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Habitat use and diet of Skylarks (*Alauda arvensis*) wintering in an intensive agricultural landscape of the Netherlands

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Abstract In recent decades, Skylark (*Alauda arvensis*) populations in Europe have declined sharply due to agricultural intensification. Insufficient reproduction rates are one reason. Increased winter mortality may also be important, but studies outside the breeding season are scarce and mostly limited to the UK. We studied habitat selection of wintering Skylarks in an agricultural area in the Netherlands. We monitored Skylarks between November 2008 and March 2009 on 10 survey plots including 77 different arable fields and permanent grasslands and covering in total 480 ha. We simultaneously measured food availability, vegetation structure and field boundary characteristics. We also analysed 158 faecal pellets collected on potato and cereal stubble fields to relate Skylark diet to seasonal changes in food availability and foraging habitat. We show that cereal stubble fields larger than 4.3 ha, surrounded by no or low boundary vegetation and a density of dietary seeds of more than 860 seeds m^{-2}, were most suitable for wintering Skylarks. Skylark group densities were low on permanent grasslands and on maize stubble fields. Densities of dietary seeds were highest in soils of potato stubble fields followed by cereal stubble fields, grasslands and maize stubble fields. Skylarks showed a strong preference for cereal grains, but their proportion in the diet fell sharply at the end of November, indicating that cereal grains were depleted and birds had to switch to less profitable food sources, such as weed seeds and leaves. We conclude that Skylarks wintering in agricultural landscapes possibly suffer from a lack of energy-rich food sources and only a few fields provide sufficient food. Conservation measures should strive to improve the wintering situation by creating food-rich habitats such as over-winter stubble with a rich layer of weeds on large fields and localised in open areas.

Keywords Nutrition · Energy intake · Droppings · Predation risk · Winter ecology · Non-breeding

Zusammenfassung

Habitatwahl und Nahrung von überwinternden Feldlerchen (*Alauda arvensis*) in einer intensiv genutzten Agrarlandschaft der Niederlande

In den vergangenen Jahrzehnten sind die europäischen Bestände der Feldlerche (*Alauda arvensis*) durch die Intensivierung der Landwirtschaft stark zurückgegangen. Geringe Fortpflanzungsraten sind ein Grund. Eine angestiegene Wintersterblichkeit ist vermutlich ebenfalls von

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Bedeutung, allerdings gibt es nur sehr wenige Studien außerhalb der Brutsaison und die wenigen sind zudem fast ausnahmslos auf Großbritannien beschränkt. Wir untersuchten die Habitatwahl von Feldlerchen in einer niederländischen Agrarlandschaft. Von November 2008 bis März 2009 zählten wir Feldlerchen auf 10 Probeflächen, die 77 verschiedene Felder und Grasländer und insgesamt 480 ha umfassten. Gleichzeitig erfassten wir die Nahrungsverfügbarkeit, die Vegetationsstruktur und Feldrandcharakteristika. Außerdem sammelten wir auf Getreidestoppelfeldern und ehemaligen Kartoffelfeldern insgesamt 158 Kotproben um die Nahrungszusammensetzung der Feldlerchen zu bestimmen. Diese setzten wir in Relation zum Nahrungsangebot und zum Habitat. Wir zeigen, dass Getreidestoppelfelder die grösser als 4.3 ha sind, kaum vertikale Randstrukturen aufweisen und mehr als 860 Samenkörner pro Quadratmeter aufweisen, bevorzugt von überwinternden Feldlerchen genutzt werden. Auf intensivem Dauergrünland und auf Maisstoppeln fanden wir nur geringe Dichten überwinternder Feldlerchen. Die Dichte von Samenkörnern, die als Nahrung von Feldlerchen dienten, war am höchsten auf vormaligen Kartoffeläckern, gefolgt von Getreidestoppelfeldern, Grünland und Maisstoppelfeldern. Feldlerchen zeigten eine starke Bevorzugung von Getreidekörnern als Nahrung, jedoch nahm deren Anteil in der Nahrung Ende November stark ab. Dies deutet darauf hin, dass bereits dann keine Getreidekörner mehr vorhanden waren und Feldlerchen auf weniger profitable Nahrungsquellen wechseln müssen, z.B. Samenkörner und Blätter von aufkommenden Wildkräutern. Wir folgern, dass überwinternde Feldlerchen in einer intensiven Agrarlandschaft vermutlich einen Mangel an energiereicher Nahrung haben und nur sehr wenige Felder im Winter als Winterhabitat geeignet sind und ausreichend Nahrung bieten. Schutzmaßnahmen sollten darauf abzielen die Wintersituation zu verbessern. Wir empfehlen die Anlage nahrungsreicher Flächen wie zum Beispiel überwinternde Stoppelfelder. Diese sollten nicht mit Herbiziden behandelt werden, sondern eine reichhaltige Krautschicht zulassen. Außerdem sollten sie in einer offenen Landschaft und mit Abstand zu vertikalen Strukturen liegen.

