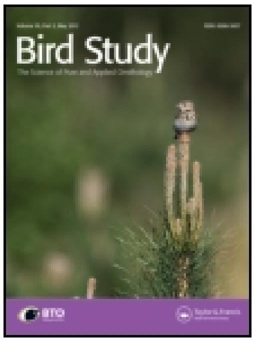

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Habitat selection by Skylarks *Alauda arvensis* wintering in Britain in 1997/98

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The results of a national survey of wintering Skylarks Alauda arvensis *undertaken by the British Trust for Ornithology (BTO) between November 1997 and February 1998 are reported here. Over three visits, volunteers counted Skylarks and mapped habitats in 541 1-km squares selected from the Skylark's winter range based on BTO* Winter Atlas *data and a stratified random sampling approach. Four landscape strata were defined from the Institute of Terrestrial Ecology landscape classification: arable, pastoral, marginal upland and saltmarsh. The survey counts underestimated Skylark abundance, but were good measures of relative abundance across habitat types. The two best predictors of Skylark presence–absence at the landscape scale were the availability of coastal and farmland habitats. Squares with saltmarsh had the highest densities and occupancy (80% of squares). At the patch scale crop stubbles, especially weedy cereal stubbles, were used significantly more than expected by chance. Oilseed rape was positively selected whereas cereal crops were used in proportion to availability and grazed grass was avoided. Skylarks avoided fields smaller than 2.5 ha and selected fields larger than 7.5 ha. We estimate that in midwinter there may be less than 1–2 ha of weedy cereal stubble per 1-km square. We recommend the retention of over-winter stubbles for the conservation of Skylarks and other farmland birds, and research on stubble management and effects on grain availability and arable weed regeneration on Skylark use.*

Recent ecological studies have attempted to identify causes of declines of farmland birds in Britain and elsewhere (Chamberlain *et al*. 2000, Fuller 2000). Numbers of breeding Skylarks *Alauda arvensis* declined by 58% in lowland British farmland habitats between 1975 and 1994 (Chamberlain & Crick 1999) but the species remains ubiquitous as a UK breeding species (Gibbons *et al*. 1993). Although the main declines occurred in the mid- to late 1970s, the species has continued to decline in recent years (Fuller 2000). Nesting success (per breeding attempt) has increased since the 1960s, indicating that the population decline is likely to have been caused either by a decrease in the number of annual nesting attempts or an increase in mortality, or a combination of both (Chamberlain & Crick 1999, Siriwardena *et al*. 2000). Changes in farm cropping have limited the number of broods Skylarks have within a season (Wilson *et al*. 1997), but one study has also demonstrated that over-winter survival of adult Skylarks was lowest during the early 1980s when the decline was greatest (Wolfenden & Peach 2001).

Most studies of Skylark ecology have focussed on the breeding season despite the gap in knowledge of requirements during the winter period for this and several other Biodiversity Action Plan species (Anon 1995a, 1995b, 1998). Farmland is the main habitat of Skylarks in winter (Lack 1986, Gillings 2001), although the importance of British farmland in

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a European context is difficult to assess. Some authors suggest that continental immigrants winter in Britain (Green in Lack 1986) whereas others find no evidence for significant wintering (Spaepen 1995), although the power to detect movements of Skylarks into Britain may be small with existing ringing data (Gillings 2001). Nonetheless, the importance of an understanding of winter habitat use is essential when designing appropriate strategies of farmland management for conserving Skylarks.

We report the results of an extensive survey of wintering Skylarks carried out in 1997/98 in lowland Britain. We set out to quantify the availability and use of habitat by Skylarks across lowland Britain and to complement intensive winter studies carried out on individual farms (e.g. Wilson *et al.* 1996, Buckingham *et al.* 1999, Robinson & Sutherland 1999, Donald *et al*. 2001).

METHODS

Selection of survey squares

The survey took place between November 1997 and February 1998. The basic sampling units were 1 km × 1 km squares (termed '1-km squares') of the Ordnance Survey national grid which were selected using a stratified random sampling approach from within the Skylark's winter range. Here winter range was defined as all 10-km squares where the 90th percentile of repeated *Winter Atlas* counts exceeded zero (64.3% of 2825 10-km squares in Britain; after Kirby & Lack 1993). Square selection was further refined by removing all 1-km squares where 40% or more of the square was attributed to the 'urban/industrial' land cover component of the Institute of Terrestrial Ecology's (ITE) *Land Cover Map of Great Britain* (Fuller & Parsell 1990). This removed densely built-up areas as being unsuitable for Sky-larks.

The remaining 1-km squares were classified using four ITE landscape types: arable, pastoral, marginal upland and upland (Bunce *et al*. 1996). Most upland squares had already been removed on the basis of being outside the Skylark's winter range. The remaining upland squares were removed because they supported extremely few Skylarks (Gillings in press) and because they were unlikely to be surveyed by volunteers in winter due to altitude, inaccessibility and severe weather.

