effect of field margins was studied at the level of individual nests, with breeding taking place in territories that did or did not contain field margins. We studied three important aspects of reproduction that are known to be linked to population dynamics: clutch size, nestling body weight and nest survival. Birds can adjust their clutch size in response to food availability (Martin 1987, Poulsen et al. 1998), which in turn can affect the productivity of a population (Chamberlain and Crick 1999). The body weight of young birds is an important reproductive parameter, because it correlates positively with future survival and reproductive success (Magrath 1991, Lindström 1999).

It is known from earlier work that the breeding performance of Skylarks differs between crops due to differences in food availability and agricultural management (Wilson et al. 1997, Poulsen et al. 1998, Donald et al. 2002). To increase the effectiveness of field margins, it is therefore important that margins are placed along crops in which Skylarks have good breeding prospects. In order to assess to what extent different crops can hamper or enhance the potential effects of field margins on reproduction, we compared the effects of field margins in three breeding crops (cereals, grassland and lucerne). We also compared these crops in terms of food availability, use as breeding habitat, survival, productivity and predation risk. Also the effect of field margins on predation risk was assessed, since earlier work suggests that field margins can attract predators or improve their access to agricultural fields (Morris and Gilroy 2008), which would hamper their use as a conservation measure.

Methods

The research was carried out from April through July in 2007 - 2012 in the province of Groningen in the northeast of the Netherlands. This province declared the stabilisation of the Skylark population one of the targets of local agri-environmental management and applies field margins as the main instrument to achieve this target (Provincie Groningen 2008). The research area of ca. 980 ha (N53°11.813, E007°7.787) is situated on marine clay and agriculture is the main land use. The main crops are winter wheat (~ 50%), permanent grassland (~ 25%), maize (~ 8%), lucerne (~ 5%), sugar beet (~ 5%) and rape seed (~ 3%). Grasslands were exclusively used for silage cutting, with cuttings taking place with a mean time interval of 33 days (SD = 5.3, based on 53 cutting intervals on 30 grasslands).

Agri-environmental management was introduced to the area more than 15 years ago. Field margins generally were 12 m wide and 500-1000 m long, sown with a mixture of grasses, forbs and cereals. Regulations required that 20-70% of a field margin was cut twice-annually to keep the vegetation open; once between March 1 and April 15 and once between July 15 and September 15. The surface area of field margins in the region varied over the years between 3 and 5% of agricultural land. The research area included both areas with and without field margins. Within Skylark territories, the surface area of field margins ranged between 0 and 24.3% (mean ±SD = 3.9 ±4.9). Other agri-environment schemes included a few patches of bird winter seed, which were grouped with field margins in the analyses because of their small surface area (less than 0.5 % of the cropped area). In 2012, two fields of set-aside were established in the area that were sown with a field margin seed mixture and some strips of lucerne.

In one part of the research area (680 ha), the number of Skylark breeding pairs was monitored annually as part of a breeding bird monitoring programme. In this area, the fraction of agri-environment schemes averaged 4.6% (± 0.96) over the six study years. Four times per year, between early April and the end of July, the area was crossed by foot and all territorial and nesting birds were mapped. After the visits, the total number of Skylark breeding pairs was estimated (Hustings et al. 1989, Van Dijk and Boele 2011).

Invertebrate sampling

Invertebrates were sampled in 2011 and 2012 to compare food abundance between field margins and crops. Each year there were five catch rounds between the middle of May and the middle of July. Five field margins were sampled in both years. Of each crop (lucerne, grassland and winter wheat), two fields were sampled in 2011 and five in 2012. The results of the 2011 sampling have been published earlier in Kuiper et al. (2013).

Invertebrates were collected by vacuum sampling using a modified leaf vacuum (McCulloch MAC GBV 345) with a 12-cm diameter suction tube. Sampling was conducted in sunny and dry weather conditions only. Each sample consisted of five subsamples of 15-s vacuum sessions within a bottomless circular frame (50 cm diameter), thus sampling a total area of 0.982 m^2 per sample. Invertebrates were identified to the order level and allocated to three size classes (3-5, 6-8 and >8 mm). Only those invertebrate groups that were recorded in the Skylark diet by Holland et al. (2006) and Smith et al. (2009) -individuals larger than 5 mm of the taxa Arachnida, Coleoptera, Diptera, Lepidoptera, Orthoptera, Hemiptera and Hymenoptera, including adults and larvae- were included in the analysis.

Survival and productivity

The effect of field margins on reproduction was studied at the level of individual nests. Skylark nests were located by searching for birds that showed signs of breeding behaviour or performed provisioning flights. The fate of nests was verified every 1-4 days either by revisiting the nest or by the observation of provisioning flights from a distance in order to minimise disturbance. A nest was considered successful when at least one nestling left the nest at the age of eight days. The number of fledglings was assumed to be equal to the number of alive nestlings that was seen during the last visit before fledging. Causes of nest failure were determined by inspection of the nest site. Egg shells, scattered feathers or nests that were found empty during incubation or early nestling stages were regarded as predated. When feathers were found intact, the predator was assumed to be a bird, and when feathers were missing the tip, they were assumed to be bitten off by a mammal. Nests with dead, underweight nestlings were considered to have failed due to starvation. When the exact failure date was unknown, it was assumed to have occurred half-way between the last two visits.

Hatching success, nest survival and nestling survival were calculated according to the methods described by Mayfield (1961, 1975) and statistically tested using a Generalised Linear Model with binomial error distribution and logit link function (see section Data analyses). Egg survival was not included in the analyses because partial clutch loss was observed only once. Overall survival S (the chance that an egg survived to a chick that successfully left the nest) was estimated as $S = H(L^8)(F^{22})$, where H is the proportion of eggs that hatch, L is the daily nestling survival rate, F is the daily nest survival rate, 8 is the duration of the nestling phase in days, and 22 is the duration of the nesting period in days (Mayfield 1975). The productivity P (the mean number of chicks successfully leaving the nest per nesting attempt) for each breeding habitat was estimated as $P = CH(L^8)(\mathrm{F}^{22})$, where C is the mean clutch size, and the other variables are as described above (adapted from Donald et al. 2002). Standard errors for survival and productivity were obtained by bootstrapping, resampling 10,000 times from the probability distributions for hatching success (beta distribution), nest survival (beta distribution), nestling survival (beta distribution) and clutch size (normal distribution). Johnson's estimator for the variance in daily survival rate was used to calculate standard errors for daily survival rates of nests and nestlings (Johnson 1979).

Estimates of hatching success were based either on the difference between clutch and brood sizes or, as most nests were found after hatching, on the presence of unhatched eggs in the nest. Since unhatched eggs were found in nests with young of all ages, this method was assumed to give a reliable estimate of true hatching success. To confirm the correctness of this assumption, a Generalised Linear Model was run with binomial error distribution and logit link function, with the number of eggs hatched relative to the number of eggs laid as the dependent factor and the explanatory factors year and nest found before or after hatching. There were no differences in apparent hatching success of nests found before or after hatching (year: Wald $\chi^2 = 5.327$, df 5, $P = 0.34$; nest found before/after hatching: Wald $\chi^2 = 0.02$, df 1, $P = 0.88$), therefore all nests were included in the calculations of hatching success. Nest survival during the incubation and nestling phase were combined into one estimate of daily nest survival (Mayfield 1975), because nest survival rates did not differ between the incubation and the nestling phase (nest days without/with losses: 290/19 during incubation phase and 631/62 during nestling phase, $\chi^2 = 0.08$, *df* 1, $P = 0.77$).

Nestling body mass

Body mass was measured to the nearest 0.1 g using a spring balance when nestlings were 5-9 days old. Tarsus length, a condition-independent indicator of growth, was measured to the nearest 0.1 mm using a pair of callipers. Rainfall and temperature may affect nestling body weight and survival (Donald et al. 2001c, Bradbury et al. 2003) and were therefore included in the analyses. Meteorological data were obtained from a weather station in the research area (Nieuw Beerta, N53°11.662, E007°8.966), owned by the Dutch meteorological institute KNMI. For analyses of the effect of temperature and rainfall on nestling weight, the mean temperature and the total duration of rainfall in hours were calculated over the day of weighing and the preceding three days. For analyses of the effect of temperature and rainfall on nest survival, the mean temperature and the total duration of rainfall in hours were calculated over the day of fledging or nest loss and the preceding three days.

Effect of field margins

In order to establish whether just the presence of a field margin would be sufficient to enhance reproduction, or whether a certain surface area of field margins or a minimum distance from the nest to a field margin would be required for positive effects to occur, three field margin measurements were tested for their effect on breeding success: (1) the presence of at least one field margin within flight distance, (2) the surface area of all field margins within flight distance and (3) the distance from the nest to the nearest field margin.

Based on the foraging distance of Skylarks in the study area, field margin presence and surface area were calculated within circles with radii of 100 and 272 m. The largest effect was expected from margins within 100 m from the nest, because the chance that a field margin was visited by a Skylark during a one- or two-hour observation was 75% for margins within 100 m from the nest and only 20% for margins further away (Kuiper et al. 2013). The 272 m radius was used because this was the 95th percentile of all foraging flight distances recorded in the research area in 2007, 2008 and 2011 (Kuiper et al. 2013). The presence and surface area of field margins and the distance from the nest to the nearest field margin were calculated in ArcGIS 10.1 (ESRI, Redlands, California), using agricultural maps of the Ministry of Economic Affairs (Dienst Regelingen).

Field margin availability was used as the explanatory variable in this study rather than the use of field margins based on foraging observations. Foraging observations conducted in the study area around the same time showed that the use of field margins by Skylarks was so high and so consistent, that we assumed that field margin availability could be used reliably as a proxy for field margin use in order to enlarge the sample size (Kuiper et al. 2013).

Data analyses

All statistical analyses were performed in SPSS 19 (IBM, Armonk, New York). Means are given with standard errors in parentheses, unless indicated otherwise. Differences in arthropod abundance between habitat types were analysed using a Linear Mixed Model. The number of prey items was square root transformed in order to achieve normality of residuals. Habitat type, catch round and year were included in the model as fixed factors. The interaction between habitat type and catch round was added to compare the change in food availability throughout the breeding season between the habitat types. When this interaction appeared significant, post-hoc tests were performed to further explore the differences. Sampling site and catch round were included as random factors, so that each sampling at the same location was regarded a repeated observation.

To examine the selection of breeding habitat, a chi-square goodness-of-fit test was performed to compare the observed number of nests per crop with the expected number of nests based on the surface area of each crop within the research area. Only data from 2011 and 2012 were used for this analysis, because in those years the research area was searched systematically for nests, with attention being paid to search all fields with equal effort. Since the surface areas of the crops did not differ much between years, the nests from 2011 and 2012 were pooled and the surface areas of the crops were averaged over the two years. When breeding habitat selection proved to be non-random, each crop was tested separately to find out which crops were used significantly more or less than expected. The Benjamini-Hochberg correction was applied to reduce the chance of false positives when performing multiple tests (Benjamini and Hochberg 1995, Waite and Campbell 2006).

