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Habitat use and diet of skylarks *Alauda arvensis* wintering on lowland farmland in southern Britain

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Summary

1. The habitat use and diet of skylarks wintering on lowland farms were studied to assess whether changes in agricultural practice could have reduced their most favoured wintering habitats or foods. Faecal samples were collected and soil seed densities were estimated. Skylarks in 122 cereal stubble fields in Oxfordshire were counted monthly to examine habitat use.
2. Cereal stubble fields were more likely to be occupied than other crops, and densities of birds in occupied fields were high. Barley stubbles were significantly more likely to be occupied than wheat stubbles. Growing cereals were weakly selected. Sugar beet stubbles held high densities of birds. Rotational set-aside was occupied more frequently and held higher densities than non-rotational set-aside.
3. Field size affected field occupancy independently of crop type, with larger fields more likely to be occupied. Fields enclosed by hedges or trees tended to be avoided. Cereal and set-aside fields that were occupied by skylarks in at least 1 month held significantly higher soil seed densities than fields that were not occupied.
4. Differences in occupancy between crops could be explained by diet. Birds in cereal stubbles fed largely on cereal grain, whereas those in winter cereals fed largely on cereal leaves. Broad-leaved weed leaves were strongly selected as food in cereal crops and farmland grass fields. In grass fields, the proportion of the diet made up by broad-leaved weeds was positively correlated with their availability. Broad-leaved weed seeds did not make up a significant dietary component in any crop.
5. Our results show that the shift from spring to autumn sowing of cereals has led to a loss of the skylark's most strongly selected wintering habitat and best food source. In winter cereals and in grass there was a high selectivity for relatively scarce, and probably declining, food resources. Our results suggest that the retention of weed-rich cereal (particularly barley) and sugar beet stubbles through the winter, particularly in large open blocks, will improve conditions for skylarks in winter. Whole-field rotational set-aside, particularly as naturally regenerating cereal stubbles, provides good winter food resources for skylarks.

Key-words: birds, ecology, habitat selection, seeds, set-aside, stubbles, weeds, winter.

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Introduction

The skylark *Alauda arvensis* L. is of high conservation concern after severe population declines across much of Britain (Chamberlain & Crick 1999) and other parts of western Europe (Tucker & Heath 1994). The species is on the Red List of UK birds of highest conservation concern (Gibbons *et al*. 1996) and has a poor conservation status throughout Europe (Tucker & Heath 1994). Britain may support internationally important wintering populations of this species due to the arrival of immigrants from the continent (Lack 1986). Many other farmland birds have also declined in numbers and range (Fuller *et al*. 1995), following the intensification of agriculture (Chamberlain *et al*. 2000; Donald, Green & Heath 2001).

It is uncertain whether the factors causing the recent decline in skylark populations operate within or outside

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the breeding season, or both. Chamberlain & Crick (1999) showed that there was no decrease during the period of population decline in the productivity of individual nesting attempts and suggested that declines were due either to fewer nesting attempts or to increased winter mortality. Robinson (1997) suggested that a decline in winter food availability was an important factor. Although habitat use in the breeding season has received considerable attention (Schläpfer 1988; Jenny 1990; Wilson *et al*. 1997; Chamberlain *et al*. 1999), determinants of habitat use and diet during the winter are less well understood. This is unfortunate because winter, particularly late winter, may be a time of particularly high mortality in many granivorous species (Crick, Donald & Greenwood 1991; Newton 1998).

The majority of skylarks wintering in Britain occur on farmland and coastal habitats, the highest densities being recorded from saltmarsh (Lack 1986; Gillings & Fuller 2001). Nationally, birds are concentrated in lowland arable areas (Gillings 2001). Winter cereal stubbles, particularly weed-rich stubbles, are an important foraging habitat for a number of declining seed-eating farmland passerines, including the skylark (Donald & Evans 1994; Evans & Smith 1994; Robinson & Sutherland 1997; Buckingham *et al*. 1999; Donald & Vickery 2000). Some of these studies have also demonstrated either avoidance by skylarks of winter cereals or a use in proportion to their availability, although skylarks make more use of winter cereals than other granivorous passerines (Wilson, Taylor & Muirhead 1996). Avoidance of grassland and small fields has also been recorded independently of crop type (Wilson, Taylor & Muirhead 1996; Gillings & Fuller 2001). So far these patterns have not been explained in terms of food availability or diet.

Due to changes in cereal management, the area of cereal stubbles has declined greatly in the UK (Shrubb 1997; Chamberlain *et al*. 2000), although this loss has been mitigated to a small extent by the introduction of set-aside in 1992 (Evans *et al*. 1997). Furthermore, the amount of grain spilt in fields during harvesting has also fallen due to improvements in harvesting machinery (Shrubb 1997). Improvements in seed cleaning and farm hygiene and a reduction in the numbers of many arable weeds through herbicide use (Donald 1998) has led to a decrease in the availability of winter food supplies to granivorous and herbivorous birds (Ewald & Aebischer 1999; Wilson *et al*. 1999; Smart *et al*. 2000). Robinson & Sutherland (1997) and Wakeham-Dawson & Aebischer (1998) both detected a positive correlation between skylark abundance and soil seed density. However, soil seed densities may have declined by two orders of magnitude since the early 1900s and skylarks will need to spend far longer feeding during the day as a result (Robinson 1997). A loss of winter stubbles has been implicated in the decline of several seed-eating farmland passerines (Evans & Smith 1994; Donald 1997; Robinson 1997; Shrubb 1997; Peach, Siriwardena & Gregory 1999) and, significantly, the provision through agricultural subsidies of grain-rich cereal stubbles in the small areas of southern Britain still occupied by cirl buntings *Emberiza cirlus* led to a rapid increase in the population of that species (Evans 1997).