Introduction

In western Europe, populations of many farmland bird species have declined in the past decades (BirdLife International 2004; EBCC 2009). The Skylark (*Alauda arvensis*) is a typical farmland bird whose populations have decreased sharply. Since 1980, European populations have declined by 48 % and an approximate 39 million Skylarks were lost during this period (PECBMS 2012). The decline is tightly associated with the general intensification of agricultural practices (Chamberlain et al. 2000a, b; Newton 2004; Donald et al. 2006). Specifically, the switch from spring cereals to winter cereals has been suggested as the main cause for the decline: Winter cereals grow taller and denser in an early phase of the breeding season and become unsuitable for Skylark nesting in early summer. As a result, the number of breeding attempts per season has significantly decreased and the number of fledglings is no longer sufficient to maintain population levels (Chamberlain and Crick 1999; Chamberlain et al. 2000a, b; Donald et al. 2002; Donald 2004; Donald and Morris 2005). The situation outside the breeding season is less well understood. An increase in winter mortality is suspected (Donald et al. 2001; Wolfenden and Peach 2001; Newton 2004; Siriwardena et al. 2007, 2008), but studies on the wintering ecology of Skylarks are scarce and mostly limited to the UK (e.g. Green 1978; Wakeham-Dawson and Aebischer 1998; Donald et al. 2001; Gillings and Fuller 2001; but see Hegemann et al. 2010, 2012a, b). Little is known about the ecology of Skylarks wintering in other parts of Europe, where most European Skylarks winter. However, a detailed understanding of Skylark wintering ecology is required if we want to understand the factors that determine winter mortality, and if we want to improve conservation action plans. Effective conservation can only be developed if based on a thorough understanding of the species' needs (Sutherland et al. 2004).

From studies in the UK, it is well documented that wintering Skylarks prefer large open fields with low boundary vegetation; they select for stubble fields, especially weedy cereal stubbles, while avoiding grasslands (Wilson et al. 1996; Robinson and Sutherland 1999; Donald et al. 2001; Gillings and Fuller 2001; Hancock and Wilson 2003; Perkins et al. 2008). Also, the composition and dominance of different vegetation types within a crop type influence habitat selection. Skylarks show a preference for some vegetation cover above bare soil and for taller over shorter stubbles (Donald et al. 2001; Gillings and Fuller 2001; Butler et al. 2005; Whittingham et al. 2006). This vegetation structure may help predator avoidance (Lima and Dill 1990) as well as influencing food searching time and thus intake rate (Butler et al. 2005; Whittingham et al. 2006). Most studies suggest that cereal grains may be an important food source on stubble fields explaining the preference for this field type, but the diet of wintering Skylarks has been studied only twice (Green 1978; Donald et al. 2001). Green (1978) showed that Skylarks feed during winter mainly on cereal grains, weed seeds and plant leaves, while invertebrates play a minor role. Meanwhile, agricultural intensification has influenced the food availability for wintering Skylarks and other granivorous birds. For example, the number of over-wintering cereal stubble fields has declined dramatically due to increased growing of maize, rape and winter-sown cereals, the use of fertilizers, herbicides and pesticides reducing the diversity of weeds and arthropods during winter, and improved harvesting techniques reducing grain spill (e.g. Stoate et al. 2001; Benton et al. 2002, 2003; Attwood et al. 2008; Billeter et al. 2008; Geiger et al. 2010). It has been suggested that these changes may have caused an important nutritional bottleneck for granivorous birds resulting in reduced winter survival (Wilson et al. 1999; Newton 2004; Siriwardena et al. 2007, 2008). Studies that have measured the availability of potential food items for Skylarks in agricultural landscapes found a positive correlation between measured seed density and Skylark abundance (Wakeham-Dawson and Aebischer 1998; Robinson and Sutherland 1999), but these studies did not measure the birds' diet. To our best knowledge, only one study simultaneously measured Skylark diet and food availability in modern agricultural landscapes while also considering field size and boundary characteristics; a design that is fundamental when striving to explain habitat selection. Donald et al. (2001) showed that, at the end of the 1990s, the diet preferences of Skylarks wintering in the UK could indeed explain habitat selection for different crop types. Skylarks preferred large stubble fields with a high density of soil seeds and low boundary vegetation characteristics. On stubble fields, Skylarks fed largely on cereal grains. However, agricultural intensification, with its negative effects on food availability, has progressed further since this time in many European countries. For example, the cultivation area of maize has further increased, the number of set-aside fields has decreased and stubble fields get ploughed after harvest ever earlier (Flade 2012; SOVON 2012). Moreover, a study investigating the habitat selection of wintering Skylarks in modern agricultural landscapes of Continental Europe, where most of the European breeding population winters, is still lacking.

In this study, we investigated food availability, diet composition, vegetation structure and field boundary characteristics in relation to the presence or absence of wintering Skylarks in an agricultural area in the northern Netherlands. Farmland areas in the Netherlands function as wintering areas for local breeding Skylarks and for Skylarks breeding in northern and eastern Europe (Hegemann et al. 2010), and can thus function as a model system for many other countries of Continental Europe. We monitored densities of Skylarks in 10 different plots totalling 480 ha, and spread over an area of 130 km^2, from November 2008 to March 2009. We simultaneously measured food abundance, field size, boundary characteristics and within-field vegetation structure. In addition, we analysed the contents of Skylark faeces to investigate their winter diet in relation to seasonal changes in food availability and to foraging habitat.