Saltmarsh is a favoured habitat of Skylarks in winter (Brown & Atkinson 1996) and may support significant numbers. However, because of its restricted distribution, few saltmarsh squares were likely to be selected by simple random sampling. Squares were redesignated for the purposes of this survey as 'landscape type = Saltmarsh' if 20% or more of the square was classified as 'saltmarsh/seaweed' in the ITE *Land Cover Map of Great Britain* (Fuller & Parsell 1990). Using this definition the distribution of 'Saltmarsh squares' broadly matched the distribution of saltmarsh given in Davidson *et al*. (1991). Based on the results of a pilot survey,[a] 1000 1-km squares were selected in four strata: 685 arable, 91 pastoral, 31 marginal upland and 193 saltmarsh.

The 1997 BTO survey of breeding Skylarks randomly selected 1000 1-km squares (Browne *et al*. 2000). Those squares that also satisfied the constraints of the winter square selection procedure were selected to achieve coverage in both seasons and to reduce preparation time for volunteers (e.g. when arranging access to private land). Accordingly, 421 squares from the summer survey were appropriately divided between the four strata for the winter survey plus 579 'new' random squares were selected to arrive at the 1000 sample.

Field methods

Fieldwork was undertaken by 469 BTO volunteer observers. Volunteers were asked to make three visits, evenly spaced between mid-November 1997 and mid-February 1998. Ideally, visits were made on calm dry days with good visibility, avoiding the first and last hours of daylight when birds may be less active and/or less detectable.

Bird and habitat recording were undertaken on a patch by patch basis within each 1-km square. A patch was defined as any area (>0.3 ha) of a single habitat type. In the majority of cases this meant a field, but in non-agricultural areas patches included, for example, woods, estuaries, moorland or saltmarsh. On each visit, volunteers surveyed as many patches as possible, approaching all parts of each patch to within 150 m. This distance was chosen as a suitable compromise between minimum flushing distances and the time taken to survey the whole square. However, based on the low densities recorded and the reported time taken to cover a square, probably few volunteers adhered to this rule (see Results and Discussion). Based on existing knowledge, patches of enclosed habitat that were clearly unsuitable for Skylarks, such as woodland or residential areas (Cramp 1988), were not visited. Observers recorded the number of Skylarks seen in each patch on each visit; birds flying high overhead and not clearly associated with a patch were ignored. Instances where Skylarks were flushed from one patch to another were noted to reduce the risk of double counting. Patches that were not visited or received incomplete coverage were identified by the observer.

Observers classified the habitat of each patch using codes based on Crick (1992) with new codes specific to winter habitats (Appendix 1). Set-aside was recorded as a stubble or grassland depending upon what it most resembled. To aid the identification of crops and stubbles, illustrated notes were provided to all volunteers and they were advised to consult the farmer on crop identity when arranging access permission. Weedy stubbles were defined as fields with arable weeds and some crop volunteers (germinating unharvested seeds from the previous crop) whereas clean stubbles lacked green cover, possibly owing to post-harvest herbicide applications to eradicate problematic weeds such as Black Grass *Alopecurus myosuroides*.

Analyses

Habitats

For subsequent analyses, the agricultural habitat codes were combined to give 14 crop types or cultivation stages (referred to hereafter as 'agricultural habitats'): cereal crop (barley, wheat, other cereals), oilseed rape crop, root crop (sugar beet, fodder roots, potatoes, carrots), other crops (all other crops listed in Appendix 1), clean cereal stubble, weedy cereal stubble, unspecified cereal stubble, oilseed rape stubble, root crop stubble, other crop stubble, bare till (ploughed, harrowed or drilled soil prior to germination), grazed grass, ungrazed grass, unspecified agricultural grass.

Habitat extent

There are currently no quantitative estimates of agricultural habitats in winter, especially cereal stubbles. Annual statistics of crop extent in June cannot be extrapolated to winter to give, for example, the area of stubble, due to the rapid turnover of habitat during the winter months. Similarly the Government's December census gives crop areas but no information on stubbles. From the area of each habitat type within each square we produced estimates of the total area in lowland Britain of the 14 agricultural habitats using a bootstrapping method.[b]

Habitat selection at two spatial scales

Habitat selection was analysed at the landscape and patch scales.

Habitat selection was examined at the landscape scale by analysing the general habitat composition of occupied and unoccupied 1-km squares. In eight separate logistic regression analyses, the presence–absence of Skylarks in each square was related to the area (ha) of one of eight broad habitat types (based on level 1 habitat codes, see Appendix). A term for visit (early, mid- or late) was included in the model since data from all three visits were entered and occupancy potentially differed between visits. After ascertaining what determined square occupancy, we planned to investigate what determined Skylark abundance in occupied squares using Poisson regression for count data (but see Results).