Habitat use in winter will be determined largely by the distribution of food, although other factors such as predator avoidance are also important (Robinson & Sutherland 1997). An analysis of diet is therefore fundamental to explaining habitat use by birds. To date the diet of skylarks in winter has received little attention, although Green (1978, 1980), working before the population decline, found that birds fed mainly on cereal grain from stubbles and from recent sowings when available, but that other food items were taken even when grain was widely available. In the absence of cereal grain, birds fed mainly on emerging winter cereal leaves or the seeds of broad-leaved weeds.

This study assessed habitat use of wintering skylarks and attempted to explain the observed patterns in terms of food availability and diet. We used the results to suggest practical conservation measures to improve farmland as a habitat for wintering skylarks.

Methods

SELECTION OF STUDY SITES

A total of 13 farms was studied in 1996–97 and 17 farms in 1997–98, involving 18 different farms in total. Farms were selected across southern England, without prior knowledge of their skylark populations, to cover as wide a variety of farming types as possible. Farms were located in East Anglia (Norfolk, Suffolk and Cambridgeshire), Oxfordshire and Dorset (Table 1).

Detailed information on the use of cereal stubbles by wintering skylarks was collected in Oxfordshire in the winters 1997–98 and 1998–99. Birds were counted monthly between October and March on 40 cereal stubble fields in 1997–98 and on 82 different cereal stubble fields in 1998–99. They ranged in size from 2·5 ha to 53·8 ha (mean = 11·3, SE = 0·71) and comprised conventional wheat (n = 67), conventional barley (n = 38) and organic stubbles (n = 17; wheat stubbles undersown with clover or grass). Of the 122 stubble fields, 54 (44%) were not set-aside and 68 (56%) were in rotational set-aside comprising naturally regenerating cereal stubbles. There were no systematic differences in farming regimes on farms with wheat and barley stubbles, both types often occurring on the same farms. However, a higher proportion of the conventional wheat stubbles was rotational set-aside than barley and organic wheat stubbles (χ^2 = 47·4, d.f. = 2, P < 0·001).

DATA COLLECTION

Main study

Birds were counted monthly on clear, dry, calm days only, in November to January in 1996–97 and November to

Table 1. Locations and descriptions of the 18 farms. Crops are listed in descending order of area based on the coverage of each in December. Crop codes: c, winter cereals; s, stubble (cereal and non-cereal); sa, set-aside; b, broad-leaf crops (mainly sugar beet and oilseed rape); g, grass (temporary and permanent); ba, bare tillage. Coverage: 'both', both winters, otherwise the single winter of coverage is given

Farm	Coverage	Region	Area (ha)	Mean field size (ha)	Crops
A	Both	East Anglia	242·8	10·12	ba,c,sa,b
B	Both	East Anglia	163·2	5·83	s,g,ba,b,c
C	Both	East Anglia	152·7	10·18	ba,c,b,s
D	Both	East Anglia	182·6	9·61	c,ba,b,s
E	Both	Oxfordshire	130·9	7·27	g,ba
F	Both	Oxfordshire	292·1	15·37	c,g,b,ba
G	Both	Oxfordshire	145·5	8·56	c,b,sa,g,ba
H	Both	Oxfordshire	153·2	17·02	c,sa,s,b,ba
J	Both	Dorset	175·6	5·46	g,b,c,s,sa,ba
K	Both	Dorset	287·4	4·64	g,sa,s,b
L	Both	Dorset	232·6	6·64	c,b,ba,s,g,sa
M	Both	Dorset	279·9	7·37	g,sa,c,s
N	1996–97	Oxfordshire	158·8	5·12	c,g,ba
P	1997–98	Dorset	167·0	5·22	c,g,s,ba,b
Q	1997–98	Oxfordshire	62·6	5·69	c,s,g,ba
R	1997–98	East Anglia	157·1	14·28	ba,s,c
S	1997–98	East Anglia	166·0	11·07	c,b,s,ba,sa
T	1997–98	East Anglia	71·6	5·97	c,ba,s,b,sa

March in 1997–98. Transects were walked across all fields so that each part was visited to within 50 m or less. We assumed that the detectability of birds did not differ between crops. The position and size of skylark flocks were recorded on maps and, when flushed, their number and direction of flight were noted to avoid double counting. Birds flying over but not landing were not counted. Crop type was recorded on each visit and in 1996–97 the cover of broad-leaved weeds and non-crop grasses was estimated monthly using quadrats from 10 evenly spaced 0·25-m^2 areas falling along each field's longest axis. Field areas and the length of field boundary were measured from maps. Field boundaries were classified into five types (no vertical structure, fence or low hedge, high hedge, hedge with trees, woodland) and the length measured around each field.

In December 1996, soil samples were collected from the top 5 mm of the soil surface at 10 evenly spaced locations in each field. Samples for each field were combined and frozen until analysis to prevent seed germination. Samples were weighed and the organic matter separated from inorganic soil contents by flotation in a super-saturated magnesium sulphate solution with a specific gravity of 1·6. Seeds were isolated from other organic matter, identified and counted under a binocular microscope, and the resulting seed densities were expressed as the number of seeds per gram of topsoil. Seeds smaller than 1 mm in length were not included in the analyses as this was the lower size limit of the smallest seeds recorded in the diet of skylarks (Green 1978).

Faecal samples were collected monthly by noting the location of feeding birds and subsequently searching the area. In virtually all cases, detection of skylarks was followed by the collection of faecal samples, suggesting that birds were feeding in all crops in which they were present. Samples were not collected when other passerines were present, although with practice it proved easy to identify skylark droppings by their size and shape. At least 10 individual faecal pellets were collected from each field where birds were present and stored in industrial methylated spirits (IMS) or frozen until analysis.