Methods

Study area

We studied wintering Skylarks in the northern Netherlands (52°57′N, 6°19′E) between 5 November 2008 and 18 March 2009. In agricultural areas of the Northern Netherlands, densities of breeding Skylarks are usually below 10 pairs/100 ha (Teunissen et al. 2009), but these areas are frequently used as wintering areas by Skylarks that breed in nearby nature reserves and by Skylarks originating from northern and eastern Europe (Hegemann et al. 2010). Within an area of 130 km^2, we selected 10 survey plots ranging from 35 to 75 ha and covering in total 480 ha (Table 1). The survey plots were on average 7.4 km apart (range 1.2–15.1 km). The 10 survey plots comprised in total 77 different arable fields and permanent grasslands. Selection criteria ensured that the survey plots included at least six replicates of former cereal, former potato and former maize fields (referred to below as cereal, potato and maize stubbles, respectively), and permanent grasslands.

Field size and boundary characteristics

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

Bird surveys

We surveyed birds nine times (every 2–3 weeks) between 5 November 2008 and 18 March 2009. Surveys were done between 1 h after sunrise and 1 h before sunset while avoiding rainy, windy and foggy weather. The order in which the survey plots were visited alternated to minimize time of day effects. All fields within survey plots were walked zigzag and the number of birds for each flock (or single birds) was mapped. We only recorded birds when

Table 1 Field size and field boundary characteristics per crop type (cereal fields, potato fields, maize fields, grasslands, unknown former crop, i.e. at the time of the surveys covered by green manure crops) surveyed for Skylarks (*Alauda arvensis*)

	Cereals	Potato	Maize	Grassland	Unknown	Total
No. fields	22	20	15	18	2	77
Total area (ha)	153.2	137.4	96.8	63.6	29.2	480.3
No. of fields occupied (%)	17 (77)	12 (60)	11 (73)	2 (11)	1 (50)	43 (56)
Skylark group density (ha^{-1})	0.121	0.063	0.054	0.005	0.067	0.07
Field size						
Mean (ha)	6.97	6.87	6.05	3.53	14.61	6.24
SD (ha)	4.38	4.12	2.67	2.22	7.4	4.06
Range (ha)	0.4–16.9	0.6–14.1	2.3–13.4	0.5–10.1	9.4–19.8	0.4–19.8
Field boundary index						
Mean (ha)	1.09	0.91	1.14	1.18	0	1.03
SD (ha)	1.06	1.01	1.39	0.78	0	1.05
Range (ha)	0–4.38	0–3.07	0–3.82	0–2.77	0–0	0–4.38

No. of fields occupied number of fields occupied by Skylarks at least once during the survey rounds; *Skylark group density* mean density averaged over all survey rounds

they were flushed or landed on the fields. Birds that were only flying over and were unrelated to a specific field were not included in the analyses. We marked landing positions of flushed birds on maps to prevent double counting.

Food abundance

To relate food abundance to bird presence, we sampled potential food items (invertebrates, seeds; Green 1978) on the same day as the bird counts. Food abundance was sampled on six fields of each of the following four field types: potato stubble, cereal stubble (combining wheat, barley and rye stubbles), maize stubble, and permanent grassland. The six fields of each type were distributed based on their availability across 6 of the 10 survey plots. On each of these 24 fields, we sampled invertebrate biomass and soil seed densities in three sampling plots of 1 × 2 m. These plots were selected 5 m distant from each other and approximately 10–20 m from one of the field borders. Soil seed and invertebrate densities at 10 m distance to the field edge are not biased by edge effects and do not differ from more central parts of the fields (e.g. Marshall and Arnold 1995; Wilson and Aebischer 1995; Hof and Bright 2010). Given this, we preferred to sample food availability at 10 m distance to the edge rather than sampling in the middle of the fields in order to minimize disturbance effects and their potential impact on Skylark behaviour and habitat use. The location of the sampling plot was different at each sampling round to prevent overlap of soil sampling.

Invertebrates were caught during 24 h with one pitfall (diameter 90 mm, filled with 4 % formaldehyde) and one sticky trap per sampling plot (Kragten et al. 2011). We sampled both ground-dwelling and flying invertebrates, because both groups belong to the diet of Skylarks (Jenny 1990), even though Skylarks mainly forage on the ground. Sticky traps (Pherobank®; 100 × 210 mm, excluding margins) were placed on a stick at about 50 cm height (Kragten et al. 2011). Invertebrates were identified to suborder (Hymenoptera, Diptera, Araneae) or family level (Coleoptera). The lengths of all invertebrates were measured, and invertebrate biomass (dry weight) was calculated using the regression equations and parameter estimations of Hodar (1996).

Soil seed densities were estimated by taking 10 soil samples per sampling plot with a bulb planter (60 mm diameter). Samples were taken to a depth of 10 mm, similar to the method used by Green (1978). The 10 subsamples were mixed into a composite sample and stored at 4 °C before processing to prevent seed germination. The soil was sieved through 2 sieves with mesh widths of 1 and 0.5 mm. These mesh sizes ensured that the majority of seeds taken by Skylarks were caught (Green 1978). The remainder from sieving (e.g. seeds, small stones, vegetation remnants) was dried (48 h, 70 °C) and sorted by hand. Weed seeds were identified to species level and counted. All or a maximum of 25 seeds per species were weighed to derive average seed weights per species.