Habitat selection was examined at the patch scale within occupied squares using the resampling approach of Wilson *et al*. (1996) to determine whether habitat use differed from what one would expect given the availability of a habitat.[c] This was performed using data from each visit separately to detect differences in habitat selection through the winter. Habitat use was assessed for 15 habitat types; these being the 14 previously defined agricultural habitat types plus 'Other habitats' – a catch-all class to include regularly occupied non-agricultural habitats (e.g. saltmarsh), rarely occupied habitats (e.g. semi-natural grassland) and some habitats that were never used (e.g. woodland).

Field size selection

Field size was investigated to test if Skylarks show preference for large over small fields through anti-predator responses (Robinson & Sutherland 1999). However an increase in field occupancy might be expected with increasing field size as a flock landing at random is more likely to occur in a large than in a small field. We investigated field size selection using a randomization procedure that produced the expected occupancy rate for fields of different sizes with which we could compare the observed rates of occupancy.[d] To aid interpretation, we tested whether field size differed between crop types using analysis of variance (ANOVA) on logged field areas, including only those fields falling entirely within each square. This analysis may suffer from non-independence due to spatial autocorrelation of field size within squares. To test for independence we performed 100 tests, where each ANOVA used a subsample of the data comprised of one field of each habitat type selected at random from within each square. We then looked at the proportion of these tests that were significant at the 5% level.

All statistics were undertaken using SAS/STAT version 6.12 (SAS Institute 1996).

RESULTS

Coverage

In all, 541 of the 1000 squares selected for coverage were surveyed (Table 1, Fig. 1). The return rate of random squares from each stratum (Table 1) did not differ significantly from the initial stratification ($\chi^2_3 = 2.96$, $P > 0.3$) indicating that there was no bias in coverage towards certain strata. Of the 541 squares surveyed, 474 were visited three times, 48 twice and 19 once. Dates of the three visits were well spaced through the winter (median and quartiles): first visit = 6 December (23 November to 15 December), second visit = 14 January (4

Figure 1. Distribution of 10-km squares containing one or more 1-km squares surveyed for Skylarks during winter 1997/98.

Table 1. Numbers of 1-km squares selected, surveyed and occupied by Skylarks in each of four landscape strata in winter 1997/98.

Stratum	Number of 1-km squares selected[a]	Number of 1-km squares surveyed[a]	Number of 1-km squares occupied[b]
Arable	685 (69)	382 (71)	240 (63)
Marginal upland	31 (3)	14 (3)	2 (14)
Pastoral	91 (9)	45 (8)	22 (49)
Saltmarsh	193 (19)	100 (19)	80 (80)
Total	1000	541	344 (64)

[a]Figures in parentheses are the percentage composition by stratum of the column total.
[b]Figures in parentheses are percentage occupancy by Skylarks, expressed as the percentage of squares surveyed that were occupied on at least one visit.

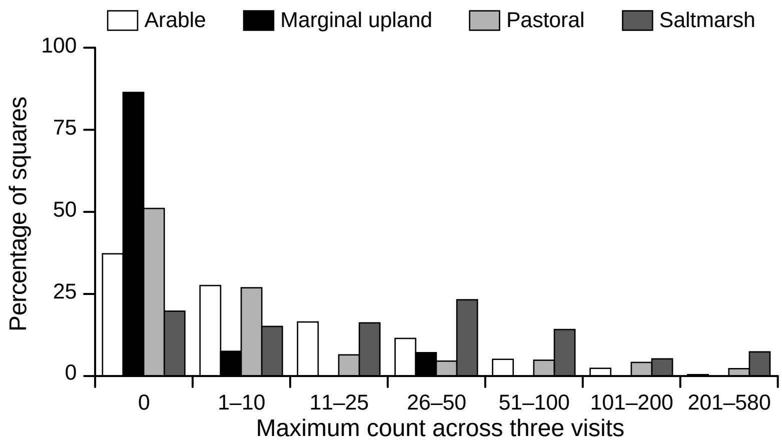

Figure 2. Frequency distribution of Skylark abundance (maximum count across three visits to each square) in a stratified random sample of 541 1-km squares.

January to 24 January) and third visit = 13 February (4 February to 17 February). Hereafter, visit is used as an approximation to season: first visit = 'early winter' (late November to mid-December based on quartiles), second visit = 'midwinter' (January) and third visit = 'late winter' (February). Note that due to a period of wet and windy weather in early 1998, some third visits were delayed to the end of February 1998. Also poor winter weather and short daylength meant that a small number of visits were undertaken in suboptimal weather conditions.