Stubble field study

Birds were counted monthly in the stubble field survey from October to March inclusive in each year. As with the main study, birds were counted by visiting all parts of each field and recording the number and position of all skylarks present. The food resources in each field were quantified from the populations of plant species (including self-sown cereals) on all stubble fields. Plant populations were assessed on percentage cover scores within a 20 × 20-cm quadrat. Forty quadrats were placed equidistantly along a diagonal transect across the field, and each non-crop species was given a percentage score relating to the amount of the quadrat it occupied.

DATA ANALYSIS

Analysis of habitat use

Main study. Many previous investigations into bird habitat selection have assumed that individual birds are distributed randomly across the landscape (Wilson, Taylor & Muirhead 1996). For this flocking species, we adopted the null hypothesis that groups of birds are distributed randomly across fields.

Birds were highly aggregated within fields, resulting in a heavily skewed and overdispersed data distribution. Furthermore, the flocking behaviour of skylarks in winter means that counts of individual birds within

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Table 2. Explanatory variables entered into models for the main study and the stubble field study

Variable	Levels	Notes
Main study		
Crop type	Winter cereals	
	Bare tillage	
	Cereal stubbles	
	Set-aside	
	Non-cereal stubbles	Mostly sugar beet and maize
	Ley grass	
	Permanent pasture	
	Broadleaf crops	Mostly sugar beet and winter oilseed rape
Region	East Anglia	
	Oxfordshire	
	Dorset	
Field size		ha
Field shape		m of boundary per ha
Hedge index		m of high (> 1·5 m) hedge or trees per ha
Seed density		Large (> 1 mm) seeds per g of topsoil
June density		Territory density the previous summer
Previous crop		Crop type in the previous summer
Farm	13 in 1996–97	
	17 in 1997–98	
Stubble study		
Field size		ha
Year	1997–98	
	1998–99	
Stubble type	Wheat	
	Barley	
	Organic wheat	
Vegetated boundaries		Number of field boundaries that were vegetated

fields are not statistically independent. We therefore attempted to identify factors explaining variation in field occupancy. Our data were replicated by month and year, allowing us to improve the resolution of the presence–absence analysis. First we used general linear models (GLM) to model the frequency of occupancy of each field (birds present on 0, 1, 2 or 3 of the three visits) as a function of a number of predictor variables describing habitat and land use (Table 2). Only fields in which crop types did not change within winters were included. Modelling was carried out in GLIM 3.77 (Payne 1987). All models assumed a binomial distribution of errors, a value of 3 being entered as the binomial denominator and a logit link function specified. The reduction in residual deviance caused by entering an explanatory variable was treated as a likelihood ratio test and its significance assessed by comparing it with the χ^2 distribution. In all models, overdispersion of the data was checked for and where the ratio of scaled deviance to degrees of freedom greatly exceeded 1, the scale parameter was reset to a value of Pearson's χ^2 divided by the residual degrees of freedom (Aitken *et al*. 1989). Data from the two winters were analysed separately. Unit and quadratic terms for each of the explanatory variables described in Table 2 were entered into a univariate model to assess their effects on field occupancy. All terms explaining significant variation in field occupancy were then entered into a multivariate model with interaction terms. Model simplification produced a minimum adequate model. Because fields within individual farms were not statistically independent, a factorial variable relating to farm was forced into each model.

Certain transitional habitats, particularly stubbles, were rarely present for the whole of the winter. Therefore a month-specific analysis was undertaken in which the effects of crop type on a binary presence–absence variable were examined using contingency tables. Adjusted standardized residuals were treated as close approximations to z-scores.

Counts of birds in occupied fields deviated greatly from normal, Poisson and negative binomial distributions, so they could not be analysed further using parametric methods. However, the relationship between counts and frequency of occupancy could be examined and, where a positive relationship was found, it was assumed that the factors explaining significant variation in field occupancy also explained variation in counts.

A second approach to determining the effects of crop type on occupancy and numbers was to use a series of paired sample tests to assess the effects of changes in cropping on the occupancy and numbers of birds on individual fields, both within and between winters. A first step was to assess whether there were systematic differences between the two winters in occupancy or numbers by comparing the proportions of fields that were occupied in each winter using a χ^2 test, and assessing any significant differences between winters in the numbers of birds in occupied fields using a Mann–Whitney *U*-test. A further check was to use paired sample McNemar tests to assess differences between winters in occupancy in the subset of fields in which the crop type was the same in both winters. McNemar tests were then used to assess the effects on occupancy of a number of possible combinations of crop changes. Where birds were present both before and after crop change, either within or between winters, Wilcoxon signed-rank tests were used to detect any systematic change in the number of birds present. In between-year comparisons, signed-rank tests were used to assess the effects of cropping change on the four-level occupancy variable.

Stubble study. The statistical distribution of the stubble data shared many of the analytical problems of the main study data. The data from both winters were combined (fields in each winter were different) and divided into three periods, early (October and November), mid (December and January) and late (February and March), and the occupancy in each period summed to give an occupancy variable of 0, 1, 2 or 3. As with the main data set, this occupancy variable was entered as the dependent variable into a GLM and the analysis repeated as for the main study.