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

Vegetation structure

To get a measure of vegetation structure within each agricultural field and crop type, we determined, for all plots on which we sampled invertebrates and seeds, the vegetation composition and an estimate for cover (percentage). This included the following vegetation types: grassy weed, dicotyledonous weed, potato stubble, maize stubble, winter cereal, volunteer cereal (i.e. cereals that arise from seed shed at or before crop harvest), and bare ground. In addition, the height of the tallest plant within a sampling plot was measured. As with food abundance, data were averaged over the three sampling plots within one field and per sampling round for further analyses.

Skylark diet measured from faeces

During the bird surveys, fresh faeces were collected where Skylarks were flushed and only if no other species were observed in the close vicinity. Faecal pellets were mixed with table salt to prevent moulding and subsequently frozen. We analysed 158 faecal pellets (8–12 per sampling round excluding the March count, when no droppings were collected, totalling 80 from cereal stubbles and 78 from potato stubbles). Droppings were dispersed by soaking them in water for 30 min and analysed under a microscope (×20 magnification) using a standard method (Flinks and Pfeifer 1987). As Skylarks do not remove the endosperm of seeds (as is done by, e.g., finches), we assumed that remains of the testa reliably reflected the diet. The quantity of ingested plant remains (epidermis of leaves or testa) was measured using a millimetre screen. The number of ingested seeds was estimated by dividing the measured area of the remains (seed coat) of the ingested seeds by the estimated surface of the reference seeds. If the ingested plant remains could not be identified by direct comparison with the reference collection, they were compared with other reference plant material at ×100–400 magnification (Rogers and Gorman 1995). Invertebrate remains were used to assess the minimum number of individuals. 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; Jenni et al. 1990).

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

Data availability

Pitfall trapping and the use of sticky traps were occasionally hampered by grazing animals and low temperatures. Four times we could not place sticky traps and pitfalls on one of the permanent grasslands because of grazing cows. Furthermore, frozen soil at the beginning of January prevented digging pitfalls into the ground and collecting soil samples. At both sampling periods in January, the glue of the sticky traps was frozen and did not stick any more. In total, data from 228 sticky traps and 259 pitfall traps, as well as soil samples, were included in the analyses. We assumed that food abundance and vegetation cover of measured fields ($n = 24$) did not differ from adjacent fields ($n = 11$) if they were cultivated in the same way.

Statistics

As Skylarks often forage in large flocks in winter, we assumed that groups of Skylarks and not individual birds were distributed randomly across fields (Cramp 1988; Donald et al. 2001). Therefore, Skylark group density, defined as the number of Skylark groups divided by the field size, was used as response variable.

As Skylarks are known to prefer large open fields with low boundary characteristics (Wilson et al. 1996; Donald et al. 2001; Gillings and Fuller 2001), we first tested for these factors. Effects of field size, perimeter-to-area ratio, field boundary index and their interactions with survey round were tested using generalised linear mixed models (GLMM) with repeated measures and the method of residual maximum likelihood in GenStat 12.1 (Payne et al. 2008). Fields nested within survey plots were included as random effect. Forward selection based on Wald tests ($P < 0.05$) was applied to select variables significantly affecting Skylark group density until variables no longer added significant effects to the model. Explanatory variables were standardized according to $(x–\mu)/s$, with x measurement, μ mean and s standard deviation, to enable comparisons of the magnitude of their effects independent of their units. We refer to these as standardised effects. If two explanatory variables were strongly correlated (Pearson correlation >0.7; see Supporting Information Table S1), only the most significant variable was included in a model. To correct for effects of field size and boundary characteristics when further testing which variables affect Skylark habitat selection in winter, significant terms from

Table 2 Differences of response and explanatory variables between crop types that were tested for their effect on Skylark group densities during winter in the Netherlands

Variable	Cat	Cereal	Potato	Maize	Grassland	*F*	*P*
Skylark group density (ha^{-1})[a]		0.12	0.06	0.06	0	12.26	<0.001
Field boundary index[a]	fb	6.97	6.87	6.45	3.53	16.19	<0.001
Perimeter-to-area ratio[a]	fb	2.34	2.36	2.27	2.44	26.96	<0.001
Field size (ha)[a]	fb	1.04	0.91	1.14	1.18	51.22	<0.001
Bare ground (%)[b]	C	76.48	91.93	89.78	5.43	465.7	<0.001
Cereal stubbles (%)[b]	c	10.29	0	0	0	81.2	<0.001
Volunteer cereals (%)[b]	f/c	4.34	0	0	0	28.53	<0.001
Maize stubbles (%)[b]	c	0	0	8.21	0	20.13	<0.001
Potato stubbles (%)[b]	c	0	3	0	0	161.82	<0.001
Total weed cover (%)[b]	f/c	8.2	6.06	1.43	92.71	1,011.77	<0.001
Dicotyledonous weeds (%)[b]	f/c	2.34	2.49	1.17	12.2	29.72	<0.001
Grassy weeds (%)[b]	f/c	6.34	3.67	0.43	82.16	893.35	<0.001
Winter cereals (%)[b]	f/c	0	0	2.13	0	58.42	<0.001
Seed density (m^{-2})[b]	f/c	1,757.25	4,609.18	1,163.21	1,332.19	30.7	<0.001
Vegetation height (cm)[b]	c	16.8	4.17	9.95	11.27	72.93	<0.001
Flying invertebrates (mg $trap^{-1}$)[c]	f	4.95	2.81	3.33	5.38	1.75	0.158
Ground-dwelling invertebrates (mg $trap^{-1}$)[b]	f	9.15	5.36	4.48	26.49	46.93	<0.001

Cat Categories; *fb* fieldsize and boundary characteristics, *f* food (f), and *c* vegetation structure variables. Mean values are given per crop type

[a] All surveyed fields are included

[b] The first survey round in January is excluded

[c] Both January survey rounds are excluded

this first analysis were included as fixed effects in subsequent analyses.