Skylark abundance

Of the 541 random squares surveyed, 64% were occupied by Skylarks on one or more visits (Table 1). Skylark presence in squares differed significantly between strata ($\chi^2_3 = 48.2$, $P < 0.01$) with 80% of saltmarsh squares occupied compared to only 14% of marginal upland squares (Table 1). The number of Skylarks in 1-km squares was heavily skewed (Fig. 2), and the median count in most strata was zero, thus Table 2 presents the percentage of squares occupied plus the median count and range in occupied squares. The median count was highest for marginal upland squares but these also had the lowest rate of occupancy (only 1–2 squares, Table 2). The median and range of densities were similar in arable and pastoral squares (Table 2). An ANOVA of logged counts confirmed that densities differed significantly between strata (ratio arable:marginal upland: pastoral:saltmarsh = 33:4:20:100; $F_{3,1619} = 38.7$, $P < 0.001$) but not visits ($F_{2,1620} = 0.4$, $P = 0.7$) indicating no temporal change in abundance.

Table 2. Skylark occupancy and densities (Skylarks per 1-km square) summarized by strata and different periods of the winter.

				Density (Skylarks per 1-km square)	
Stratum	Period	*N*	%	Median	Range
Arable	Early	382	45%	11	1–320
	Mid	371	44%	10	1–214
	Late	359	54%	11	1–126
Marginal upland	Early	14	7%	28	–
	Mid	14	0%	–	–
	Late	13	15%	24	5–43
Pastoral	Early	45	29%	11	1–232
	Mid	42	38%	5	1–120
	Late	35	49%	10	1–102
Saltmarsh	Early	98	70%	20	1–421
	Mid	99	68%	21	1–580
	Late	82	72%	20	1–230

N, number of squares surveyed; %, percentage of surveyed squares occupied by Skylarks. Median and range refer to the number of Skylarks recorded in occupied squares only. Note that none of the 14 marginal upland squares surveyed in midwinter were occupied so no density summary is given.

Habitat extent

Table 3 gives estimates of the area of the 14 agricultural habitats within the Skylark's winter range in 1997/98. For each habitat type, figures are only presented for the midwinter period since confidence limits overlapped across all three periods. Grazed grass was the most widespread habitat, covering 4.1 million hectares and 37% of farmland. Cereal crops accounted for 24% and ungrazed grass a further 14% of farmland. Cereal stubbles covered 5.7% of farmland (629 000 ha), of which 46% was weedy (Table 3). When broken down by strata, cereal stubbles were concentrated within the arable stratum (47%), the remainder being divided almost equally between pastoral and marginal upland strata. Fifty eight percent of weedy cereal stubbles were within the arable stratum.

Habitat selection at different scales

At the landscape scale, certain habitat types were associated with the presence of Skylarks and others with the absence of Skylarks (Table 4). Squares with a large amount of coastal habitat or farmland tended to be occupied whereas squares with a large amount of woodland tended to be unoccupied, either because woodland is avoided by Skylarks or because the presence of woodland precludes the presence of a more preferred habitat within the square (Table 4). These results should be interpreted

Table 3. Estimates of the area of 14 agricultural habitat types during midwinter for the Skylark's winter range (broadly lowland Britain). Figures are only given for the midwinter period since confidence limits for all three periods overlapped.

Habitat	Area (ha)	95% Confidence Limits
Cereal crop	2700 000	2200 000–3000 000
Oilseed rape crop	440 000	300 000–560 000
Root crop	120 000	81 000–160 000
Other crop	200 000	130 000–270 000
Clean cereal stubble	270 000	110 000–520 000
Weedy cereal stubble	290 000	190 000–420 000
Unspecified cereal stubble	69 000	43 000–110 000
Oilseed rape stubble	21 000	4 500–45 000
Root crop stubble	22 000	11 000–37 000
Other crop stubble	130 000	46 000–170 000
Bare till	850 000	590 000–1200 000
Grazed grass	4100 000	3300 000–5100 000
Ungrazed grass	1500 000	1200 000–2000 000
Unspecified agricultural grass	350 000	840 000–690 000

Table 4. Results of eight logistic regression analyses relating Skylark presence–absence in 1-km squares to eight broad habitat variables. Each regression modelled the area (ha) of one broad habitat type within 1-km squares. Data from all three visits were combined and models included a visit term. Level 1 code indicates which habitats were combined in each broad habitat type (see Appendix 1 for definitions of the codes); Parameter is the parameter estimating the relationship between habitat area and probability of Skylark occurrence on the logit scale; $P(100)$ is the probability of Skylarks occurring in a 1-km square consisting wholly of one habitat type.