Dietary analysis

One faecal pellet was selected at random from the 10 or more collected from each field visit, and spread thinly in water over a microscope slide. Staining was not necessary. The samples were examined at × 45 under a binocular microscope following the methods of Green (1978). The relative area of each diet item was estimated by counting the number of times (out of 50 'hits') that it fell directly under the calibration marks of an eyepiece-mounted graticule scale. Items were identified to Green's (1978) categories using reference material. Particular care was taken to avoid overlooking dicotyledon epidermis and the skin of cereal grain, as these could be virtually transparent. Green (1978) calculated weighting factors to correct the area of each diet item to its proportion of the dry weight of material ingested by captive skylarks. The weighting factors were calculated relative to an arbitrary reference, in this case cereal leaf. The proportion of each item in the sample was calculated as the number of hits multiplied by the appropriate weighting factor and divided by the weighted sum of hits of all the diet items present. This approach does not adequately quantify earthworm biomass. Where earthworm chaetae were present (in just three samples), 10% of the total number of hits were arbitrarily set to earthworms and included with other invertebrates. The resulting measures represented the proportion of each of seven food types (broad-leaved weed leaf, cereal leaf, grass leaf, arthropods, cereal grain, broad-leaved weed seed and other), totalling one for each pellet. GLM were used to assess differences in the proportion of dietary items taken in different crop types or in different months, as compositional analysis was found to be unsuited to the data distribution. Models again assumed a binomial distribution of errors (Crawley 1993) with a unit denominator and overdispersion was checked and corrected for as above. Principal components analysis (PCA) was used to identify similarities or differences between crops in the diet of birds feeding there.

Results

FIELD OCCUPANCY

A total of 342 fields (covering 2560 ha) was visited monthly in 1996–97 and 388 fields (3000 ha) in 1997–98. Non-zero counts of skylarks were recorded in 25·8% and 27·8% of field visits in 1996–97 and 1997–98, respectively. The median number of skylarks in occupied fields was 7·5 in 1996–97 and 6·0 in 1997–98; this difference was not statistically significant (Mann–Whitney U-test, $U_{266,316} = 39315{\cdot}0$, $P = 0{\cdot}18$). There were no significant differences between winters in the proportion of occupied fields ($\chi^2 = 1{\cdot}04$, d.f. = 1, $P = 0{\cdot}31$) nor in the highest number of birds recorded on fields in which crop type was the same (Wilcoxon signed-rank test for maximum number, $Z_{179} = -1{\cdot}75$, $P = 0{\cdot}08$). Patterns of occupancy by skylarks of fields of different crop types did not change significantly through the course of either winter (Kruskal–Wallis tests, $P > 0{\cdot}05$ in all cases).

In both winters, the same variables explained variation in field occupancy (Table 3). The factorial dummy variable relating to farm had a significant effect and was retained in all further models. The crop type and field size, shape and hedgerow terms each had additional effects independently of farm effects in both winters. Field occupancy by skylarks increased with increasing field size, but decreased with increasing field boundary length per hectare of field and with increasing length of tall hedgerow or woodland in the field boundary.

Table 3. Results of univariate models of field occupancy. The figures shown relate to the reduction in residual scaled deviance caused by the entry of each variable to a model into which a dummy variable relating to farm had already been forced and their significance derived by comparison with the χ^2 distribution. The direction of the effect of continuous variables on increasing field occupancy is given in parentheses. Variables in bold relate to the four variables in each winter retained in a multivariate model. The explanatory variables are described in Table 1. *$P < 0{\cdot}05$; **$P < 0{\cdot}005$; ***$P < 0{\cdot}0005$

Variable	d.f.	1996–97	1997–98
Farm	12 or 16	**65·7*****	**63·1*****
Region	3	NS	NS
Crop type	7	**48·8*****	**42·7*****
Previous crop	8	NS	NS
Field size	1	**39·8***** (+)	**64·2***** (+)
Field shape	1	**49·7***** (–)	35·4*** (–)
Hedge index	1	15·4*** (–)	**41·5***** (–)
Seed density	1	NS	NS
June density	1	NS	NS

Table 4. Significant differences in the frequency of occupancy classes (0–3) between crop types. +, more than expected by chance; –, fewer than expected by chance. All significant at $P < 0.05$

	1996–97				1997–98			
	0	1	2	3	0	1	2	3
Winter cereals	–	+			–	+		
Cereal stubbles	–			+	–		+	
Non-cereal stubbles								
Bare tillage								
Set-aside				+				+
Grass ley								–
Permanent pasture	+	–	–	–	+	–		–
Broad-leaved crops	–			+	–			+

Table 5. Results of month-specific comparisons of occupancy. Numbers shown (out of a maximum of 6) are significant (at $P < 0.05$) positive and negative deviations from expected use, derived from contingency tables

	Significant + deviations	Significant – deviations
Winter cereals	1	0
Cereal stubbles	6	0
Non-cereal stubbles	0	0
Bare tillage	0	0
Set-aside	2	0
Ley grass	0	2
Permanent pasture	0	6
Broad-leaved crops	5	0

Multivariate models showed that a number of factors independently explained significant variation in skylark field occupancy. In 1996–97, the best multivariate model retained the dummy variable denoting farm, crop type and field shape terms and field area. In 1997–98, the final multivariate model held the same variables except that the field shape term was replaced by the hedge index term, although the two were strongly correlated ($r_{345} = 0{\cdot}61$, $P < 0{\cdot}0001$). There were no significant interaction terms in either of the two models. In both cases, the regression coefficient was positive for field area, indicating a selection for larger fields independent of crop type, and negative for field shape or hedge index, indicating an avoidance of small, enclosed, fields.

Winter cereals showed a positive deviation from mean usage due to a significantly higher number of cases of infrequent occupancy (Table 4) and a lower number of cases of complete absence than expected by chance. Stubbles, set-aside and broad-leaved crops all had positive deviations from mean use (although not always significantly so due to small sample sizes) due to a higher than expected incidence of frequent or permanent occupancy (Table 4). This was supported by analysis of the stubble field data, with 66% of stubble fields occupied in at least one month (October to March inclusive) being occupied in all months, and a further 18% being occupied in 5 out of 6 months. Permanent pasture and grass leys were avoided.