We then analysed whether the Skylark group density was related to food abundance as well as to vegetation structure and survey round. We did this for the 35 fields for which data on food abundance and vegetation structure were available. We used repeated measures in GLMM and forward selection as described above, including either 8 food variables (Table 2) or 11 vegetation cover variables (Table 2).

To investigate which of the tested variables are most important for Skylark habitat effects, we also analysed the effects of field size, boundary characteristics, food availability, vegetation cover and their interactions with survey round on Skylark groups in one analysis. At first, field size and boundary characteristics were included in the model. Then, forward selection using all food and cover variables, was applied. Significant interactions between explanatory variables and survey round were further investigated by analysing the effect of the respective explanatory variable on Skylark group density per survey round. This was done using GLMM, fields nested within survey plots as a random effect and the explanatory variable as a fixed effect.

To test for relationships between time of winter, foraging habitat and Skylark diet, the effects of survey round, temperature and crop type on Skylark diet were examined. Single effects of crop type, survey round and mean temperature (of the 3 days preceding the collection of the faeces) were analysed on the proportion of dry weight of different food types in the Skylark faeces. Temperature data were available from a weather station approximately 20 km distant from the study area (Hoogeveen, Dutch national weather station KNMI). GLMM with repeated measures were applied, including survey plot, survey round and crop type (for the analyses regarding the effects of survey round and temperature) as random effects.

Results

Habitat selection in relation to crop type, field size and boundary characteristics

More than 2,000 Skylarks assembled in 304 groups were observed during the 9 survey rounds using 43 of the 77 fields (Table 1). Skylark group densities differed significantly between fields of different crop types, with densities being highest on cereal stubbles and lowest on permanent grasslands (Table 2). When analysing the effects of field size and boundary characteristics on Skylark group density, the interaction between field size and survey round had the

Table 3 Effects of field size and boundary characteristics on Skylark group density in the Netherlands during winter

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

Forward selection of variables of field size and boundary characteristics (see Table 2) resulted in the presented model

β Standardized effects

strongest single effect, followed by the field boundary index (Table S2). Skylark group density was only significantly positively related to field size in the last two survey rounds (Table 3). Furthermore, Skylark group density was negatively related to the field boundary index. The smallest field occupied by Skylarks was 1.8 ha in size and 90 % of the Skylark groups were observed on fields larger than 4.3 ha. The highest field boundary index of occupied fields was 3.7 and 90 % of all Skylark groups were found on fields with a boundary index smaller than 1.5. Such a value can be interpreted as, for example, a field with a forest along a third of its perimeter or with lower vertical structures along a relative larger perimeter.

Habitat selection in relation to vegetation structure

Skylark group density was negatively related to the vegetation height in early November, but positively from February onwards (Table 4). On average, vegetation was tallest on cereal stubbles and shortest on potato stubbles (Table 2). Additionally, Skylark group density was negatively related to maize stubbles and total weed cover. Total weed cover (monocotyledonous and dicotyledonous weeds) was highest on grasslands with on average more than 93 % in comparison to 8 %, 6 % and 1 % on cereal, potato and maize stubbles, respectively (Table 2). Weed cover was no longer significantly related to Skylark group density when grassland was excluded from the analysis ($F = 1.45$, $P = 0.231$). The effect of volunteer cereals differed between survey rounds. Finally, Skylark group density was positively related to cereal stubbles.

Table 4 Effects of field size and boundary characteristics, vegetation structure and food abundance on Skylark group density in an agricultural area of the Netherlands during winter

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

Forward selection of cover only variables and all explanatory variables (including seed density)

β Standardized effects

Food availability

The most abundant seed species found in the soil samples belonged to the family Chenopodiaceae (44 %), followed by *Poa annua* (12 %), *Stellaria media* (9 %), *Solanum* sp. (9 %) and *Polygonum persicaria* (7 %), all of which were part of the Skylark diet. The remaining 17 % belonged to 42 different species. Cereal grains accounted for less than 0.1 % of the sampled seeds and were found in only three soil samples. Seed densities significantly differed between crop types. Densities of dietary seeds were highest in soils of potato stubbles followed by cereal stubbles, grasslands and maize stubbles (Table 2). Average densities of seeds declined significantly in grasslands in the course of the winter, and showed a negative trend on potato stubbles

($F = 14.89$, $P < 0.001$ and $F = 3.45$, $P = 0.063$, respectively). Soil seed densities on maize fields increased ($F = 13.32$, $P < 0.001$), while they did not change significantly on cereal stubbles ($F = 0.45$, $P = 0.503$).