Level 1 code	Broad habitat type	Parameter ± se	$P(100)$
D	Heath & bog	–0.028 ± 0.010	0.06
G	Water bodies	–0.006 ± 0.027	0.36
M, N, P, Q	Farmland	0.006 ± 0.002	0.64
R	Coastal	0.017 ± 0.002	0.84
C	Semi-natural grassland	–0.004 ± 0.005	0.39
A, B	Wood and scrub	–0.033 ± 0.005	0.04
F	Human sites	–0.021 ± 0.004	0.11
I	Inland rock	–0.024 ± 0.026	0.09

with caution as demonstrated by the high predicted occupancy of squares consisting solely of open water (Table 4). This apparent preference for water is more likely the result of selection for a habitat that tends to occur in squares containing open water (e.g. saltmarsh). Attempts to model Skylark abundance in occupied squares using Poisson regression failed due to poor model fit caused by severe over-dispersion arising from the aggregation of birds into flocks.

At the patch scale, agricultural habitats accounted for 60% of Skylarks (n = 20 289 birds), coastal habitats a further 35% and the remaining 5% comprised non-agricultural grassland types (e.g. ungrazed dry grass, playing fields, airfields and golf courses). Within coastal patches, most Skylarks were in the occasionally inundated mid-saltmarsh (67%). Three-quarters of Skylarks in agricultural patches were on stubbles and crops. Cereals and oilseed rape accounted for most Skylarks on crops, with most in patches with vegetation more than 5cm tall. Cereal stubbles accounted for most stubble-dwelling Skylarks, especially weedy stubble fields (Table 5). On pastures, most Skylarks were recorded on ungrazed grass (Table 5).

Taking habitat availability into account using the randomization procedure demonstrated that cereal stubble was the major habitat used more than expected by chance throughout the winter. Weedy stubble fields were used more than clean cereal stubble fields (Figure 3). Stubbles of oilseed rape, root crops and other crops were rare (Table 3), but were used more than expected during at least one third of the winter (Fig. 3). Oilseed rape crops were used in proportion to their availability in early winter but were positively selected in mid- and late winter; other crops were mostly used in proportion to their availability. Use of cereal crops was in proportion to their availability and use kept pace as more crops were sown through the winter.

Table 5. Total number of Skylarks recorded in (a) agricultural grass, (b) crops and (c) stubbles during winter. Figures are summed across all squares and all visits and are presented for the major grass, crop and stubble types. Note that no account has been taken of habitat availability in the production of these figures.

a

Agricultural grass	Ungrazed	Recently grazed	Currently grazed	Unspecified
Improved	330	249	119	9
Unimproved	288	179	140	0
Temporary	200	3	57	180
Unspecified	125	21	24	25

b

Crops	Less than 5cm tall	More than 5cm tall	Grazed
Wheat	647	1413	0
Barley	108	207	0
Unspecified cereal	179	130	0
Oilseed rape	230	972	18

c

Stubbles	Clean	Weedy	Grazed	Undersown
Wheat	576	1035	111	74
Barley	254	1472	30	136
Unspecified cereal	110	599	41	64
Oilseed rape	17	41	36	26
Maize/sweetcorn	8	42	0	0
Sugar beet	19	14	6	0
Potato	0	228	0	0