Nestling weight was analysed using Generalised Linear Mixed Models (type III sums of squares) with nest as random variable. Body mass was log-transformed to achieve normality of residuals. Nest survival was modelled using Generalised Linear Models with binomial error distribution and logit link function (i.e. Mayfield logistic regression; Aebischer 1999, Hazler 2004). Clutch size was analysed using General Linear Models (type III sums of squares), including only the nests that were found during the incubation phase or on the day of hatching. For all three analyses, only nests located in the most used breeding habitats were included, which were grassland, lucerne, cereals (mainly winter wheat but a few nests in spring wheat and barley) and non-crop habitat (including field margins, set-aside, road verges and ditch banks).

In a first step, the dependent variables (nestling weight, nest survival and clutch size) were each tested in a model containing all variables that were expected to explain some of the observed variation, with exception of the field margin variables. The aim of this step was to construct a basic model, to which the field margin variables could be added at a later stage. The models of all three dependent variables included the factors year and breeding habitat and the covariates temperature, rainfall and laying date (the estimated date that the first egg of a clutch was laid). Brood size was added as a covariate to the models for nest survival and nestling weight. The model for nestling weight contained the covariate tarsus length to control for differences in nestling age and structural size (Gilroy et al. 2009, Labocha and Hayes 2012) as well as the interaction between tarsus length and year, because we expected that the relation between body weight and tarsus length would differ between years as a result of varying weather conditions and food availability.

In a second step, separate models were constructed to test the effect of the five field margin variables, which were the presence of a field margin within 100 m and 272 m, the surface area of field margins within 100 m and 272 m and distance to the nearest field margin. Only those variables that were significant in the models described above were added to the field margin models. For analyses of nestling weight and nest survival, the field margin variables were tested in interaction with breeding habitat, because it was expected that the effect of field margins would be more pronounced when nests were located in crops with lower invertebrate availability. For the analyses of the effect of field margins on clutch size this was not done because breeding habitat did not have any significant effect on clutch size.
Nests found in non-crop habitat were excluded from the analyses of field margin effects, because almost all of these nests had a field margin present close to the nest.

To assess whether nests located closer to field margins experienced increased predation rates (e.g. Morris and Gilroy 2008), a Generalised Linear Model with binomial error distribution and logit link function (i.e. Mayfield logistic regression; Aebischer 1999, Hazler 2004) was used to model predation as a binary variable (predated or not predated) relative to the nest exposure time. For nests that failed due to other causes than predation, the last nest exposure day was omitted and only the days that the nest survived and was not predated were counted. Breeding habitat and field margin presence within 100 m from the nest were entered as factors. Only nests located in grassland, lucerne and cereals were included in this analysis.

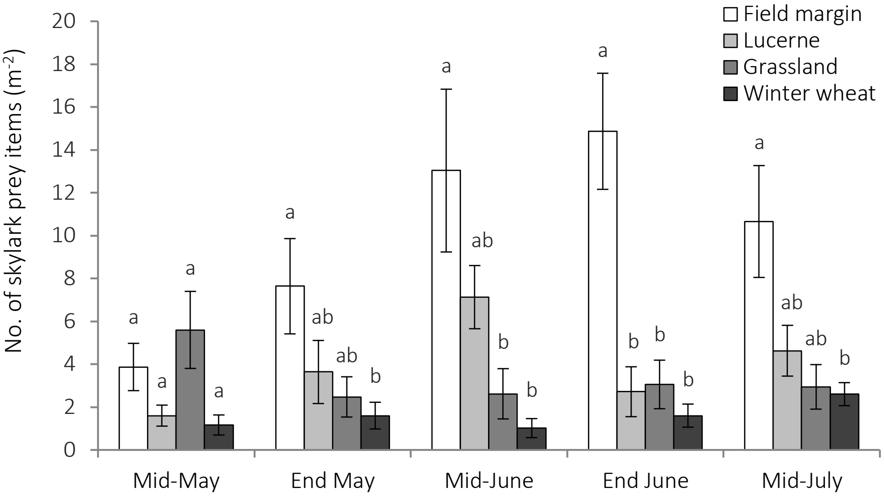

Figure 1. Invertebrate prey availability in field margins and crops throughout the beeding season, averaged over 2011 and 2012. Letter denote signficiant differences between habitat types within catch rounds ($P < 0.05$).

Results

Food abundance

Invertebrate prey abundance differed significantly between the four habitat types that were sampled (field margins, grassland, lucerne and winter wheat; $F_{3,23} = 10.0$, $P < 0.001$), but not between the five catch rounds ($F_{4,27} = 2.5$, $P = 0.070$) or study years ($F_{1,27} = 0.0$, $P = 0.99$). The interaction between habitat type and catch round was significant ($F_{12,27} = 4.5$, $P < 0.001$), indicating that the differences in prey abundance between habitat types changed over time. During the first catch round in the middle of May there were no differences in prey abundance between habitat types. Throughout the rest of the sampling period (from the end of May until the middle of July), prey abundance was significantly higher in field margins than in winter wheat (Figure 1). Field margins contained more prey than grassland in the middle and end of June, and more prey than lucerne in the end of June. Prey densities in the three crops did not differ from each other at any point in time, although densities were generally lower in winter wheat than in grassland and lucerne.

Breeding habitat selection and population trend

Over the six study years, 237 nests were found. Most nests were located in silage grassland (87), lucerne (62) and winter wheat (48). Smaller numbers were found in spring wheat (6), sugar beet (7), barley (4), rape seed (1) and maize (1). Some nests were found on extensively managed agricultural land, including field margins (10) and set-aside (6). A few nests were located in road verges (4) and ditch banks (1). When comparing the distribution of nests over the most abundant crops in 2011 and 2012 to the surface area of these crops, the selection of breeding habitat proved to be significantly non-random ($\chi^2 = 143.7$, *df* 5, $P < 0.001$). Lucerne and grassland were used more than expected based on their surface area, while cereals and maize were avoided (Table 1).

The number of Skylark breeding pairs in the central part of the research area was monitored annually and decreased steadily from 63 pairs (9.3 per 100 ha) in 2007 to 38 pairs (5.6 per 100 ha) in 2012, which is an overall decrease of 40%.

Clutch size

The average clutch size of nests found during the incubation phase was 3.85 eggs (Table 2). None of the tested variables explained any variation in clutch size (Table 3). Clutch size tended to be higher in cereals than in grassland, but this trend was not significant. The presence of field margins around the nest did not have a significant effect on clutch size, neither did the surface area of field margins or the distance from the nest to the nearest field margin (Table 4).

Table 1. Observed and expected number of Skylark nests per breeding crop in 2011 and 2012. Only crops with an expected number of nests > 5 were included.

Breeding crop	Nests found	Nests expected	χ^2
Cereals	41 (27%)	75 (49.8%)	25.51***
Field margins	3 (2%)	6 (4.1%)	1.56
Grassland	62 (41%)	40 (26.4%)	20.26***
Lucerne	38 (25%)	9 (5.68%)	118.8***
Maize	0 (0%)	13 (8.68%)	12.12**
Sugar beet	7 (5%)	8 (5.35%)	0.132

**$P < 0.01$, ***$P < 0.001$, significance after Benjamini-Hochberg correction

Nestling body weight

Nestling body mass differed significantly between breeding habitats (Table 3; n = 121 broods). The weight of nestlings was lower in cereals compared to grassland ($P < 0.001$), lucerne ($P < 0.01$) and non-crop habitat ($P < 0.05$). Nestling mean body mass varied significantly between years, which also significantly affected the relationship between tarsus growth and weight gain (tarsus x year, Table 3). Brood size, temperature and rainfall did not affect nestling body mass (Table 3), nor did the presence or surface area of field margins around the nest or the distance to the nearest field margin (Table 4).

Survival and productivity

47 unhatched eggs were found among 747 eggs and nestlings in 202 nests, giving a mean hatching success of 0.936 (Table 2). Partial brood loss was observed for 21 nests, with 29 nestlings being lost during 2401 nestling exposure days. The loss of nine nestlings could be attributed to starvation. In all other cases the cause of partial brood loss could not be established. The daily nestling survival rate was 0.988 (Table 2), resulting in a nestling survival probability of 90.7% (± 1.6) for the entire nestling period of eight days.

Table 2. Survival and production of Skylark nests located in the four most used breeding habitats and the total of all nests, averaged over the years 2007 - 2012. Data show means ± SE.

	Nests	Nest days	Nests lost	Nestling days	Nestlings lost	Clutch size[b]	Hatching success[c]	Daily nest survival	Daily nestling survival[d]	Overall survival[e]
Cereals	48	231	15	633	2	4.10 (0.23)	0.933 (0.018)	0.935 (0.016)	0.997 (0.002)	0.208 (0.079)
Grassland	73	314	41	725	10	3.65 (0.18)	0.921 (0.017)	0.869 (0.019)	0.986 (0.004)	0.038 (0.020)
Lucerne	48	301	14	672	13	3.95 (0.14)	0.960 (0.014)	0.953 (0.012)	0.981 (0.005)	0.288 (0.081)
Non-crop[a]	18	77	7	257	4	3.63 (0.26)	0.933 (0.028)	0.909 (0.032)	0.984 (0.008)	0.101 (0.090)
All habitats	195	1002	81	2401	29	3.85 (0.09)	0.936 (0.009)	0.919 (0.009)	0.988 (0.002)	0.133 (0.027)

[a] Set-aside, field margins, road verges and ditch banks
[b] Clutch size of nests found in incubation phase
[c] Hatching success of eggs present at hatching time
[d] Daily survival of individual nestlings in surviving nests
[e] Product of hatching success, nest survival over 22 days and nestling survival over 8 days

Table 3. Factors influencing Skylark nestling body weight (GLM, n = 121 nests, adjusted r^2 = 0.927), nest survival (Mayfield logistic regression, n=186) and clutch size (GLM, n = 68, adjusted r^2 = -0.07). Only nests located in cereals, grassland, lucerne and non-crop habitat were included. Data were collected between 2007 and 2012. Significant variables in bold.