The most abundant invertebrate groups caught with sticky traps ("flying invertebrates") were from the orders Brachycera (83 %) and Nematocera (7 %). Biomass of flying invertebrates did not differ between crop types (Table 2), but differed significantly between survey rounds, with highest biomass in the first round and lower biomass in subsequent rounds ($F = 212.8$, $P < 0.001$). Almost no flying invertebrates were caught between the beginning of December and late February.

Coleoptera larvae, including 38 % Carabidae and 12 % Staphylinidae, accounted for more than half of the invertebrate biomass caught in pitfall traps ("ground-dwelling invertebrates"). Imagos of Coleoptera accounted for 22 % of the biomass in pitfalls and Diptera for 13 %. Biomass of ground-dwelling invertebrates differed significantly between crop types, with highest biomass caught in grassland and the lowest on maize stubbles (Table 2). Biomass of ground-dwelling invertebrates also differed significantly between survey rounds and was highest in the first survey round and subsequently lower, but increased again slightly at the end of the winter ($F = 17.8$, $P < 0.001$).

Habitat selection in relation to food availability

Of the 35 fields for which data on food abundance and vegetation cover were available, 23 were occupied by Skylarks at least once during the bird surveys (Table 1), and a total of 1,107 Skylarks in 153 groups were counted (Fig. 1). The biomass of ground-dwelling invertebrates significantly affected Skylark group density (Table S2). Consequently, all further analyses were performed without the first survey round in January (when we could not place pitfalls; see "Data availability"). Skylark group density was positively related to the interaction between the cover of volunteer cereals and survey round and negatively to the biomass of ground-dwelling invertebrates (Table S3). Density of Skylark groups was positively related to the cover of volunteer cereals in mid-December and late February.

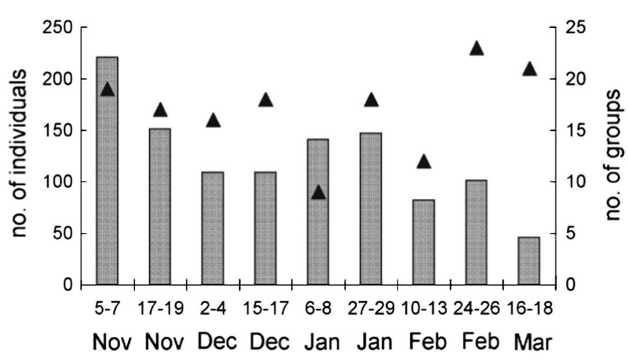

Fig. 1 Skylark (*Alauda arvensis*) numbers (*grey bar*, primary *y* axis) and numbers of Skylark groups (*black triangles* secondary *y* axis) per survey round on plots in the northern Netherlands in the winter 2008/2009. The figure includes only Skylarks observed on fields for which data about food abundance and vegetation cover were available

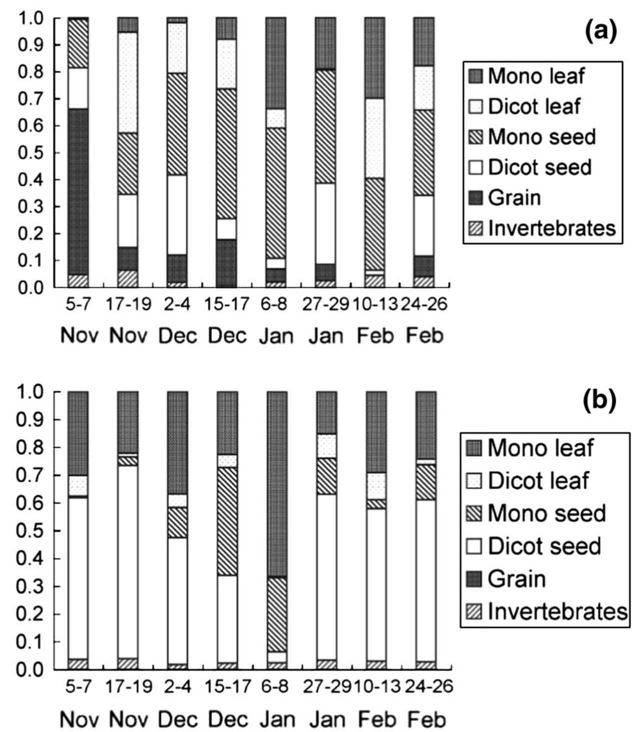

Fig. 2 Average proportion of different food types in Skylark faeces collected on former (**a**) cereal and (**b**) potato fields during winter in the northern Netherlands. *Mono leaf* monocotyledonous leaf, *dicot leaf* dicotyledonous leaf, *mono seed* monocotyledonous seed, including flowers and fruit inflorescence; *dicot seed* dicotyledonous seed, including flowers and fruit inflorescence; and invertebrates

Skylark diet based on faecal analysis

The contents of Skylark faeces differed between samples collected on potato and cereal stubbles (Fig. 2). The proportion of dicotyledonous seeds was significantly higher in faecal pellets collected on potato stubbles, whereas the proportion of cereal grains was significantly higher in faeces collected on cereal stubbles (Table 5). The most frequent food types found in faeces collected on potato stubbles were seeds of Chenopodiaceae, present in 65 % of the pellets, followed by leaves and seeds of *Poa annua* (58 and 35 %, respectively), seeds of *Solanum* sp. (33 %) and *Stellaria media* (32 %). This roughly reflects the order in the abundance of seed species found in the soil samples. On cereal stubbles, seeds of Chenopodiaceae were found in most of the faecal pellets (53 %), too. Furthermore, 45 % of the faecal pellets contained seeds of *Polygonum convolvulus*, 42 %