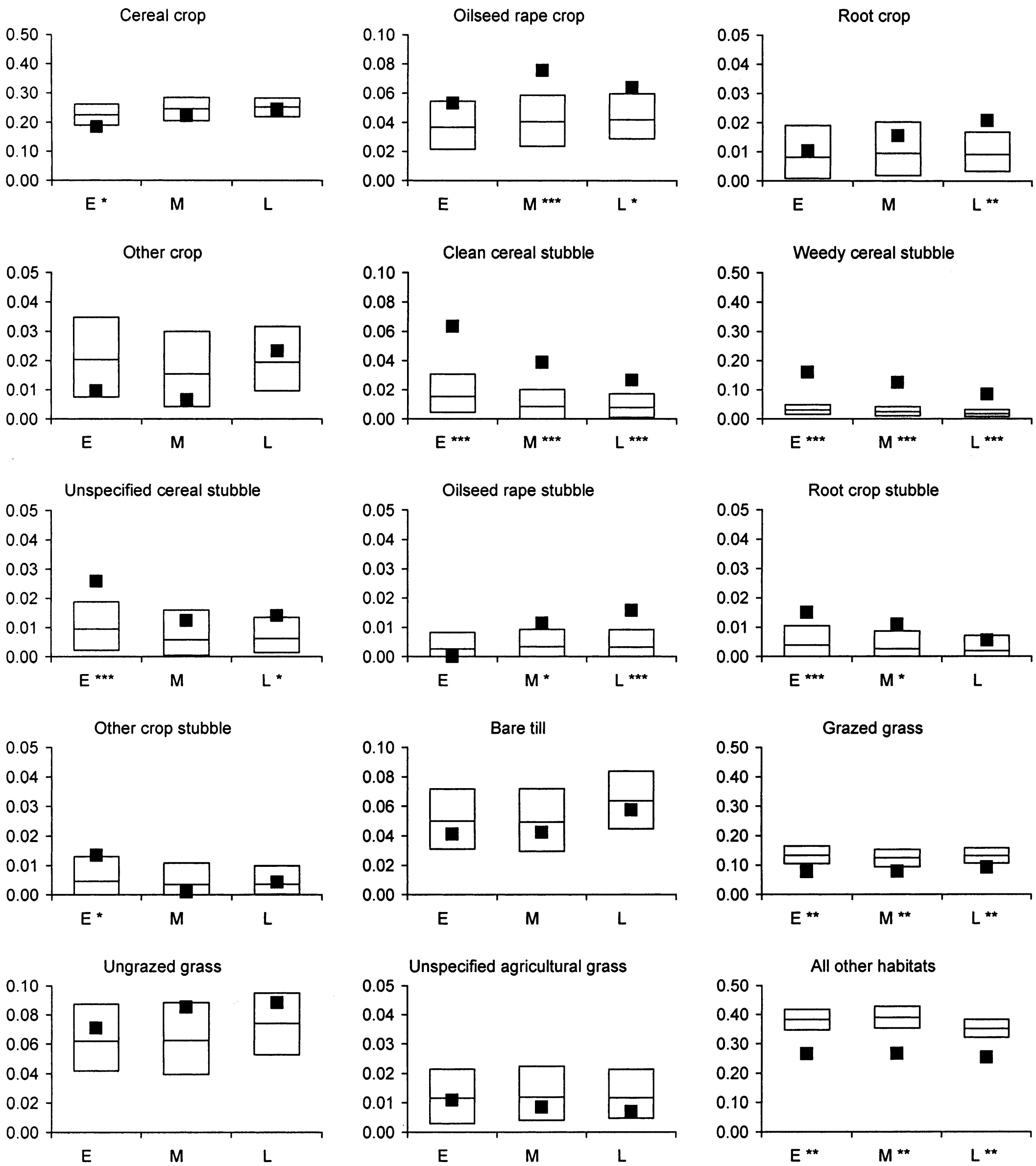

Figure 3. Observed (■) and expected (▭) use of habitats by Skylarks in winter. For each habitat type three sets of squares and bars are given indicating observed and expected use from early winter (E), midwinter (M) and late winter (L) visits. Squares falling within bars indicate use of a habitat type in proportion to its availability, i.e. no selection; squares falling above or below bars indicate significant positive habitat selection or habitat avoidance respectively, where significance is denoted as follows: $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Note that for clarity, three different *y*-axis scales are used, representing 5%, 10% and 50% of habitat use.

The randomization procedure was repeated with more specific habitat categories but few appreciable differences were detected. No differences were detected in the use of wheat versus barley crops or wheat versus barley stubbles. Cereal crops were used in proportion to availability irrespective of their height and improved grass was marginally avoided whereas unimproved grass was used in proportion to availability.

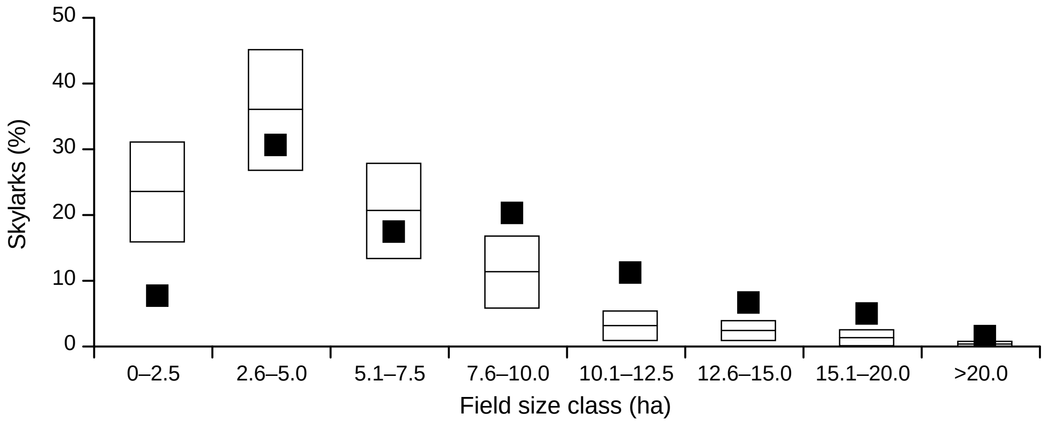

Figure 4. Observed (■) and expected (▭) use of fields of varying size by Skylarks in winter. Squares falling within bars indicate use of a field size category in proportion to its availability, i.e. no selection; squares falling above or below bars indicate significant (P < 0.05) positive field size selection or field size avoidance respectively.