Seed density differed significantly between crop types (Kruskal–Wallis test, $\chi^2 = 32{\cdot}05$, d.f. = 7, $P < 0{\cdot}0001$), with set-aside holding significantly more seeds than winter cereals or permanent pasture. Soil seed sample sizes for cereal stubbles were too small to compare with other crops. Soil surface seed density did not explain significant variation in field occupancy in any of the univariate or multivariate models and was not significantly correlated with the density of birds in occupied fields ($r_{71} = -0{\cdot}03$, $P > 0{\cdot}5$). However, winter cereal fields that were occupied at least once during the winter held significantly higher soil seed densities than fields that were never occupied (Mann–Whitney $U_{31,34} = 258{\cdot}0$, $P < 0{\cdot}0001$). The same was found for set-aside fields ($U_{12,13} = 22{\cdot}0$, $P = 0{\cdot}002$), and there was a difference approaching significance in bare tillage ($U_{7,12} = 20{\cdot}0$, $P = 0{\cdot}06$). These differences were unlikely to have been due to systematic differences between farms, as there was no significant correlation between mean farm seed density and mean farm field occupancy ($r_s = 0{\cdot}22$, $n = 13$, $P = 0{\cdot}45$), and there were no significant differences in mean field seed density between farms ($F_{12,278} = 0{\cdot}62$, $P > 0{\cdot}8$).

The territory density of breeding birds the previous summer had no predictive effect on field occupancy or density, although significantly higher proportions of fields were occupied or unoccupied in both summer and winter than would be expected by chance ($\chi^2 = 78{\cdot}8$, d.f. = 1, $P < 0{\cdot}0001$). This suggests that at least some of the environmental factors determining field use in the breeding season apply in winter. Because crop type changed in most fields between summer and winter, these factors are likely to be related to field size and structure.

In each of the 6 months, cereal stubble fields were occupied more frequently and permanent pasture less frequently than would be expected by the random distribution of birds across fields (Table 5). Winter cereals were used more than would be expected by chance in 1 of the 6 months, although the effect of multiple testing on type I errors was not controlled.

Of the 236 fields that were occupied in at least one winter, in only 57 (24·2%) did crop type change between the two winters. Numbers of skylarks increased when fields changed from winter cereals to other crops (Wilcoxon signed rank test, $Z_{28} = -2{\cdot}38$, $P < 0{\cdot}02$) and decreased when fields changed to winter cereals ($Z_{17} = -2{\cdot}4$, $P < 0{\cdot}02$). Changes in cropping between consecutive visits to fields within winters were recorded 73 times. Changes from cereal stubbles to bare tillage resulted in a significant decrease in the number of skylarks present (Wilcoxon signed rank test, $Z_{15} = -2{\cdot}61$, $P < 0{\cdot}01$).

ABUNDANCE

There was a positive relationship between likelihood of occupancy and the maximum recorded density (Fig. 1),

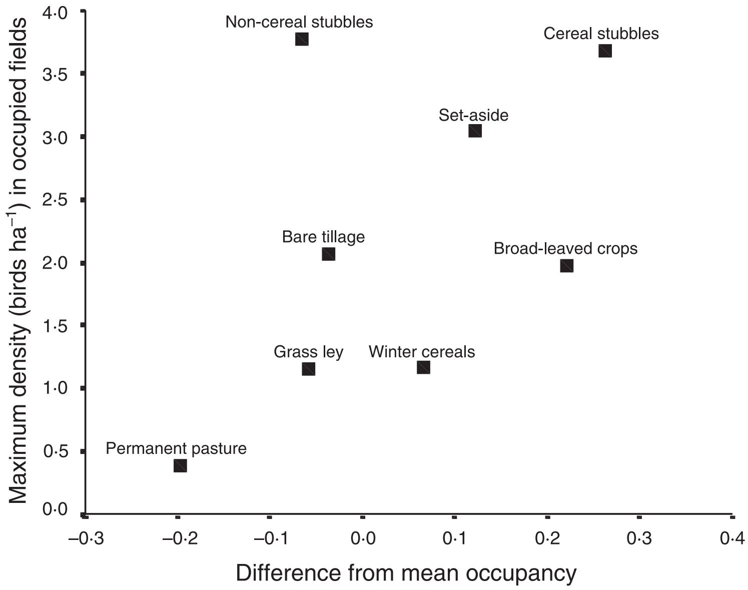

Fig. 1. Relationship between recorded density (mean of maximum counts in occupied fields) and deviations from mean occupancy (from GLM). The relationship was not significant when non-cereal stubbles were included ($r_s = 0{\cdot}36$, $n = 8$, $P > 0{\cdot}05$) but achieved significance when that point was removed ($r_s = 0{\cdot}71$, $n = 7$, $P < 0{\cdot}05$). See text for interpretation.

suggesting that the factors explaining significant variation in field occupancy also explained significant variation in numbers.

Densities of birds in occupied rotational set-aside fields were higher than those in occupied non-rotational set-aside fields ($U_{27,88} = 838{\cdot}5$, $P = 0{\cdot}02$), and a significantly higher proportion of rotational set-aside fields was occupied than was the case with non-rotational set-aside ($\chi^2 = 4{\cdot}5$, d.f. = 1, $P < 0{\cdot}05$).

An obvious outlier in Fig. 1 was non-cereal stubbles, which held higher numbers of skylarks than would be expected by their occupancy rate. The two most frequent types of non-cereal stubble were maize and sugar beet stubbles. A higher proportion of sugar beet stubbles was occupied than maize stubbles ($\chi^2 = 32{\cdot}5$, d.f. = 1, $P < 0{\cdot}$s) and maximum numbers of birds in occupied sugar beet fields were higher ($U_{17,6} = 20$, $P = 0{\cdot}03$).