	Nestling weight			Nest survival			Clutch size		
	F	df	P	Wald χ^2	df	P	F	df	P
Intercept	124.4	1	<0.001	10.0	1	<0.01	51	1	<0.001
Year	13.0	5	<0.001	4.56	5	0.47	0.49	5	0.78
Breeding habitat	5.92	3	<0.001	10.1	3	<0.05	0.70	2	0.50
Lay date	3.99	1	<0.05	0.29	1	0.59	0.00	1	0.98
Temperature	0.22	1	0.63	0.69	1	0.41	0.09	1	0.76
Rainfall	0.90	1	0.34	0.85	1	0.36	1.26	1	0.27
Brood size	0.43	1	0.51	0.78	1	0.38			
Tarsus length	717.0	1	<0.001						
Tarsus x year	28.87	5	<0.001						

The daily nest survival rate was 0.919 (Table 2), equalling a nest survival probability of 15.7% (± 3.2) over the whole nesting period. Nest survival differed significantly between breeding crops (Table 3). Survival in grassland was lower than in lucerne (*P* < 0.001) and in cereals (*P* < 0.01; Table 2). Nest survival in non-crop habitat was slightly higher than in grassland but the difference was statistically non-significant (*P* = 0.060). There were no differences in nest survival between years nor between nests with different clutch or brood sizes (Table 3). Also weather conditions and the time of egg laying did not affect nest survival. The presence, surface area or distance to field margins had no effect on nest survival (Table 4). The number of fledglings produced per nesting attempt in was 0.14 (±0.07) in grassland, 0.37 (±0.33) in non-crop habitat, 0.85 (±0.33) in cereals and 1.14 (±0.32) in lucerne (Figure 2).

Mowing and predation were the most important causes of nest loss (Table 5). Of the 34 nests that were lost to mowing, 30 were located in grassland and four in lucerne. The proximity of nests to field margins did not affect predation rates (Wald χ^2 = 0.02, *df* 1, *P* = 0.88), neither did predation rates differ between breeding crops (Wald χ^2 = 2.6, *df* 3, *P* = 0.27; Table 5). For ten nests, the predator type could be identified based on feather remains. In seven cases the predator was a bird and in three cases a mammal. Ten broods were lost due to starvation or abandonment and three to unknown or other causes, including a nest located in a road verge that failed after one of the adult birds was killed by traffic.

Table 4. Effects of field margin presence and surface area around the nest and distance to the nearest field margin on Skylark nestling body weight (GLM; n = 111 nests), nest survival (Mayfield logistic regression; n=169 nests) and clutch size (GLM; n = 68 nests). Only nests located in cereals, grassland and lucerne were included. Data were collected between 2007 and 2012.

	Nestling weight			Nest survival			Clutch size		
	F	df	P	Wald χ^2	df	P	F	df	P
Presence within 100 m	0.11	1	0.75	0.17	1	0.68	0.28	1	0.60
Presence within 272 m	2.41	1	0.12	0.95	1	0.33	0.27	1	0.61
Surface area within 100 m	1.70	1	0.19	0.56	1	0.46	0.99	1	0.32
Surface area within 272 m	2.52	1	0.11	0.27	1	0.60	0.46	1	0.46
Distance to nearest	0.20	1	0.65	0.34	1	0.56	0.22	1	0.64
Presence within 100 m x Breeding habitat	2.88	2	0.06	0.78	2	0.68			
Presence within 272 m x Breeding habitat	0.73	2	0.48	2.29	2	0.32			
Surface area within 100 m x Breeding habitat	0.74	2	0.48	1.39	2	0.50			
Surface area within 272 m x Breeding habitat	0.52	2	0.60	0.87	2	0.65			
Distance to nearest x Breeding habitat	0.04	2	0.96	1.67	2	0.43			

Table 5. Causes of Skylark nest failure in the four most used breeding habitats and in total, summed over the years 2007 - 2012. In parentheses the percentage of nests lost relative to the total number of nests found within the breeding habitat.

	Cereals	Grassland	Lucerne	Non-crop [a]	All
Mowing	0 (0%)	30 (41%)	4 (8%)	0 (0%)	34 (17%)
Predation	12 (25%)	7 (10%)	9 (19%)	4 (22%)	34 (17%)
Starvation/Abandonment	3 (6%)	3 (4%)	0 (0%)	3 (17%)	10 (5%)
Other/Unknown	0 (0%)	1 (1%)	1 (2%)	1 (6%)	3 (2%)
Total	15 (31%)	41 (56%)	14 (29%)	8 (44%)	81 (42%)

[a] Set-aside, field margins, road verges and ditch banks

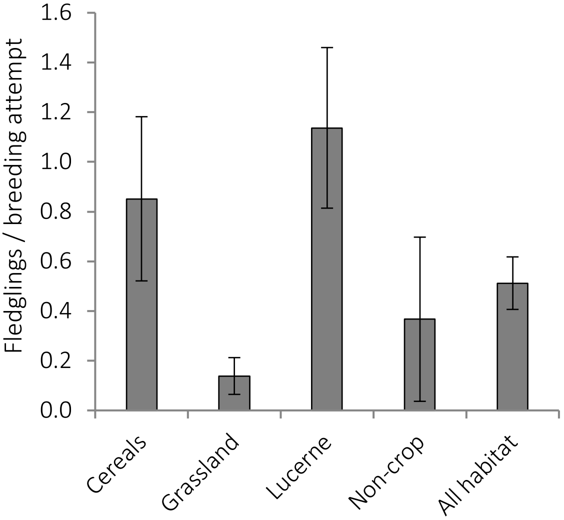

Figure 2. Mean number of Skylark fledglings produced per breeding attempt (± SE) in the four most used breeding habitats and in total, averaged over the years 2007 - 2012.

Discussion

Low food availability in present-day agricultural landscapes has been identified as one of the causes behind the declines of farmland bird populations in Western Europe (Newton 2004, Butler et al. 2007). The establishment of agri-environment schemes that increase food availability, such as field margins, was expected to improve bird reproductive performance. Yet, the relationship between food availability and nestling condition or nestling survival is not consistently positive.

Although some studies found improved nestling weight and survival when the food availability around the nest was higher, for example for Yellowhammer *Emberiza citrinella* (Hart et al. 2006), Linnet *Carduelis cannabina* (Bradbury et al. 2003) and Corn bunting *Miliaria calandra* (Brickle et al. 2000, Boatman et al. 2004), other studies could not detect such correlations for Chaffinch *Fringilla coelebs* (Bradbury et al. 2003), Yellowhammer (Bradbury et al. 2003) and Yellow wagtail *Motacilla flava* (Gilroy et al. 2009).

For Skylarks there are indications that nestling condition is significantly affected by the abundance of chick food within 100 m from the nest (Boatman et al. 2004). Our results point in the same direction, with broods located in winter wheat, the crop with the lowest food abundance, being in poorer condition than broods in grassland or lucerne. This suggests that the establishment of invertebrate-rich elements such as field margins would be most effective in wheat fields. Surprisingly, however, we did not find a positive effect of field margins on nestling weight in any of the breeding crops, even when taking into account field margin surface area and the distance from the nest to the nearest field margin. This is unexpected, since food abundance was on average 4.4 times higher in field margins than in the sampled crops. We have shown previously that field margins are widely and frequently used by the Skylarks in this area, so the vegetation composition and management of the margins do not seem to hamper their use (Kuiper et al. 2013). The lack of effect can also not be explained by an increase in clutch size near field margins (Donald et al. 2001c), since clutch size was not affected by the availability of field margins nor by breeding habitat.

A possible explanation is that Skylark parents were able to compensate for a poorer environment by increasing their foraging efforts (Bradbury et al. 2003, Gilroy et al. 2009). However, when parents make longer or more frequent foraging flights, this can ultimately lead to reduced condition, elevated mortality rates or a reduced number of breeding attempts per year (Martin 1995, Siriwardena et al. 2000). An alternative possibility is that Skylark nestlings were able to maintain a normal growth rate also under poor conditions on the cost of lowered immune functioning. In this case the body weight can indicate good health, while the deprived immune system reduces long-term survival (Chin et al. 2005, Hegemann et al. 2012).

We found no effect of field margin availability on nest survival rates. Most likely, food abundance was not the limiting factor for nest survival. Only a small fraction of nests was lost due to starvation, while the majority of nest failures was caused by agricultural practices and predation. Some studies have suggested that nest predation rates increase in the direct proximity of field margins (Morris and Gilroy 2008), but this was not the case in our study area. Rather, our field observations led to the idea that predation risk was enhanced by food shortage. Nests with underweight nestlings or abandoned broods were often found predated at a later visit, although this was not further quantified. It is known that hungry nestlings increase the frequency and volume of their begging calls, which attracts the attention of predators and increases predation rates (Redondo and Castro 1992, Evans et al. 1997).

Grassland was one of the most used breeding habitats, but, in line with earlier work, nest survival rates in grassland were very low (Jenny 1990b, Wilson et al. 1997, Donald et al. 2002). The studied fields were cut in their entirety on average every 33 days to collect silage, a time interval that is generally too short for Skylarks to complete their nesting cycle. It is therefore not surprising that the mean number of chicks produced per nest in grassland was only 0.14. The number of nestlings that survive until independence will probably be even lower, considering that nests that were destroyed in the incubation stage may have been missed and that productivity was calculated up to the moment that the chicks left the nest, while they can only fly short distances and escape from cutting machinery after several more days. The high cutting frequency of grasslands, enhanced by the use of fertilizer, improved drainage and fast-growing grass species, is a strong limitation for successful breeding in grassland (Chamberlain and Vickery 2000). In non-grassland habitat there were little or no agricultural practices that directly affected nest survival. In lucerne, a legume which is cut two to three times per year for silage, nest survival and productivity were the highest of the four considered breeding habitats. We suspect that few nests were lost to mowing in lucerne because this crop grows tall and dense quite fast, while Skylarks prefer to nest in low and sparse vegetation (Wilson et al. 1997, Toepfer and Stubbe 2001), so that the majority of nests was initiated shortly after mowing.

Data on adult and juvenile survival rates are not available for the study population, but we can estimate the minimum reproduction rate necessary for a stable population based on a different Skylark population in the Netherlands, which showed average annual return rates of 0.7 for adults and 0.2 for juveniles (Hegemann 2012). Assuming that the same return rates apply for our population, it would require on average three fledglings per pair per year in order to maintain the population size. With 2.5 to 3 breeding attempts per year (Delius 1965), the minimum number of fledglings required per breeding attempt is 1.0 – 1.2. In our study site the mean number of fledglings produced per breeding attempt, averaged over all study years and all breeding habitats, was only 0.51, and probably this is an underestimation because nests that fail during the early nesting stages are often missed (Jenny 1990b). The annual monitoring of Skylark breeding pairs confirmed that this reproduction rate was insufficient, showing a gradual decline of 9.5% per year between 2006 and 2012. Lucerne was the only crop in which reproductive output exceeded the minimum, with 1.14 nestlings produced per breeding attempt. There is not sufficient data on emigration, immigration and juvenile and adult survival to draw final conclusions, but the low productivity rates in cereals and particularly grassland seem at least partly responsible for the population decline.