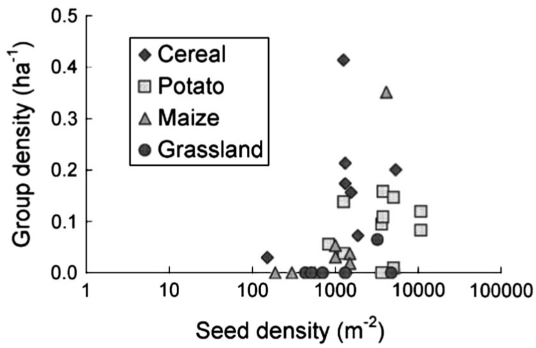

Fig. 3 Relationship between the density of dietary seeds (m^{-2}, log-scale) and Skylark group density (ha^{-1}) during winter in the northern Netherlands. Presented data are averaged over all survey rounds

seeds of *Echinochloa crus-galli* and 40 % cereal grains. Cereal grains were only found in faeces collected on cereal stubbles. The proportion of cereal grains in the faeces was related to sampling round. In the beginning of November, the proportion of cereal grains in the faeces was about 60 %, but dropped below 20 % in December and in subsequent months below 10 % (Table 5; Fig. 2a). Green parts of plants were part of the Skylark diet throughout winter on potato as well as on cereal stubbles (Fig. 2; Table 5). Their proportion was highest in January and February, when leaves of dicotyledonous and especially monocotyledonous could together form more than 50 % of the Skylark diet (Fig. 2). Most droppings (73 %) contained a low percentage (on average 3 %) of small invertebrates ($\geq$5 mm) (Fig. 2). The most important prey types were Coleoptera (89 % of all pellets) and Araneae (25 %). The proportion of invertebrates in the faeces was positively related to temperature, but not to crop type (Table 5).

Habitat selection: all factors combined

Simultaneous investigation of all explanatory variables showed which variables had most impact on Skylark group density: the field boundary index, vegetation height and total weed cover had a negative effect and seed density a positive effect. Furthermore, Skylarks avoided maize stubbles and preferred cereal stubbles (Table 4). 90 % of the Skylark groups were observed on fields with more than 860 dietary seeds m^{-2} (Fig. 3). Neither field size nor its interaction with survey round was related to Skylark group density in this dataset of 35 fields for which food availability data and vegetation structure were available.

Discussion

Habitat selection by Skylarks wintering in an agricultural area of the Netherlands was associated with food abundance, vegetation cover, field size and boundary characteristics. Of all Skylark groups observed across the winter, 90 % foraged on fields larger than 4.3 ha and with low boundary characteristics. Furthermore, Skylarks avoided maize stubbles and grasslands. Thus, our study supports data from the UK, where a preference of Skylarks for wintering on large stubble fields with low boundary characteristics has been documented (Robinson and Sutherland 1999; Donald et al. 2001; Gillings and Fuller 2001). In addition to these data, we provide evidence that potato stubble fields are an important habitat for wintering Skylarks in the Netherlands.

Table 5 Single effects of crop type (potato and cereal), temperature (mean of the 3 days preceding faeces collection) and survey round on the proportion of different food types in faecal pellets of Skylarks foraging during winter on potato and cereal stubble fields in the Netherlands

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

Mean proportions of the different food types in Skylark faeces are given per crop type (cereal and potato). Generalised linear mixed models with repeated measures were applied, including survey plot, survey round and crop type (for the analyses regarding the effects of survey round and temperature) as random effects

Dicot leaf dicotyledonous leaves; *dicot seed* dicotyledonous seeds, fruit inflorescence and flowers; *mono leaf* monocotyledonous leaves; *mono seed* monocotyledonous seeds, fruit inflorescence and flowers; β Standardized effects

Significant values ($P < 0.05$) in bold

Analyses of faeces collected on potato and cereal stubble fields revealed differences between the diet of Skylarks foraging on these two field types. Cereal grains were only found in faeces collected on cereal stubbles, and the proportion of cereal grains in the faeces declined sharply over the course of the winter. Cereal grains were found in only three of the soil samples collected throughout the winter. Thus, despite the meagre cereal grain abundance in the soil samples, the grain content was relatively high in faeces collected at the beginning of November. This suggests that Skylarks have a strong preference for cereal grains, even though we cannot rule out that cereal grains were highly aggregated within fields, which may contribute to the observed pattern. However, a strong selection of cereal grains is likely, because of their high energy content. Green (1978) showed that, although grain and weed seeds have a similar metabolizable energy per unit weight, grains were much more profitable because of their bigger size. Therefore, Skylarks probably take cereal grains as long as they are available and switch to other, less profitable, food types when the grain supply is depleted. This may cause an important bottleneck in the energy balance of wintering Skylarks.