Table 6. Results of univariate and multivariate models of occupancy of cereal stubble fields. The values represent the change in scaled deviance (significance assessed by comparison with the χ^2 distribution) caused by addition of variables separately (univariate models) or removal of unitary or interaction terms from a maximal model containing all terms (multivariate model). *$P < 0{\cdot}05$; **$P < 0{\cdot}01$; ***$P < 0{\cdot}001$. Fitted values of the multivariate model are plotted in Fig. 2

		Model	
	d.f.	Univariate	Multivariate
Field area	1	23·8***	27·1***
Year	1	NS	NS
Stubble type	2	6·2*	9·5**
Vegetation boundary	1	NS	NS
Interactions			
Area–year	2		NS
Area–stubble type	2		7·1*

STUBBLE FIELD STUDY

The results of the stubble field study (Table 6) supported the findings of the main study, particularly with regard to the importance of field size. A significant interaction term showed that barley stubbles were more likely to hold skylarks than wheat stubbles of the same size (Fig. 2). The likelihood of occupancy of a field of barley stubble approached 100% at around 6 ha, whereas that of a wheat stubble of the same size was only around 60%. The number of weed species recorded was higher in barley than in wheat stubbles ($F_{1,103} = 11{\cdot}0$, $P = 0{\cdot}001$), and the cover of volunteer cereals was higher in wheat than in barley stubbles ($F_{1,103} = 8{\cdot}1$, $P = 0{\cdot}005$). Total cover of stubble stems and bare ground did not differ significantly between wheat and barley stubbles ($F_{1,103} = 3{\cdot}0$, $P > 0{\cdot}05$).

DIET

A total of 166 faecal pellets was analysed for the period November to February, each relating to a different field visit. Seven major food types were identified (Table 7). There were significant differences in the proportions of four identified foods in the diets of birds from different crop types from November to February (Table 7). Cereal grain made up a significantly higher proportion of the diet in cereal stubbles and bare tillage than in other crops, whereas in winter cereals, cereal leaves made up the largest component. Birds wintering in winter barley had a significantly higher proportion of cereal leaves in their diet than birds in winter wheat ($\chi^2 = 6{\cdot}6$, d.f. = 1, $P = 0{\cdot}01$). Broad-leaved weed leaves were significant dietary components in all crops. In farmland grass fields, grass leaves made up a high proportion of the diet but

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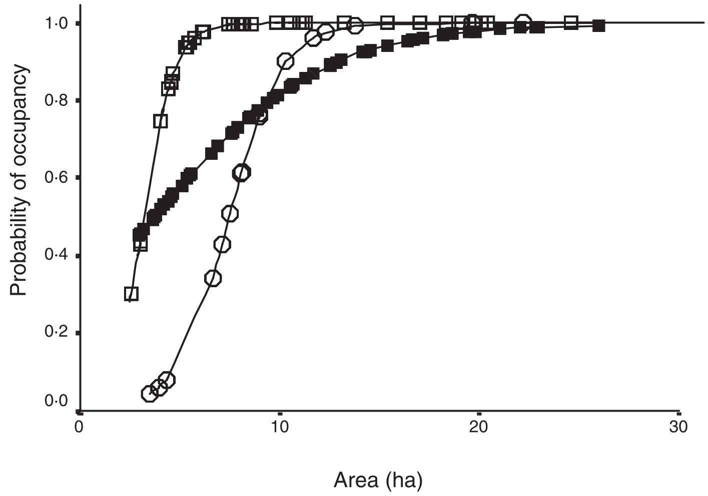

Fig. 2. Effects of field size on probability of occupancy of stubble fields of different types, derived from fitted values from regression model parameters (Table 6). Open squares, barley stubble; filled squares, conventional wheat stubble; open circles, organic wheat stubble. Lines were fitted from a simultaneous model, not calculated for each stubble type independently.

Table 7. Mean proportion of diet in different crops made up by each of seven food types. The food group 'Other' comprised grass flowers and seed and other small seeds; Blf, broad-leaved. Differences between crops in the proportions of each food type are assessed from GLM. For four food types there were significant differences between crop types in their contribution to total dietary intake (*$P < 0.05$, **$P < 0.005$, ***$P < 0.0005$). Directions of significant ($P < 0.05$) deviations from the overall mean of all crops combined are shown as superscripts

		Food item (mean proportion)						
Crop	n	Cereal grain	Cereal leaf	Blf leaf	Blf seed	Grass leaf	Arthropods	Other
Winter cereals	38	$0·13^{-}$	$0·54^{+}$	$0·24^{-}$	0·05	$0·00^{-}$	0·03	0·01
Cereal stubbles	24	$0·47^{+}$	$0·12^{-}$	0·31	0·05	0·02	0·01	0·02
Non-cereal stubbles	6	0·07	$0·00^{-}$	$0·88^{+}$	0·01	0·01	0·03	0·01
Bare tillage	12	$0·28^{+}$	$0·03^{-}$	$0·56^{+}$	0·07	0·01	0·04	0·01
Set-aside	24	0·14	$0·04^{-}$	$0·65^{+}$	0·02	0·08	0·07	0·00
Ley grass	25	0·06	$0·00^{-}$	$0·42^{+}$	0·09	$0·36^{+}$	0·05	0·02
Permanent pasture	11	0·16	$0·00^{-}$	$0·51^{+}$	0·02	$0·23^{+}$	0·07	0·01
Broadleaf crops	26	$0·02^{-}$	$0·00^{-}$	$0·96^{+}$	0·01	0·01	0·00	0·00
χ^2 (with 7 d.f.)		21·8**	56·6***	44·5***	NS	29·6***	NS	NS

this was a rare food item in other crop types. Broad-leaf weed seeds made up a small proportion of the diet in all crop types and their abundance was not correlated with soil seed availability ($r_s = 0·04$, $n = 134$, $P > 0·5$).

Broad-leaved weed leaves made up 46·3% of the diet in grass fields and 24·0% of the diet in winter cereals, yet accounted for an average of only 2·6% and 0·73% of total vegetated area in occupied fields, respectively, suggesting strong selection. In grass fields, the proportion of the diet made up by broad-leaved weed leaves was positively correlated with their availability in the field ($r_s = 0·46$, $n = 30$, $P = 0·02$). However, the cover of broad-leaved weeds had no effect on field occupancy or bird density in any crop type.