Implications for agri-environment management

In order to conserve this species in agricultural areas, it is essential that measures are taken that do not only improve food availability, but foremost provide safe nesting habitat. Based on our findings we see two main possibilities to increase the availability of safe nesting habitat for Skylarks in the study area and in similar agricultural landscapes. First, the safety of grassland as a breeding habitat could be improved by reducing the number of silage cuts, preferentially accompanied by lowered inputs of fertilizer to reduce grass growth, thereby lengthening the cutting interval and allowing the birds more time to raise their brood (Wilson et al. 1997, Vickery et al. 2001, Donald et al. 2002). This is particularly important because Skylarks highly preferred grassland as a breeding habitat, especially in June and July when winter wheat became too tall and other suitable crops were only scarcely available.

Late-season availability of suitable breeding crops can be improved by increasing the use of spring-sown cereals (Chamberlain et al. 1999, Kragten et al. 2008b, Eggers et al. 2011) or lucerne (Eraud and Boutin 2002). In the present study, lucerne was the only breeding habitat in which the average productivity per nesting attempt reached the minimum required to maintain a stable population. The low-frequency mowing of lucerne allows sufficient time for Skylarks to raise their young but also repeatedly returns the vegetation to a height and coverage that is suitable for nesting, explaining the high use of this crop as a breeding habitat throughout the entire breeding season. Another advantage of lucerne is the relatively high availability of invertebrates compared to other crops, probably because lucerne is a perennial crop and requires no pesticide applications (Bretagnolle et al. 2011).

Despite high nest-level productivity, lucerne may or may not act as a source population for skylarks, depending on the speed of re-nesting and number of nesting attempts per year. Due to the suitable sward structure, we predict that these parameters are good in lucerne fields, but further work is required to confirm that lucerne does indeed deliver high annual productivity. Previous work has suggested that increasing the surface area of lucerne may also benefit other bird species. For the Montagu's Harrier, lucerne is one of the most preferred hunting habitats, especially shortly after mowing, when voles and mice become more easily visible (Trierweiler et al. 2010). In France, an increase in the surface area of extensively managed lucerne has helped to locally reverse the decline of the endangered Little bustard *Tetrax tetrax* (Bretagnolle et al. 2011), while simultaneously slowing down the decline of the non-targeted Skylark (Brodier et al. 2013).

An important advantage of promoting certain production crops for agri-environmental purposes is that such measures are more cost-effective than non-productive agri-environment schemes. In the study area, farmers received a payment of approximately €2150 for each ha of field margin to fully compensate the loss of income associated with not using the land to grow winter wheat, the most profitable crop in the region. In comparison, the sum required to compensate the income difference between lucerne and winter wheat would be approximately €1200 per ha, or €1000 when the positive effects of lucerne on soil quality and future pest pressure are incorporated (pers. comm. local farmers). Thus, by promoting crops such as lucerne as agri-environmental measures, farmers can provide safe breeding habitat for birds at relatively low costs, even when additional measures are taken that reduce farming intensity (e.g. limited number of silage cuts per year) in order to increase the ecological value of the crop.

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With its efforts hooked to the sun, a swinging ladder
With its song
A labour of its whole body
Thatching the sun with bird-joy

To keep off the rains of weariness
The snows of extinction

With its labour
Of a useless excess, lifting what can only fall

With its crest
Which it intends to put on the sun

Which it meanwhile wears itself
So earth can be crested

With its song
Erected between dark and dark

The lark that lives and dies
In the service of its crest

T. Hughes (The Thought-Fox, 1995)

Chapter 6

Improving agri-environmental management for arable farmland birds - a synthesis

To halt the ongoing declines of farmland birds, two things are of great importance. First, the underlying mechanisms and their interactions need to be identified in order to understand how various components of agricultural intensification have affected food availability, reproduction and survival of farmland bird species. Second, based on this knowledge, ecologically effective measures and policies need to be developed that can counteract the negative effects of agricultural intensification and stabilise populations. Without doubt, the second aspect is the most challenging of the two. After several decades of research into farmland birds, the ecology of most species is well known and the reasons behind the population declines are reasonably well understood (Potts 1986, Donald et al. 2001b, Stoate et al. 2001, Robinson and Sutherland 2002, Newton 2004, Wretenberg et al. 2006, Stoate et al. 2009, Geiger 2011). Yet the development of agri-environmental measures that are ecologically effective and economically efficient has proven notoriously difficult (Berendse et al. 2004, Kleijn et al. 2011, Whittingham 2011a).

This synthesis evaluates the value of agri-environmental management for farmland birds, with special attention for the function of field margins. The central question of the research in this thesis was 'How effective are field margins as a measure to support farmland birds in intensively managed agricultural areas?'. Here, I will answer that question by summarising the findings of my own research and combining them with results from previous studies. Based on this evaluation, suggestions are given to improve the effectiveness of existing conservation measures, as well as to develop new agri-environment schemes for farmland birds.

The value of field margins for farmland birds, and the Skylark in particular

Field margins are widely implemented throughout Europe and constitute the most common agri-environment scheme in most arable areas in the Netherlands (Figure 1). In this thesis, the value of field margins for farmland birds was evaluated from various angles. At first sight, the results may seem quite variable, showing positive effects of field margins in some situations, while neutral or negative effects were seen when a different aspect of bird ecology or behaviour was under consideration. Yet on closer examination, the overall picture provides a clear insight in the ecological function of field margins for birds and gives explanations for the seemingly mixed results.

Figure 1. Field margin with grasses, cereals and forbs in the first year after sowing. Ganzedijk, the Netherlands, July 2010.

Foraging habitat

A first step to assess the value of field margins to birds is to verify whether, and for what purpose, field margins are used. Although some birds nest in field margins, such as Yellowhammer *Emberiza citrinella* and Whitethroat *Sylvia communis* (Stoate and Szczur 2001), few researchers seem to consider the provisioning of breeding habitat an important function of field margins. The far majority of studies concerns the value of field margins as a foraging habitat (Vickery et al. 2009). Regarding the Skylark, we found that field margins were indeed hardly used as breeding habitat (chapter 5), but the use as foraging habitat was multiple times larger than expected based on surface area (chapter 3). Also other bird species such as Yellowhammer, Corn bunting *E. calandra* and Common kestrel *Falco tinnunculus* prefer field margins for foraging (Brickle et al. 2000, Perkins et al. 2002, Aschwanden et al. 2005, Douglas et al. 2009).

Field margins generally contain higher densities of invertebrate and plant food items than crops or grassland, especially when they have a complex sward structure and a high diversity of plant species (chapter 5, Barker and Reynolds 1999, Thomas and Marshall 1999, Vickery et al. 2009, Hyvönen and Huusela-Veistola 2011). Also the diversity of invertebrates is larger in field margins, so that prey groups become available to birds that are rare on conventional agricultural fields (chapter 4, Vickery et al. 2002, Noordijk et al. 2010). Reduced pesticide use and the absence of soil disturbance by ploughing results in higher densities of important dietary items such as sawfly larvae (Hymenoptera), caterpillars (Lepidoptera), hoppers (Orthoptera) and plant bugs (Hemiptera) (chapter 4, Barker and Reynolds 1999, Vickery et al. 2002).

The larger prey diversity in field margins is reflected in the nestling diet: when parents forage in field margins, the diet of Skylark nestlings contains a significantly larger diversity of invertebrate orders and families (chapter 4). This indicates that field margins have the potential to improve nestling health and weight via the foraging behaviour of the parents. Various studies show that improved diet diversity positively influences the health and growth of young birds (Tinbergen 1980, Johnston 1993, Donald et al. 2001c, Ramsay and Houston 2003), but more research is needed to examine the importance of prey diversity for farmland birds. Specifically, it would be interesting to assess the effect of diet diversity, or differing proportions of certain prey groups, on immune functioning, as there are indications that these are linked (Hegemann et al. 2013). Considering that not only the abundance but also the diversity of invertebrate and seed foods has decreased in agricultural landscapes over the past decades (Wilson et al. 1999), the effects of diet diversity and composition on bird health are in clear need of more research.

Effects on nestling weight, survival and population growth

Field margins improve food availability for birds in agricultural landscapes, they are a favoured foraging habitat for Skylarks and other farmland birds and improve the diversity of the nestling diet. Still, these results are not sufficient to determine the effectiveness of field margins as a conservation tool. In order to stabilise declining populations, it will be necessary to improve reproduction and survival. Do the positive effects of field margins on food availability and diet translate into higher chick survival or improved reproductive success? This question was answered by measuring the effect of field margins on three important reproductive parameters: Skylark clutch size, nestling weight and nest survival. Unexpectedly, the presence of a field margin in the vicinity of a Skylark nest did not have any measurable effect on nestling weight, even when taking into account the surface area of field margins and the distance from the nest to the nearest margin. Also clutch size was unaffected, and the survival of Skylark nests was not improved. The last finding is easily explained by the fact that only a small part of all nestlings was lost to starvation: most nests were destroyed by agricultural operations and predation. The reason why field margins did not improve nestling weight is less clear. Food availability did seem to influence nestling weight, since nestlings in winter wheat, the crop with the lowest prey densities, had the lowest weight. Perhaps parents could compensate lower food availability by making longer or more frequent foraging flights, or nestlings might have been able to maintain normal growth rates by trading off growth against a poorer immune system (Hegemann et al. 2013).

The finding that field margins did not improve the reproductive performance of Skylarks was confirmed by a population decrease of 40% that was observed in the study area between 2007 and 2012 (chapter 5). A comparison of Skylark population trends in areas with and without field margins showed no effect of field margins on growth rates (chapter 2). Also the short-term population trends of nine other bird species were unaffected. In the UK, positive effects of field margins were found on the population growth rates of a few bird species, but negative effects were also found and the results varied considerably between farming types (i.e. pastoral, mixed or arable landscapes) and between regions (Davey et al. 2010b, Baker et al. 2012). In contrast to the lack of effect of field margins on population growth rates, areas with field margins did exhibit higher bird species richness and higher densities of several species (chapter 2), a result similar to findings from Switzerland and the UK (Henderson et al. 2012, Meichtry-Stier et al. 2014). However, as long as population trends are not improved and reproduction and survival remain unaffected, the higher bird abundances may as well reflect the preference of farmers or administrators to establish field margins in areas with higher bird densities, or a preference of birds to establish themselves in areas with field margins even though this has no direct effect on reproduction or population growth.