Field size

Skylark flocks did not settle at random with respect to field size, but showed positive selection of large fields (Fig. 4). Field size differed between crop types (ANOVA, $F_{13,3516}$ = 613.4, P < 0.0001)[e] meaning that this relationship was potentially influenced by positive selection of a habitat type usually found in large fields but this seems unlikely based on mean field sizes for various crop types. The largest fields were oilseed rape crops (7.0 ± 0.5 ha, mean ± 1 se) and cereal crops (6.6 ± 0.2 ha) which were occasionally selected and used in proportion to availability respectively. In contrast, positively selected weedy and clean cereal stubble fields were only 5.6 ± 0.5 ha and 5.4 ± 0.4 ha respectively. The smallest fields were grass fields (3.1 ± 0.1 ha) which were used in proportion to availability or avoided. It should be noted that the restriction of using only fields falling wholly within the 1-km square meant that the frequency distribution of field sizes was truncated, with the largest field being only 46.8 ha.

DISCUSSION

Skylark detectability

Tucker (1992) suggested that extensive field surveys of wintering farmland birds should exclude species smaller than thrushes (*Turdidae*) on detectability grounds. The method used in this survey of walking across habitat patches to within 150 m of all points partially alleviated this problem because Skylarks were flushed. However, this method did not record all Skylarks because they have flushing distances smaller than 150 m and because it was not always possible to traverse fields (e.g. because of potential crop damage). This is a problem only if detectability differed between habitat types, thus confounding comparisons of habitat use. To test this, data from this survey were compared with Skylark counts collected on 18 farms for an intensive study undertaken by the Royal Society for the Protection of Birds (RSPB). In the latter study, fields were thoroughly searched to ensure that all Skylarks were recorded to give values approaching absolute abundance (P.F. Donald pers. comm.). This more intensive approach resulted in a higher proportion of fields being recorded as occupied by Skylarks and larger mean flock sizes in the RSPB study than reported here. Importantly, these differences were consistent across all habitats, indicating that the Skylark counts from this study were unbiased estimates of relative abundance and could be used to draw valid comparisons between habitats.

Habitat selection – landscape scale

Skylarks selected coastal habitats and farmland in winter. Although coastal squares had the highest rates of occupancy and contained high densities of Skylarks, the saltmarsh with which they were associated only accounts for an estimated 44 370 ha of Britain (Davidson *et al.* 1991) and so can support only a fraction of the national winter population. Most concerns over the Skylark's status relate to the farmland environment but saltmarsh is also under considerable pressure, both through changing management (e.g. Norris *et al*. 1998) and potential sea-level rise (Brown & Atkinson 1996).

Farmland was the next most important habitat and this is where the majority of Skylarks occur in winter (Green in Lack 1986, Gillings 2001). Arable and pastoral landscapes held similar median densities of Skylarks, although the rate of occupancy was higher for arable 1-km squares compared to pastoral 1-km squares. The *Winter Atlas* maps showed that the greatest numbers of Skylarks were found in lowland mixed and arable farmland (Green in Lack 1986). Marginal upland landscapes were of minor importance for Skylarks and in such landscapes small areas of lowland farmland types are important in determining Skylark occurrence both in the winter (Gillings 2001) and also in summer (Atkinson & Robinson 2000).

Habitat selection – patch scale

At the patch scale most Skylarks selected saltmarshes and agricultural fields (see below) with fewer in a variety of open grassy habitats including downland, grazing marshes, parks, playing fields and golf courses. On the coast, more Skylarks occupied the occasionally inundated mid-saltmarsh than either high or low saltmarsh although this takes no account of relative abundance of these habitat types.

Patch scale habitat selection on farmland largely agreed with previous intensive studies. Cereal stubble fields, especially those with abundant weeds, were the most positively selected farmland habitat type as found by Wilson *et al.* (1996), Chaney *et al.* (1997), Wakeham-Dawson & Aebischer (1998), Buckingham *et al*. (1999), Robinson & Sutherland (1999), and Donald *et al*. (2001). No difference was found between barley and wheat stubbles despite the fact that barley stubbles support greater cover of crop volunteers and broad-leaved weeds (Robinson & Norris 2001). Furthermore, two studies found greater selection of barley stubbles than wheat stubbles (Buckingham *et al*. 1999, Donald *et al*. 2001).

In this study, cereal crops were used in proportion to availability and previous studies have ranged from reporting limited selection (Donald *et al*. 2001) to avoidance (Wilson *et al*. 1996, Buckingham *et al*. 1999, Robinson & Sutherland 1999). Contrary to Wilson *et al*. (1996), this study found positive selection of oilseed rape crops and stubbles and root crop stubbles. No effect of crop height was found in agreement with Robinson (1997). In pasture, Skylarks utilized ungrazed grass in proportion to availability but they significantly avoided grazed grassland as reported by Wilson *et al*. (1996) and Wakeham-Dawson & Aebischer (1998).