The winter period was broken down into three periods, early (November and December), mid (January and February) and late (March and April), to assess seasonal changes in diet. No dietary component changed significantly within any crop type over the course of the winter ($P > 0·05$ in all cases).

PCA (Fig. 3) suggested that diet in cereal stubble was most similar to that in winter cereals, the component scores showing that this was due to the high proportion of cereal leaves and grain in the diet. The diet of skylarks in non-cereal stubbles, broad-leaved crops and, to a lesser extent, set-aside were also similar, due to the high proportion of broad-leaved leaves in the diet. Diets of birds on bare tillage were not dominated by any individual food item, suggesting a high diversity of food types.

Discussion

FACTORS AFFECTING HABITAT USE

The results of this study demonstrate a clear preference by wintering skylarks for arable farmland, with both temporary (ley) grass and permanent pasture being strongly avoided. Wilson, Taylor & Muirhead (1996), Gillings & Fuller (2001) and Buckingham *et al.* (1999) also showed avoidance of grassland by wintering skylarks,

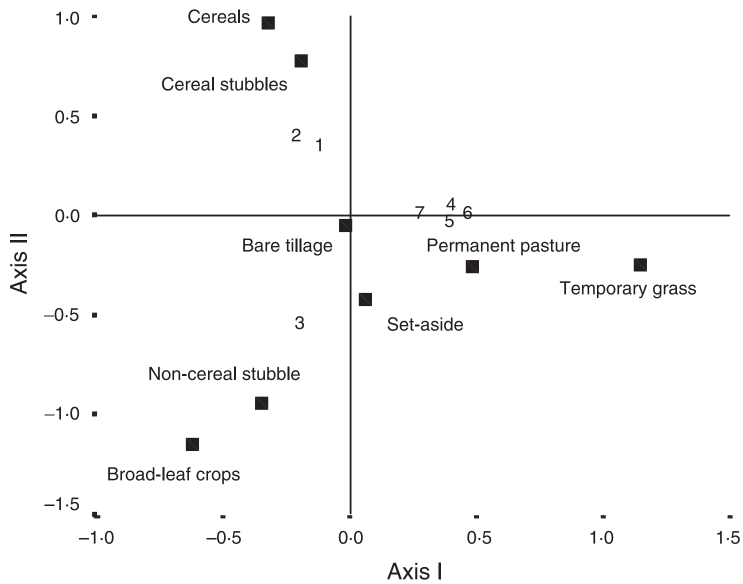

Fig. 3. Ordination of crops by composition of skylark diet in winter. Axes represent the first two axes of a PCA that between them explained 45% of the variance in the data set. Points represent the mean axis scores for each crop type. Numbers show the component weighting scores of each dietary group (1, cereal grain; 2, cereal leaf; 3, broad-leaf leaf; 4, broad-leaf seed; 5, grass leaf; 6, arthropods; 7, other).

while Wakeham-Dawson & Aebischer (1998) found that land converted from arable to grass was used by skylarks until sward closure, when numbers declined. Grass structure therefore appears to be an important determinant of use by skylarks. Within grassland, a higher proportion of the diet was made up of grass leaves than was the case in any other crop type, and within permanent pasture there appeared to be a strong selection of broad-leaved weed leaves. The high proportion of cereal grain (16%) in the diet of birds in permanent pasture was due to birds feeding on grain put out as supplementary food for livestock. Previous work on wintering birds has shown that agricultural grasslands tend to be dominated by invertebrate-feeders (Tucker 1992), although arthropods were no more frequent in faecal samples from grassland than from other crop types in this study. Invertebrate-feeders and granivorous bird species appear to be spatially separated in Britain in winter, with invertebrate-feeders occurring almost entirely on grassland, some avoiding even cereal stubbles (Tucker 1992), and granivorous species occurring almost entirely on arable land, many of them strongly selecting stubbles (Wilson, Taylor & Muirhead 1996).

Within arable landscapes, there were significant differences in skylark habitat use and diet between crop types. This study supports previous work (Wilson, Taylor & Muirhead 1996; Robinson 1997; Wakeham-Dawson & Aebischer 1998; Buckingham *et al.* 1999; Gillings & Fuller 2001) in suggesting that cereal stubbles are the most highly selected wintering habitat of skylarks. Barley stubbles were preferred to wheat stubbles, a preference also found by Buckingham *et al.* (1999). Stubble fields and rotational set-aside left as naturally regenerating stubble tended to be occupied throughout the winter and to hold higher densities of birds than other field types. The addition in this study of information on diet further suggests that this positive selection is linked to the availability of cereal grain, shown by Green (1978) to be the most energetically profitable food available to wintering skylarks. Growing winter cereal fields were not avoided, but the use of individual fields was infrequent, suggesting a higher degree of movement between fields than was the case with stubbles or set-aside. Although the largest single dietary component of skylarks in winter cereals was cereal leaves, around a third of dietary intake comprised cereal grain and broad-leaved weed leaves, the latter making up a very small proportion of the vegetated area of cereal fields. This suggests a very strong positive selection by birds wintering in cereal fields of broad-leaved weed leaves.

Small fields, fields with a high boundary length to area ratio and fields with tall hedges tended to be avoided. The resulting apparent selection for large fields could have been real, although it could arise for stochastic reasons, large fields being more likely to hold birds distributed at random than small fields simply because they cover a larger area. However, there are good reasons for assuming that large fields are positively selected compared with small ones, as a similar avoidance of small, enclosed, fields was found by Gillings & Fuller (2001) and Robinson (1997), who presented evidence that avoidance of field boundaries was likely to be a precaution against predation. Whitehead, Wright & Cotton (1995) found that starlings *Sturnus vulgaris* did not select larger fields but did avoid vertical field boundaries, again probably as a way of minimizing predation risk. The finding of Chamberlain, Wilson & Fuller (1999) that skylark densities in winter did not differ between organic and conventional fields, despite the higher food availability on organic farms (Gardner

& Brown 1998), may have been due to the smaller field sizes of the organic systems studied.