Combining the results presented in this thesis and the findings from earlier studies from various countries, a careful attempt can be made to evaluate the value of field margins for breeding farmland birds. Overall, field margins seem to do what they are designed for, that is offering a rich foraging habitat that is appreciated by Skylarks and other farmland birds (Brickle et al. 2000, Perkins et al. 2002, Aschwanden et al. 2005, Kuiper et al. 2013). Yet, increased food availability is only expected to improve population growth rates when food scarcity is the main factor that limits reproduction and survival. When other bottlenecks exist, the establishment of field margins will be of limited value. This is illustrated by our case study of the Skylark, in which the main factors limiting reproduction were silage cutting of grassland and predation, two factors that are not ameliorated by the presence of field margins. A similar result was found for the Corn bunting in Scotland, where increased food availability only reversed population trends when additional measures were taken to delay mowing (Perkins et al. 2011). Therefore I conclude that in our study area and in other areas with similar cropping systems, field margins are not sufficient as a prime agri-environmental option to conserve the Skylark, although they can be valuable in addition to other measures. Regarding other species, more detailed studies are needed, but so far it seems that the effect of field margins is limited when no other measures are taken (Perkins et al. 2011, Baker et al. 2012, chapter 2).

In the following section, the main causes for the population declines of the Skylark are discussed and suggestions are given to improve agri-environmental management.

Skylark reproduction: bottlenecks and solutions

Since the 1980s, the Skylark declined by 48% in Europe, a loss of approximately 39 million birds (EBCC 2013). The difficulties that Skylarks experience on present-day farmland can roughly be divided into three categories: low invertebrate availability in summer, low seed availability in winter and a lack of safe and suitable breeding habitat. Different aspects of agricultural intensification underlie these factors, that are discussed below.

Food availability

Food availability for Skylarks on farmland has diminished over the past decades, mainly due to the disappearance of foraging habitat, the intensification of grassland management and the increased use of fungicides, herbicides and insecticides (Wilson et al. 1999). Bird abundance and species richness generally correlate negatively with increased pesticide use (Rands 1985, Geiger et al. 2010, Hallmann et al. 2014). Pesticides reduce food availability directly by killing invertebrates and seed-bearing weeds, as well as indirectly, by reducing the diversity and structure of plant communities that provide food and a living environment for invertebrates (De Snoo 1999, Taylor et al. 2006). Winter food availability has furthermore decreased due to the increasing popularity of winter cereals, which are sown before winter so that the area of over-winter stubbles, a favoured foraging habitat of the Skylark, has been reduced (Gillings et al. 2005, Siriwardena et al. 2008, Geiger et al. 2013).

Since invertebrates are the primary food source for young Skylarks, the establishment of invertebrate-rich foraging habitat is important to support populations, in particular in areas where food availability is low due to large field sizes, high pesticide inputs, low crop diversity and low availability of semi-natural landscape elements. In such landscapes, also the establishment of winter foraging habitats such as stubble fields or sown food patches is widely recommended to improve population growth rates (Donald et al. 2001a, Gillings et al. 2005, Siriwardena et al. 2007).

Safe and suitable breeding habitat

Skylarks have a well-documented preference to breed in low and open vegetation. The height of the vegetation should generally lie between 15 and 60 cm, with a vegetation cover not exceeding 60% (Wilson et al. 1997, Toepfer and Stubbe 2001). Crops of this height and structure should be available from the end of April until the end of July, during which time Skylarks produce an average of three clutches. This high productivity is needed to balance the relatively low adult longevity and high juvenile mortality (Donald 2004). However, over the past decades the number of breeding attempts that Skylark pairs undertake per year has decreased significantly, so that the number of fledglings is no longer sufficient to maintain population levels (Wilson et al. 1997, Chamberlain and Crick 1999, Chamberlain and Vickery 2000). The reason behind this decrease is probably a shortage of suitable breeding habitat, caused by reductions in crop diversity at the farm and landscape scale (Chamberlain and Vickery 2000, Kragten et al. 2008b). A high crop diversity offers spatial as well as temporal heterogeneity, so that Skylarks can find suitable breeding habitat throughout the breeding season. The shift from spring to winter cereals has also been important in this respect, because winter cereals have an earlier growing season and already become too tall for nesting in late May or early June (Chamberlain et al. 1999, Donald et al. 2002).

To offer Skylarks the possibility to fulfil their full breeding potential, it is recommended to increase crop diversity to such an extent that Skylarks will be able to find crops of a suitable height during the entire breeding season. One option is to introduce fields of set-aside, where Skylark fledgling productivity is generally high because of large clutch sizes, good nest success and high territory densities (Poulsen et al. 1998, Eraud and Boutin 2002). However, sometimes lower survival rates are found in set-aside, mainly because of high predation rates (Weibel 1999, Donald et al. 2002). Another disadvantage of set-aside is that it is relatively expensive, because the land is taken out of production entirely. Costs can be reduced when specific crops are promoted for agri-environmental purposes, for example spring cereals (Bos et al. 2010) or winter cereals that are sown with slight changes in crop density (Evans and Green 2007). Also lucerne, mown three times per year or less, can be a valuable crop, because Skylark fledgling production is high and the vegetation height is suitable for nesting throughout the entire breeding season (chapter 5, Eraud and Boutin 2002). The good nest survival rates and relatively high nestling body mass that were found in lucerne are promising (chapter 5), but large-scale experiments are needed to determine the effects of increased surface areas of lucerne on population growth rates.

Apart from some crops being unsuitable for breeding, there is a problem with some breeding crops being unsafe. Although long-term changes in the causes of nest failure are unknown for Skylarks, it is highly likely that the proportion of nest failures that can be attributed to silage cutting of grasslands has increased. At present, the growth of monocultures of highly productive grass species and large fertiliser inputs allow cutting intervals of only 34 days, which is too short for Skylarks to complete their nesting cycle (chapter 5). In common with studies from other countries (Jenny 1990b, Poulsen et al. 1998, Donald et al. 2002), the frequent mowing of silage grassland caused very high nest failure rates in our study area (chapter 5). Grasslands are an attractive nesting habitat for Skylarks because of the short vegetation, in particular during the second half of the breeding season, when most other crops have reached an unsuitable vegetation height. In areas where grassland is frequently mown, measures are therefore needed to reduce nest losses. For example, the number of silage cuts could be reduced, thereby lengthening the intervals between the mowing events (Donald et al. 2002).

Predation

Although the effect of predation on breeding success varies per region, predation was one of the most important causes of nest failure in our study area (chapter 5) and on British lowland farmland (Donald et al. 2002). Studies suggest that predation pressure on farmland birds has increased over the past decades due to increasing predator densities (Macdonald and Bolton 2008), but also because intensive farming enhances predation through for example decreased vegetation cover and reduced body condition, so that birds are less well able to hide or escape from predators (Whittingham and Evans 2004, Schekkerman et al. 2009). Low food availability may furthermore enhance the predation of young birds, because hungry nestlings call louder and more frequently for their parents, thereby increasing the chance that they are discovered by predators (Redondo and Castro 1992, Evans et al. 1997). In this context the establishment of field margins may help to reduce predation by increasing food availability, but they may as well increase predation because predators are also attracted to these habitats. A British study found that predation rates of Skylark nests increased with decreasing distance to field margins (Morris and Gilroy 2008), although this effect did not exist in our study area (chapter 5).

It is likely that predator densities have indeed increased since the 1960s, but on the other hand predation was already the most important cause of Skylark nest loss before 1965 (Delius 1965). Skylarks and many other farmland birds are adapted to predation by their ability to lay several clutches per year and to start relaying soon after nest loss. They are able to handle a certain degree of predation when nest failures due to other causes are not too frequent. When other causes are frequent, however, predation contributes to the poor population growth rates. Intensive predator control can increase nest survival rates (Tapper et al. 1996, Donald et al. 2002), but demands substantial efforts and it is questionable whether this is in general desirable. Although the culling of foxes is common in the Netherlands, it is generally not accepted to control mustelids or birds of prey. On the contrary, several conservation groups aim to increase the populations of these predatory animals and restore a more complete food web on farmland. Predator control does therefore not seem to be a feasible option for the conservation of farmland birds.

Conservation measures for Skylarks

The best strategy to conserve the Skylark seems to be to offer a number of integrated agri-environmental measures that target exactly those key factors that limit population growth in the landscape or region under consideration. For example, in the north of the Netherlands, conservation measures should include summer food availability, winter food availability and the availability of suitable nesting habitat. Summer food resources can be provided by means of field margins, but the current management would be improved when a higher proportion of field margins was placed alongside suitable breeding crops such as cereals or sugar beets, instead of along unsuitable habitats such as roads, canals, maize, trees or buildings (chapter 3). To supply winter food, sown winter food patches and fields with stubbles of for example barley, sugar beet or wheat are recommended (Donald et al. 2001a, Geiger et al. 2013). As opposed to the preferences of most other species of farmland passerines, these fields should be relatively large and not enclosed by hedges or trees to meet the requirements of the Skylark. Currently, conservation actions focus almost exclusively on the provisioning of food, while the lack of safe breeding habitat is not addressed (Figure 2). In areas with silage grasslands, a management plan is needed to reduce nest losses, for example by reducing the frequency of silage cuts (Donald et al. 2002, chapter 3). In areas with low crop diversity it is furthermore recommended to provision suitable (late-season) breeding habitat, such as lucerne.

In a more general sense it can be concluded that current conservation measures for birds on arable farmland are very general and often not sufficiently tailored to the requirements of declining species to be successful (Perkins et al. 2011, Pywell et al. 2012). In the next section, this problem and possible improvements of agri-environmental policy are discussed.

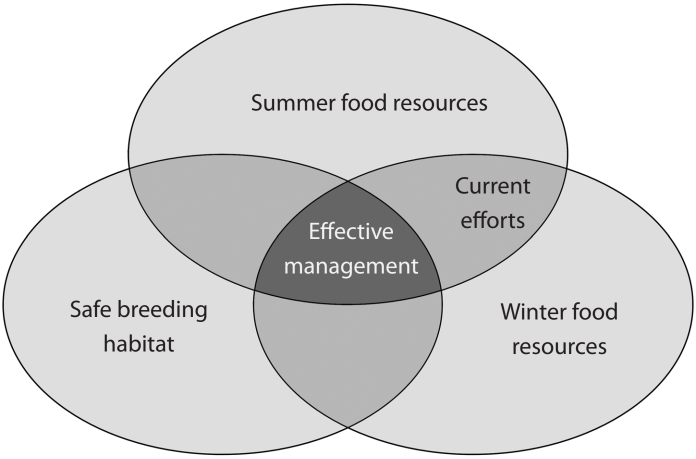

Figure 2. Required managament actions for Skylarks in the north of the Netherlands. Current conservation efforts focus almost exclusively on providing food resources, while effective management should incorporate the provisioning of suitable and safe breeding habitat.