As cereal grains were depleted early, dicotyledonous and monocotyledonous seeds were an important part of the Skylark diet throughout most of the winter in our study. Skylarks especially selected seeds of *Polygonum convolvulus* and *Echinochloa crus-gallis*. These seeds were numerically only marginally present in the soil samples (3 and <1 %, respectively, of all seeds found in the soil samples), but were found in almost half of all droppings. This suggested that these plants are an important food source in winter, although we cannot rule out that these seeds were highly aggregated within fields, which may contribute to the observed pattern. Invertebrates were of minor importance (see also Green 1978), and their proportion in the diet only increased when temperatures were relatively high, probably causing a higher abundance and mobility of invertebrates. That the biomass of ground-dwelling invertebrates significantly affected Skylark group density might be an artefact, because invertebrates are most common on fields with low pesticide use and a high density of plant material, and thus are most numerous on the same fields as Skylarks. Alternatively, but not mutually exclusively, Skylarks might need a certain amount of invertebrates in their diet to fulfil specific nutrient requirements, e.g. to maintain their immune system. A higher proportion of dicotyledonous seeds were eaten by Skylarks foraging on potato compared to cereal stubbles. Soil seed densities (i.e. weed and grain seeds) were on average higher on potato than on cereal stubbles. Moreover, seeds were possibly more accessible on potato stubbles due to a higher percentage of bare earth (Whittingham and Markland 2002). Strikingly, and in contrast to studies that found seed depletion in soils of cereal stubble fields over the winter period (Robinson and Sutherland 1999; Moorcroft et al. 2002; Butler et al. 2005), seed densities decreased significantly only in grasslands and slightly, but non-significantly, on potato stubbles. This suggests that potato stubbles can provide food for Skylarks throughout the winter. Interestingly, in early January, when the soil was frozen and most seeds were probably unavailable for foraging birds, Skylarks fed almost exclusively on monocotyledonous leaves and seeds. Both leaves and seeds were possibly taken from grassy weeds that had been growing and setting seeds during autumn and throughout the winter, which indicates their importance as emergency food during harsh times. However, pesticides are often applied on stubble fields to prevent their growth.

Although dietary seeds which make part of the Skylark diet were more abundant on potato stubbles and Skylark group density was positively related to seed density, the average Skylark group density was higher on cereal stubbles. Besides the preference for high energy-containing cereal grains, the higher vegetation cover on cereal stubble fields might add to this effect. Potato stubble fields contained more bare soil in contrast to cereal stubble fields, which were mostly covered by stubbles. Skylarks have been shown to prefer some vegetation cover above bare soil and taller over shorter stubbles (Donald et al. 2001; Gillings and Fuller 2001; Butler et al. 2005; Whittingham et al. 2006), probably because they rely on crouching to avoid detection by a predator (Butler et al. 2005), but potentially also because some vegetation structures may provide a better micro-climate during cold winter weather by providing shelter from wind.

Half of the maize stubble fields and grasslands in this study contained less than 860 seeds m^{-2}. On fields with seed densities below this threshold, Skylark group density decreased sharply. On these fields, searching time may increase and, consequently, energy intake rate may be reduced to a suboptimal level. Furthermore, in most grasslands, food was probably less accessible due to the dense vegetation impeding bird movement (Wakeham-Dawson and Aebischer 1998; Whittingham and Markland 2002). In the current study, we recorded two occasions when Skylarks foraged on grassland. On both occasions, sheep and cattle, respectively, had grazed the grassland shortly before, thereby causing open areas in the grass sod. The combination of lower seed densities and the lack of suitable vegetation cover on maize stubbles might explain the relatively low Skylark group densities recorded on these fields.

Conclusion

Our findings suggest that cereal stubble fields larger than 4.3 ha, surrounded by no or low boundary vegetation and containing a density of dietary seed species of more than 860 seeds m^{-2} were most suitable for Skylarks wintering in agricultural lands of the Netherlands. Skylarks showed a strong preference for feeding on cereal grains, one of the most profitable food types in winter (Green 1978). However, cereal grains were already depleted by the end of November. When cereal grains were depleted, birds switched to weed seeds and leaves, and fed throughout the winter roughly in line with the food types that were most abundant and most easily accessible in a particular habitat. Foraging on weed seeds and leaves may, however, be less profitable than foraging on cereal grains (Green 1978). Additionally, overwintering stubble fields are rather rare and, furthermore, often treated with herbicides that prevent weed growth, one of the most important alternative food resource for Skylarks in winter. Consequently, Skylarks wintering in Dutch agricultural landscapes may suffer from a lack of energy-rich food resources throughout the winter and might experience difficulties in meeting their daily energy requirements. Therefore, improving the wintering food situation of Skylarks may increase winter survival and help to slow population declines. We recommend improving the food supply available to Skylarks in winter by providing more overwinter stubble fields that are not treated with herbicides and allow seed-rich weeds to proliferate, or even unharvested cereal fields. Fields that are not treated by herbicides but allow weeds to grow after harvest have already been proven to be of high conservation importance for other species (Bradbury et al. 2008), and are particularly important during harsh winter weather conditions when seeds cannot be accessed in frozen ground. Fields that aim to improve the Skylark food situation outside the breeding season should be large and situated in open areas. In the Netherlands, the most suitable areas for such measures have been identified (Bos et al. 2010). However, measures have so far only been introduced on local and regional scales, and their implementation on the national scale is still under political discussion (Bos et al. 2009, 2010; Kragten and Koks 2011).

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Conflict of interest The authors declare that they have no conflict of interest.

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