DIET AND FOOD AVAILABILITY

Dietary analysis revealed four main types of winter diet. Birds in cereals and stubbles fed largely on cereal products (either grain or growing cereal leaves), birds in grassland fed mainly on grass leaves, birds in broad-leaved crops and non-cereal stubbles fed mainly on broad-leaved leaves (a mixture of crop and weeds), and birds in bare tillage and non-stubble set-aside had mixed diets not dominated by any one food source. However, in grass and cereal fields there was a strong selection for broad-leaved weed leaves, which are likely to have declined in both habitats due to the use of dicotyledon-specific herbicides (Ewald & Aebischer 1999; Smart *et al*. 2000). The positive selection of broad-leaved weed leaves from cereal and grass crops is likely to be due to the low energetic intake of birds feeding on cereal or grass leaves (Green 1978). Robinson (1997) showed that in north Norfolk, stubble fields held virtually all the spilt cereal grain, very little being present in winter cereals. It seems likely, therefore, that the cereal grain in the diet of birds in winter cereals is germinating grain of the sown crop. As much of this is dressed with chemicals, birds could be ingesting toxic chemicals, although many dressed seeds are coated with agents designed to make them unpalatable to birds and at least some are avoided (McKay *et al*. 1999). Green (1978) also noted birds uprooting and eating germinating grain, and suggested this was a response to a shortage of weeds and weed seeds.

There is no firm evidence that declines in survival due to reduced winter food supplies are responsible for recent population declines of skylarks. However, there is a correlation between population trends and survival rates in other farmland species (Siriwardena, Baillie & Wilson 1999); although declines in survival rates could not be ascribed to increased winter mortality through food shortage, increased predation rates seem unlikely to be responsible (Thomson *et al*. 1998). Peach, Siriwardena & Gregory (1999) showed that declines in over-winter survival could largely explain the decline in British reed bunting *Emberiza schoeniclus* populations and ascribed this to the loss of small weed and grass seeds. Robinson (1997) noted that seed-eating farmland bird species that make use of the abundant food provided during the winter in gardens or other non-farmland habitats suffered significantly lower population declines than those species wintering primarily on farmland. Analysis of ringing recoveries of seed-eating species suggested that late winter is a period of high mortality (Crick, Donald & Greenwood 1991). Whatever demographic change has caused the observed population declines, reversing that process is not necessarily the only way of restoring populations (Green 1995); an increase in winter survival resulting from improved winter conditions might be expected to go some way to compensating for any reductions in productivity.

IMPLICATIONS FOR CONSERVATION

The results of this work suggest a number of management options that would be likely to improve winter conditions for skylarks and other declining farmland species. An increase in the area of cereal stubbles, shown to be the most favoured feeding habitat, would benefit skylarks. Although not documented, the area of cereal stubbles currently available comprises a very small proportion of the area it could potentially occupy; the extent of non-set-aside stubbles on our study sites fell from 7·6% of total arable area in November to 2% in January. An increase in stubble area could be brought about by increasing the area of spring cereals and by encouraging farmers to leave stubbles unploughed for as long as possible after harvest. A return to spring tillage is also likely to improve conditions for skylarks during the breeding season (Chamberlain *et al*. 1999; Chamberlain, Vickery & Gough 2000; Donald & Vickery 2000). Currently no national agri-environment schemes subsidize farmers to plant spring cereals or maintain winter stubbles, although both are options in the Arable Stewardship Scheme currently being piloted in two areas of England. A further way of maintaining cereal stubbles, even in winter tillage systems, is to direct drill winter crops into the stubbles of the previous crop. Much of the current winter stubble area in Britain exists through the set-aside scheme. Maintaining this scheme and encouraging farmers to leave their set-aside in the form of naturally regenerating stubbles is likely to be of considerable importance in the future conservation of this and other declining farmland species (Henderson *et al*. 2000). The possible withdrawal of the set-aside scheme being considered under the current round of changes to the Common Agricultural Policy (CAP) would lead to a massive reduction in stubble area.

The results of this study suggest that there are several ways of maximizing the benefits of cereal stubbles to skylarks. Stubbles provided in large, open, blocks away from tall field boundaries are far more likely to be used than those provided in small blocks. Furthermore, barley stubbles are more likely to be occupied than wheat stubbles, particularly in fields smaller than 10 ha.

Sugar beet stubbles were found to hold particularly high densities of skylarks. Given the long harvesting period of this crop (September to February), this could provide food throughout the winter in the large areas of eastern Britain where this crop is grown. However, in most cases, harvesting is followed quickly by ploughing. Postponing the ploughing in of beet stubbles could increase the availability of an important food resource.

In both agricultural grassland and winter cereals, broad-leaved weed leaves were strongly selected food items, making up a far higher proportion of dietary intake than their availability in the field. Measures taken to increase the availability of broad-leaved weeds in grass and cereals would therefore have a positive effect on birds in these habitats. Such measures include the use of mechanical rather than chemical weed control and the use of scarifying techniques after harvest to encourage the germination of weed seeds in autumn. The availability of broad-leaved weeds has declined since the introduction of dicotyledon-specific herbicides. Postponing the application of herbicides until late winter would increase the availability of broad-leaved weeds to wintering birds without reducing subsequent yields. The low proportion of the diet made up by broad-leaved weed seeds could be the result of greatly reduced soil seed banks. These could be re-established by minimizing pesticide usage through integrated pest control methods.

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