The future of agri-environmental management for farmland birds

With a globally rapidly increasing demand for agricultural products, it can be difficult to find commitment as well as resources to carry out conservation measures that decrease productivity (Tilman et al. 2002). The European Parliament acknowledges the importance of biodiversity for "the existence of human life and the well-being of societies, both directly and indirectly through the ecosystem services it provides" and also "stresses the urgent need for action" (EU 2012). Despite these encouraging words, the last 'greening' of the Common Agricultural Policy is considered a failure by conservationists, because the environmental prescriptions are diluted and have so many exemptions that they are unlikely to benefit biodiversity (Pe'er et al. 2014). On top of that, a considerable part of all conservation efforts that have been taken over the past years to halt biodiversity declines on farmland were of relatively little value, despite being costly and requiring substantial effort from farmers (Kleijn et al. 2006, Blomqvist et al. 2009, Breeuwer et al. 2009, Baker et al. 2012).

Yet, not all is lost for agri-environmental management. Large-scale changes in agriculture policy have the potential to change the state of farmland biodiversity, as was evident from the generally positive bird population trends during the 'set-aside period' in which the EU stimulated farmers to leave large areas of land uncultivated (Koks and Van Scharenburg 1997, Wretenberg et al. 2007). Positive results have also been achieved with local, high-effort management that was based on scientific knowledge or expert judgement. These examples of successful agri-environmental management show that it is possible to restore biodiversity on farmland when measures are tailored to local circumstances (Table 1).

Regional conservation plans

A wrong assumption underlying many of the earliest -but still common- agri-environment schemes was perhaps that, since bird population declines were attributable to general effects of agricultural intensification that were similar over large geographic areas (Newton 2004, Stoate et al. 2009), the solutions would also be general and only required relatively simple interventions that could be applied uniformly across different landscapes. Over the past decade, however, it has become clear that the responses of birds to their environment depend on landscape composition and that effects of agri-environmental measures show a high degree of spatial variability (Kleijn et al. 2006, Whittingham et al. 2007, Davey et al. 2010a, Kleijn et al. 2011). This means that measures of the type 'one-size-fits-all' often lack functionality and do not connect to the landscape-specific factors that limit a species' reproduction and survival (Concepción et al. 2008, Batáry et al. 2012, Concepción et al. 2012, this thesis).

One of the reasons why agri-environmental management in the Netherlands has been organised around a number of standard packages was probably to reduce the costs of development, implementation and administration (Smits et al. 2008). Expressed as a percentage of the total subsidy to the farmers, these costs range from approximately 10% in Austria, Germany and Sweden to 48% in the UK, 63% in Belgium and 87% in France (Falconer and Whitby, 1999 in Smits et al. 2008). It seems a sensible aspiration to reduce these costs as much as possible, but a trade-off exists between transaction costs and the ecological efficacy of the conservation programme (Smits et al. 2008). Allocating subsidies to the proposals with the highest potential environmental impact requires a larger administrative effort, but can also improve efficacy and, ultimately, efficiency in the use of financial resources.

Although some researchers campaign for larger-scale studies that evaluate the effects of agri-environmental management on a national or even continental scale (Kleijn et al. 2011), the idea that bird population trends can be reversed on this scale might be outdated. Such a reverse would require a substantial upscaling of agri-environmental management (Wilson et al. 2010), but with demands for agricultural products projected to continue increasing over the next decades (Tilman et al., 2001), it might not be feasible to expect that this upscaling will take place, or that former national levels of bird abundances and diversity on farmland will ever be restored. In order to ensure the continued existence of declining species, it seems a more promising tactic to target the most viable populations at locations with the best pre-conditions than to invest in nation-wide, but diluted, agri-environmental measures that often have limited conservation value (Wrbka et al. 2008, Baker et al. 2012, Elts and Lõhmus 2012, Pywell et al. 2012). Such a regional approach to agri-environmental management would furthermore allow a better control of variables that need to be coordinated at the landscape level, such as ground water level, and variables of which the influence exceeds the scale of the field or farm, such as pesticide use (Kleijn et al. 2004, Geiger et al. 2010).

Of course, when promoting a more tailored, regional approach to agri-environmental management, it is important to not let the cohesion between conservation efforts escape our attention. Fragmentation or isolation of management areas can pose problems for the protection of species, since small or isolated areas may expose populations to the risk of a narrow gene pool or extinction following disease, catastrophic events or high predation rates (Hodge 2001, Olff and Ritchie 2002, Tscharntke et al. 2002). Additionally, the effectiveness of agri-environmental management is enhanced by the vicinity of nature reserves (Leng et al. 2010, Van Dijk et al. 2014), and vice versa, the value of nature reserves can be improved when they are connected by means of agri-environmental measures (Donald and Evans 2006). A regional approach to agri-environmental management thus requires a good collaboration among local stakeholders, and a shift from a system in which individual farmers can select which measures to apply on their farm to a system in which an integrated plan is developed for an entire region. To achieve this in the Netherlands, a better cooperation between farmers' environmental co-operatives and nature organisations is required and the provinces would need to take a more prominent role in the development and coordination of agri-environmental policy.

Table 1. Examples of successful conservation of bird species on farmland.

Species	Location	Achievement	Measures taken	Reference
Cirl bunting *Emberiza cirlus*	England, UK	Population increase	Grass margins around arable fields, weedy winter stubbles, open patches of grassland next to scrub	Peach et al. 2001
Little bustard *Tetrax tetrax*	France	Recovery of depleted population	Establishment of lucerne and grassland with reduced mowing and grazing to improve nest and female survival, increasing food availability by prohibiting the use of pesticides	Bretagnolle et al. 2011
Stone curlew *Burhinus oedicnemus*	England, UK	Population increase	Heavy grazing and tilling of fields to maintain short and open vegetation, nest protection	Aebischer et al. 1999
Corn Bunting *Emberiza calandra*	Scotland, UK	Stabilising a declining population	Increasing summer food availability	Perkins et al. 2011
		Turning population decline into growth	As above, plus winter food patches and delayed mowing of grassland to improve nest survival	Perkins et al. 2011
Montagu's harrier *Circus pygargus*	The Netherlands	Restoration of a stable population	Arable field margins and set-aside to improve food availability, nest protection	Koks and Visser 2002

Better targeted and more stringent management

Apart from tailoring measures to local circumstances, the effectiveness of agri-environment schemes in the Netherlands would be enhanced by more demanding and better targeted management. To that purpose, clear scheme objectives should be formulated that differentiate between enhancing the abundance of common species or ecosystem services (for example conserving common bee species for pollination), which can be achieved by relatively simple modifications in farming practices, and stimulating the diversity or abundance of declining and rare species, which requires more targeted and sometimes more demanding conservation actions (Kleijn et al. 2006, Pywell et al. 2012). In the United Kingdom, such a distinction exists since 2005 with the introduction of the Environmental Stewardship (ES). The ES contains both 'broad-and-shallow' management options, which are relatively simple, low-cost and operate at the national scale (Entry-Level Stewardship), and 'narrow-and-deep' management options, which require more intensive or complicated management, are often species-specific and are available only in regions where the species is most viable (Higher-Level Stewardship) (Evans and Green 2007, Baker et al. 2012).

Currently, Dutch management options for the protection of meadow birds (waders such as the Black-tailed godwit *Limosa limosa*) can resemble the Higher-Level Stewardship in their degree of management complexity and the required cooperation between multiple farmers to create a landscape-scale mosaic of different management prescriptions (Schekkerman et al. 2008). In arable and mixed agricultural areas in the Netherlands, however, Higher-Level Stewardship for birds does not exist. This study on Skylarks demonstrates that general management options are not sufficient to stabilise the declining populations, a result that mirrors findings from other locations regarding a range of species (Birrer et al. 2007, Perkins et al. 2011, Baker et al. 2012, Marja et al. 2014, Meichtry-Stier et al. 2014). It is likely that the effectiveness of agri-environmental management in the Netherlands would increase when more 'narrow-and-deep' measures would be developed, in particular for vulnerable or rare bird species that occur on arable land. Such measures could be embedded in a two-tier system similar to that in the UK (Figure 3).

The examples of successful agri-environmental management listed in table 1 have in common that they relied on a thorough assessment of the causes of population declines, followed by species-specific management actions that were tailored to local circumstances. It is important to note in this context, though, that even management that is called 'species-specific' often benefits a wider range of taxa (Perkins et al. 2011). For example, lengthening the cutting intervals of grasslands in mixed agricultural areas in the Netherlands, as suggested in chapter 5 of this thesis, will not only benefit the Skylark, but likely also other species that breed in grassland, such as Meadow pipit *Anthus pratensis*, Yellow wagtail *Motacilla flava* and Eurasian curlew *Numenius arquata*. In most cases it will be possible to design management options that fulfil the requirements of a number of species that share similar landscape and habitat preferences. It is in this respect also interesting to note that, while general measures usually only benefit common species, measures that are designed to provide the requirements of sensitive target species increase the abundance of these sensitive species as well as common species (Kleijn et al. 2006, Pywell et al. 2012). Targeted measures will thus eventually benefit a wider range of taxa, increasing not only the effectiveness but also the efficiency of the management (Pywell et al. 2012).

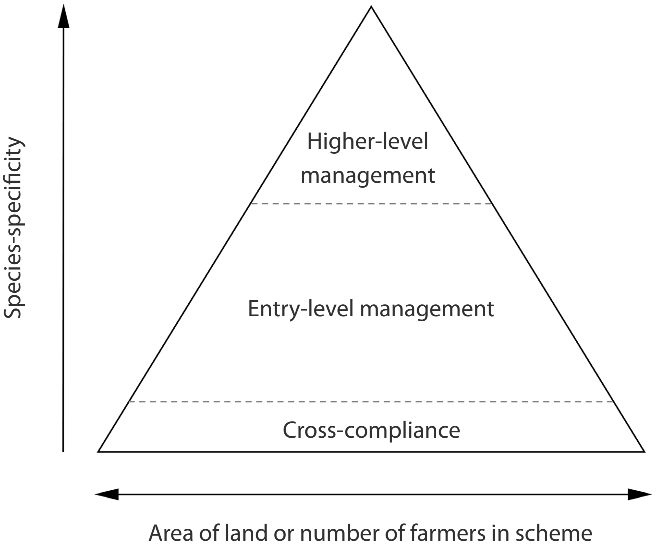

Figure 3. Diagrammatic representation of a possible two-tier system for agri-environmental management in the Netherlands, based on the Environmental Stewardship in the UK (figure adapted from Evans et al. 2007). Cross-compliance covers the basic standards that are required to obtain EU farming subsidies. Entry-level management involves relatively simple and general measures that are available nation-wide. Higher-level managementinvolves measures that are available in certain regions only, targeted at certain species or species groups.

Farmers and conservationists

It is without question that a good collaboration with farmers is indispensable for successful agri-environmental management. Only they know how to manage a farm and have a full overview of all agricultural practices and new developments therein. Such knowledge is essential to deliver agri-environmental prescriptions that are efficient, cost-effective and fit in the daily farming practice. Moreover, since most forms of agri-environmental management are on a voluntary basis, the involvement of a sufficient number of farmers depends solely on their motivation to participate. It is therefore important to achieve a better understanding of the behaviour of farmers and their motivations to participate in agri-environmental management (De Snoo et al. 2012a, Van Dijk 2014).

As self-employers having to take care of their business and families, farmers are inclined to make choices that are largely based on economic grounds (Wossink and van Wenum 2003). This is illustrated by the situation that developed when the Entry-Level Stewardship was first introduced in the UK, and farmers were free to choose which types of environmental management they wanted to carry out from a long list containing 60 options. It soon turned out that their choice was restricted to only a few options, that were perceived as easier to execute or a better fit to their farming practice, rather than choosing options that were most suited to tackle the environmental issues on their farm (Evans and Green 2007, Radley 2013). Options that involve managing the land within the crop itself are particularly unpopular, even though such in-field options have substantial benefits for biodiversity (Evans and Green 2007, Whittingham 2011b).

It is perhaps unrealistic to expect that farmers will know the complex ecology of plant and animal species, or that they always foresee how the measures they take to improve the economic position of their farm restrict the chances of survival of these species and the success of nature conservation measures (Kleijn et al. 2001). For this reason, the guidance, support and advice from (local) experienced ecologists and conservationists, who know the area and the species living in it, is very important for successful conservation on farmland (Whittingham 2011b, Radley 2013). Educational and advisory programmes can help farmers to understand why certain management is required and how to perform it well, which helps to positively influence farmers' attitudes towards agri-environmental management and to reduce tendencies to 'cut corners' (La Haye et al. 2010, Lobley et al. 2010). It is believed that direct contact between project officers and farmers has been one of the keys to the success of the recovery programmes for Stone-curlew, Corncrake and Cirl bunting in the UK (Evans and Green 2007). The judgement of experts should also receive a more prominent role in for example the selection of viable species and populations, the proportional and absolute quantities of different management options, the locations of measures at the farm and landscape level and the choice of management actions that are allowed or required.

Monitoring, research and adaptive management

Monitoring and research are very important to evaluate and improve agri-environmental management and to ensure that subsidies are directed towards the most effective schemes (Arroyo et al. 2002, Hails 2002, La Haye et al. 2010, Radley 2013). Considering the large sums of money spent on agri-environmental schemes by both the European Union and national governments, it is surprising that proper evaluations of the effectiveness of these schemes came to a very slow start and were limited to only a few countries (Kleijn and Sutherland 2003). The term 'agri-environment' first appeared in the literature in 1993 (Potter et al. 1993). Since then, the number of publications on this subject rose to 87 per year in 2003 and 221 in 2013 (search in Scopus performed September 2014). This steep increase was probably stimulated by the fact that early evaluations returned pessimistic results regarding the effectiveness of schemes (Kleijn et al. 2001, Kleijn and Sutherland 2003), which clarified the need for more research.

In the ideal situation, the introduction of any new agri-environment scheme should be accompanied by a proper monitoring and evaluation plan, including the collection of baseline data (Kleijn and Sutherland, 2003). At the moment this is often not the case, and evaluations are sometimes based on incomplete or biased data (Kleijn and Sutherland 2003, Berendse et al. 2004, Kleijn et al. 2011), which is dangerous because the results can be misleading (Legg and Nagy 2006). Although monitoring consumes time and money that could otherwise be spent on (experimental) research and conservation management (Hauser et al. 2006, McDonald-Madden et al. 2010), in the case of agri-environmental management it is often feasible to make this investment, also because a considerable part of the monitoring work is performed by volunteers. Long-term and large-scale monitoring is needed to detect national trends, to assess past and future changes and to evaluate the effect of management actions on larger geographic scales (Hails 2002, Kleijn et al. 2011). Furthermore, monitoring provides the data that can convince policymakers and other stakeholders of the fact that action is needed, thereby making more resources available. Yet, for all of these purposes, a short (for example annual) monitoring interval is not necessarily needed; it is more important that monitoring is continued over a long period of time and covers large geographic areas (Hauser et al. 2006).

The Dutch Meetnet Agrarische Soorten (Monitoring Network for Farmland Species), that exists since 2009 and is based on randomly placed census points, is very suitable for monitoring purposes. The MAS monitoring network generates the type of data that is needed to calculate population trends and distributions, compare population trends between different areas, and assess the effects of habitat characteristics and agri-environmental management (chapter 2). The random placement of points increases the reliability of inferred distribution maps and population trends, because there is no bias towards 'good' birding areas as often happens when volunteers are allowed to select their own monitoring locations (Roodbergen et al., 2011). The point count method allows the monitoring of large areas with a relatively small time investment compared to methods that monitor larger, continuous blocks. It is important that the MAS network is continued over the following years, so that it will become possible to calculate population trends over longer periods of time, and compare population trends in areas with and without agri-environmental management.

Furthermore, monitoring is important because it enables adaptive management, a process in which management actions are directly modified based on new research insights (McDonald-Madden et al. 2010, Whittingham 2011b). For example, research can identify new management options or point out how existing options can be refined to better suit local conditions (Perkins et al., 2011, Baker et al., 2012). Adaptive management seems particularly valuable in species-specific management programmes with a limited geographical range (Mackenzie and Keith 2009, Perkins et al. 2011). Since the success of management is often dependent on local conditions, a smaller geographical range enables a more precise adjustment of the management (Whittingham et al. 2007, Whittingham 2011b). The success of adaptive management will furthermore be influenced by how well conservationists are able to explain management changes to farmers and offer them practical guidance (Perkins et al. 2011). It would be interesting to test the value of adaptive management for the conservation of farmland birds in the Netherlands, because the current political framework only allows changes in agri-environment schemes to take place at intervals of six years. Six years is a long time considering the speed of decline of many bird populations, and adaptive management could speed up the process of refining agri-environmental prescriptions.

Concluding remarks

This thesis provides information for a better understanding of the foraging and breeding behaviour of Dutch Skylarks living on farmland. Regarding the value of field margins for the conservation of the Skylark and other farmland birds, there is good news as well as bad news.

The good news is that:

- Arable field margins provide more abundant and more diverse invertebrate food resources for breeding birds than conventionally managed crops (chapters 3, 4 and 5).
- Skylarks highly prefer field margins as foraging habitat during the breeding season (chapter 3).
- Foraging in field margins provides Skylark nestlings with a more diverse diet (chapter 4).
- Several bird species, including the Skylark, are present in higher densities in areas with field margins than in areas without, although the relationship differs between regions for all considered taxa (chapter 2).
- Bird species richness is higher in areas with field margins, regardless of region (chapter 2).

The bad news is that:

- Short-term population growth rates of the Skylark and other farmland bird species are not positively influenced by field margins (chapter 2).
- Field margins do not increase Skylark clutch size, nestling condition or nest survival (chapter 5).
- The largest bottleneck for Skylark reproduction on Dutch farmland is the lack of sufficient suitable and safe nesting habitat (chapter 5).
- The largest threats to Skylark nests and nestlings on farmland are silage cutting of grassland and predation (chapter 5).
- Despite the establishment of arable field margins in the study area, the decline of the Skylark continues at an alarming rate (chapter 5) .

In conclusion, my thesis shows that field margins are suitable to increase summer food availability and food diversity for birds in agricultural landscapes. However, field margins are unlikely to benefit Skylark reproduction sufficiently to enhance populations. Better targeted measures, specifically providing safe nesting habitat, are required to conserve this species on Dutch farmland.

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Summary

Agriculture in Europe has greatly intensified over the past 50 years, bringing about large changes in agricultural practices and landscape composition. Yields increased considerably during this period, but simultaneously the diversity of plants, invertebrates and birds on farmland decreased. To halt the ongoing biodiversity decline, various agri-environment schemes have been established in the Netherlands and other European countries. One of these schemes is the arable field margin, an extensively managed strip of land sown with grasses and forbs, often established to provide a foraging and breeding habitat for birds. In this thesis, the value of field margins for farmland birds, and the Skylark in particular, is evaluated.

A 5-year dataset of bird counts covering the whole province of Groningen, the Netherlands, was used to establish relationships between landscape composition and the abundance and population growth rates of ten farmland bird species. Analyses were conducted for four geographic areas: the province as a whole and three regions within the province that differ in soil type and cropping plan. Bird species richness was higher on locations with field margins in each of the geographic areas. Also the abundance of eight species was positively affected by field margin area in at least one of the geographic areas. However, the population trends of none of the ten species was significantly more positive in areas with field margins than in areas without. Although this may be due to the short study period, it may also be an indication that management areas were already richer in birds before field margins were established. Alternatively, birds could have preferred areas with field margins for establishing their territory even though this did not deliver substantial benefits for reproduction or survival.

To investigate in more detail if and how field margins influence breeding birds, the Skylark was chosen as the species for a case study. Although still widespread, the Skylark has decreased dramatically in the Netherlands and is often a target species for agri-environmental management. The field work for this case study was conducted in an area with mixed agriculture in the east of Groningen. As expected, the Skylark rarely used field margins as breeding habitat. However, as foraging habitat field margins were preferred over all other habitat types. Grassland and lucerne were also used for food collection, while maize and winter cereals, both annual crops with high pesticide inputs, were actively avoided. An invertebrate sampling campaign confirmed that food availability was 2.5 - 5.5 times higher in field margins than in crops, with lowest densities found in winter cereals. Also the diversity of invertebrates was larger in field margins, providing a number of prey groups rarely found in crops. This might be an additional benefit, because larger prey diversity is generally associated with a better health and growth of young birds. When parents provided their young with food from field margins, the diet of the nestlings contained significantly more invertebrate groups.

Between 2007 and 2012, detailed information on the breeding biology of the Skylark was collected in the same study area. The overall reproductive success was very low, leading the study population to decline by 40% over the six-year study period. Neither clutch size, nestling condition nor nest survival was positively affected by field margins, even when taking into account field margin surface area or the distance to the nearest margin. This result did not differ between breeding crops. However, breeding crop in itself had an important effect. Nestling weight was significantly lower in cereals, which corresponds with the low prey availability in this crop. Nest survival was lowest in grassland because of the frequent silage cuts. Since grassland was a preferred breeding habitat, silage cutting of grassland was the most important cause of nest loss. Nest survival in cereals was intermediate, while only in lucerne survival was probably sufficient for a stable population.

The results of this study demonstrate that field margins are not sufficient to reverse the negative population development of the Skylark. In order to maintain this species in agricultural areas, it is essential that measures are taken that do not only improve food availability, but foremost provide safe and suitable nesting habitat. This conclusion echoes the findings of a range of studies demonstrating that birds typically do not respond, or respond only marginally, to general ‘broad and shallow’ agri-environment schemes. Since these schemes are not sufficiently targeted, they do not address all key factors that limit survival or reproduction. Based on a number of cases of successful conservation management for birds, it is argued that the conservation of declining bird species is better achieved by regionally coordinated management programmes with species-specific measures.

Samenvatting

De afgelopen 60 jaar is de landbouw sterk geïntensiveerd. Dit bracht veranderingen teweeg in zowel de agrarische werkzaamheden als de samenstelling van het landschap: het gebruik van bestrijdingsmiddelen en (kunst)mest nam toe, percelen werden groter, de diversiteit aan gewassen liep terug en natuurlijke elementen werden uit het landschap verwijderd. De gewasopbrengsten namen hierdoor sterk toe, maar tegelijkertijd holde de diversiteit van planten, insecten en vogels achteruit. Om het nog altijd doorgaande verlies van biodiversiteit te stoppen is het agrarisch natuurbeheer ingevoerd in Nederland en andere Europese landen. In akkerbouwgebieden komt met name de akkerrand veel voor, een strook langs de akker die is ingezaaid met grassen en bloeiende planten. Het doel van deze beheersmaatregel is onder meer het bieden van foerageer- en broedgelegenheid voor vogels. In dit proefschrift wordt de waarde van akkerranden voor vogels geëvalueerd, met speciale aandacht voor de Veldleeuwerik.

Om op grote schaal de effecten van akkerranden op de aantallen en populatietrends van tien vogelsoorten te onderzoeken, werd gebruik gemaakt van een dataset van punttelingen uit de provincie Groningen. Vier gebieden werden onderzocht: de provincie als geheel en drie regio's binnen de provincie die verschillen in bodemtype en gewassamenstelling. Uit de tellingen bleek dat een groter areaal aan akkerranden binnen de telcirkels samenhing met een grotere diversiteit van vogels. Dit gold in alle vier de gebieden. Ook de aantallen van acht vogelsoorten namen toe met een toenemend oppervlakte aan akkerranden in ten minste één van de gebieden. Echter, de vijfjarige populatieontwikkeling werd voor geen van de vogelsoorten positief beïnvloed door de aanwezigheid van akkerranden. Dit zou kunnen komen door de korte studieperiode, maar het kan ook een aanwijzing zijn dat gebieden met akkerranden weliswaar worden geprefereerd door vogels, maar geen wezenlijke bijdrage leveren om het broedsucces te verhogen. Ook is het mogelijk dat er hogere aantallen vogels werden geteld in de omgeving van akkerranden omdat deze juist op plekken met veel vogels kunnen zijn aangelegd.

Om in meer detail te onderzoeken of, en hoe, akkerranden broedende vogels kunnen helpen, werd de Veldleeuwerik gekozen als voorbeeldsoort. Hoewel de Veldleeuwerik nog steeds wijd verspreid is, is de soort in Nederland met 96% afgenomen sinds de jaren 1960. De Veldleeuwerik is dan ook vaak een doelsoort voor agrarisch natuurbeheer. Het veldwerk voor dit onderzoek werd gedaan in een gebied met gemengde landbouw in het oosten van de provincie Groningen. Zoals

verwacht werden akkerranden door Veldleeuweriken nauwelijks gebruikt om in te broeden, waarschijnlijk om het risico op predatie te mijden. Als foerageerhabitat werden akkerranden echter geprefereerd boven alle andere habitattypen. Ook bermen, grasland en luzerne werden graag gebruikt als foerageerhabitat, terwijl tarwe en maïs (beide éénjarige gewassen met veel gebruik van bestrijdingsmiddelen) werden vermeden. Insectenvangsten bevestigden dat akkerranden 2,5 tot 5,5 keer zoveel insecten bevatten dan gewassen. Ook de diversiteit van insecten was groter in akkerranden, zodat vogels toegang hadden tot insectengroepen die in gewassen nauwelijks voorkomen. Dit zou een extra voordeel kunnen zijn, want een hogere prooidiversiteit heeft over het algemeen gunstige effecten op de gezondheid en groei van jonge vogels. Inderdaad bevatte het dieet van jonge vogels een hogere diversiteit aan prooigroepen wanneer oudervogels toegang hadden tot akkerranden.

Tussen 2007 en 2012 werd in hetzelfde gebied gedetailleerde informatie verzameld over de broedbiologie van de Veldleeuwerik. Het gemiddelde broedsucces was erg laag, waardoor de studiepopulatie in de loop van zes jaar met 40% afnam. Akkerranden hadden geen invloed op het broedsucces: zowel legselgrootte, het gewicht van de jongen als de nestoverleving bleven gelijk. Wat wel een belangrijke invloed had op het broedsucces, was het gewas waar de Veldleeuweriken in broedden. Het gewicht van de jongen was het laagst in nesten in tarwe, overeenkomstig met de lage hoeveelheden insecten die in dit gewas voorkomen. De nestoverleving was het laagst in grasland, wat kwam door het frequente maaien. Omdat grasland vanwege de geschikte vegetatiehoogte door Veldleeuweriken juist sterk geprefereerd werd om in te broeden, was het maaien van gras de belangrijkste oorzaak van nestverliezen. De overleving in tarwe was gemiddeld, en de overleving in luzerne was het hoogst. Uit een populatiemodel bleek dat alleen de reproductie in luzerne voldoende is voor een stabiele populatie, in alle andere gewassen was de overleving te laag. Echter, de totale oppervlakte luzerne is zo gering dat het voor de populatie als geheel onvoldoende is om te blijven bestaan.

De resultaten van dit onderzoek tonen aan dat akkerranden niet voldoende zijn om de negatieve populatieontwikkeling van de Veldleeuwerik om te keren. Om deze soort in agrarische gebieden te behouden zijn aanvullende maatregelen nodig die niet alleen het voedselaanbod verhogen, maar vooral geschikt en veilig broedhabitat bieden. Dit kan in de vorm van natuurbraak, maar ook door bijvoorbeeld het areaal luzerne te vergroten. Op grasland zijn daarnaast maatregelen nodig om de maaifrequentie te verlagen. Deze conclusie lijkt op de bevindingen van andere onderzoeken uit binnen- en buitenland die aantonen dat vogels doorgaans niet of nauwelijks reageren op maatregelen die heel algemeen zijn, zoals akkerranden. Dergelijke algemene maatregelen bieden vaak geen oplossingen voor juist díe sleutelfactoren die de overleving of voortplanting beperken. Uit een aantal gevallen van succesvol agrarisch natuurbeheer kan worden afgeleid dat de bescherming van vogels in het agrarisch gebied het beste werkt in de vorm van regionaal gecoördineerde programma's, met maatregelen die specifiek zijn voor een bepaalde soort of groep van soorten. Onderzoek is daarbij nodig om uit te wijzen wat precies de probleempunten zijn, zodat het beheer zich daarop kan richten en daardoor zo efficiënt en effectief mogelijk kan worden uitgevoerd.

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Curriculum vitae

Marije Kuiper was born on the 2nd of August 1985 in Finsterwolde, the Netherlands. She grew up in Midwolda where she attended primary school. In 2003 she obtained her VWO degree at the Dollard College in Winschoten. She subsequently enrolled in the study Scandinavian languages and Cultures at the University of Groningen. After obtaining her propaedeutic in Swedish, she decided to move to Amsterdam to study Biology at the University of Amsterdam. She specialised in ecology, obtaining her BSc and MSc degrees with honours. In the third year of the Bachelor, she studied at Lund University in Sweden for five months, taking courses in biology and improving her Swedish language skills. From 2007-2009 she was a student member of the Study Programme Committee of the study Biology. During her Masters she wrote two MSc theses. The first thesis was conducted at the University of Amsterdam in collaboration with the National Herbarium in Leiden and focused on the reproductive isolation and possible speciation of a European orchid subspecies in the Dutch dunes. The second thesis was conducted at Wageningen University and concerned the relation between migration and parental care in geese. In 2010 Marije started as a PhD candidate in the chair group Nature Conservation and Plant Ecology at Wageningen University on a project that developed in close collaboration with the Dutch Montagu's Harrier Foundation. In this project she studied the effectiveness of agri-environment schemes for farmland birds, which resulted in this thesis.

Publications

Ottens HJ, Kuiper MW, Flinks H, Van Ruijven J, Siepel H, Koks BJ, Berendse F, De Snoo GR (2014). *Do field margins enrich the diet of the Eurasian Skylark Alauda arvensis on intensive farmland?* Ardea 102 (2) in press.

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PE&RC Training and Education Statement

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

Writing of project proposal (3 ECTS)

- The potential of arable field margins to restore biodiversity in agricultural landscapes (2010)

Post-graduate courses (5.7 ECTS)

- Mixed linear models; PE&RC (2010)
- Generalised linear models; PE&RC (2010)
- Spatial ecology; PE&RC (2011)
- iGis; PE&RC (2011)

Invited review of (unpublished) journal manuscript (1 ECTS)

- Agriculture, Ecosystems & Environment: contribution of woody habitat islands to conservation of birds and their potential ecosystem services in an extensive Colombian rangeland (2013)

Deficiency, refresh, brush-up courses (3 ECTS)

- Introduction geo-information science (2011)

Competence strengthening / skills courses (4.5 ECTS)

- PhD Competence assessment; WGS (2010)
- Scientific writing; Language Services (2011)
- Didactic skills; Education and Competence Studies (2014)

PE&RC Annual meetings, seminars and the PE&RC weekend (1.2 ECTS)

- PE&RC Day: extreme life (2012)
- PE&RC Weekend; final year (2013)

Discussion groups / local seminars / other scientific meetings (7 ECTS)

- Seminar Biodiversity and Ecosystem Dynamics; IBED, University of Amsterdam (2010)
- Wageningen Ecology & Evolution Seminars (2010-2013)
- Ecological theory and application PhD discussion group (2010-2014)
- Netherlands Annual Ecology Meeting (NERN) (2010-2014)
- Symposium Linking Green Economics, Forests and Biodiversity; Utrecht University (2011)
- Minisymposium leerstoel Agrarisch Natuurbeheer (2013)
- Minisymposium: orde uit chaos; CBS (2013)

International symposia, workshops and conferences (6.2 ECTS)

- Netherlands Annual Ecology Meeting; poster presentation (2013)
- Annual Meeting of the Gesellschaft für Ökologie: integrating ecological knowledge into nature conservation and ecosystem management; oral presentation; Hildesheim, Germany (2014)
- 26th International Ornithological Congress; poster presentation; Tokyo, Japan (2014)

Lecturing / supervision of practicals / tutorials (3 ECTS)

- Supervision Bsc thesis (2010)
- Ecologie (2010, 2012, 2013)
- Forest and nature conservation (2011-2013)
- Lecture: agri-environmental management (2013, 2014)

Supervision of MSc students (3 ECTS)

- Foraging behaviour of farmland birds

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