CONCLUSIONS

The patterns of habitat use by Skylarks can be explained by our current knowledge of their diet and foraging ecology. In winter, Skylarks have a broad diet consisting of a variety of small seeds, fresh vegetation and germinating seedlings. However, when feeding in cereal crops they consume mostly cereal leaves, whereas on stubble fields they consume mostly seeds, especially grain (Green 1978, Robinson 1997, Donald *et al.* 2001). This difference presumably reflects the fact that spilt cereal grain and weed seeds occur at lower densities in germinated cereal crops compared with stubble fields (Robinson & Sutherland 1999). Although food is abundant in cereal fields in the form of cereal leaves, these are of lower energetic content than seeds (Green 1978) and cereal fields may present suboptimal feeding conditions (Robinson 2001).

Skylark use of ungrazed grassland may be related to food availability or predation. Perkins *et al.* (2000) showed that Skylarks were most abundant in pastures with abundant seeding grasses and Wakeham-Dawson & Aebischer (1998) found that Skylark density was positively correlated with the number of dicotyledon seeds. Heavy grazing decreases the abundance of fruiting plants so that seed availability is lowered (Vickery *et al*. 2001). Also, heavily grazed grasslands are typically those that have been intensively managed and improved and consequently have reduced botanical diversity and seed resources (Donald *et al*. 2001). Alternatively, shorter swards may be avoided because they provide little cover from predators (Wakeham-Dawson & Aebischer 1998). Both Perkins *et al.*

(2000) and Wakeham-Dawson & Aebischer (1998) suggest that low intensity grazing by cattle may be beneficial because it promotes tall open swards with bare ground patches ideal for foraging Skylarks.

Although stubbles are clearly important for Skylarks and several other farmland birds (Evans 1997), several aspects of their management may affect their suitability as feeding areas. Post-harvest herbicide applications can prevent regeneration of weeds and crop volunteers, preventing the development of weedy stubble fields. If waste straw is chopped and spread over the field rather than baled, seed availability may be reduced because the straw forms a dense mat suppressing broad-leaved weeds and trapping moisture that promotes germination of spilt grain (P.N. Watts pers. comm.). The location of stubble blocks may also be important. Most stubble is present as a precursor to set-aside which is often situated as marginal strips along field edges. Given that field size is important in determining Skylark occupancy (this study and Donald *et al*. 2001), and that Skylarks actively avoid hedges (Robinson & Sutherland 1999), small or narrow stubble patches alongside hedges may not benefit Skylarks (although they may be of greater benefit for other species such as Yellowhammer *Emberiza citrinella*). Future work could investigate mechanisms such as those by which stubble fields may be made more attractive to Skylarks through measures that are practical and inexpensive for farmers to implement. A major new area of research will be the effects that genetically modified crops and their new management techniques have on weeds, seed abundance and the distribution of species such as the Skylark (e.g. Watkinson *et al.* 2000).

One consequence of the switch from spring sowing to autumn sowing of cereals (Chamberlain *et al.* 2000) has been to decrease the availability of over-wintering stubbles. We estimate that in January some 630 000 ha of cereal stubble were available to Skylarks through a combination of fields intended for set-aside or spring crops. By the same method we estimated 2.7 million hectares of autumn-sown cereal which compares favourably with Government June agricultural census data (approximately 3 million hectares) giving confidence in the method. These figures suggest that of the stubbles that are created immediately post-harvest, 23% remain to midwinter, equating to *c*. 3 ha of cereal stubble per 1-km square in lowland Britain (3.7 ha per 1 km in arable squares). Since only 46% of stubbles were weedy, the average area of ideal foraging conditions is further reduced to 1–2 ha per 1-km square. Furthermore, since Skylarks avoid fields smaller than 2.5 ha and select those over 7.5 ha, much of this may be effectively unavailable to foraging Skylarks. Exactly how these stubble areas relate to the requirements of a typical Skylark flock is unknown. Although Skylarks have a wide diet, stubble fields containing spilt cereal grain and weed seeds must provide the best foraging conditions. An increase in the availability of weedy stubble fields so that Skylarks are not forced to feed nomadically in cereal crops must be beneficial for winter survival and possibly help to offset declining annual productivity.

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ENDNOTES

a. In winter 1996/97, a pilot survey was conducted in which 20 randomly selected squares from each stratum were surveyed for Skylarks. Formulae from Greenwood (1996, pp.101–103) were applied to these counts to produce an optimal allocation of squares to the strata in a way that maximized precision of population estimates (which subsequently were not calculated because it was considered that the survey counts were underestimates; see Discussion).

b. Area estimates were calculated with 95% confidence limits in a way analogous to calculating population estimates using a bootstrapping method of 1000 resamples (Manly 1991). The area estimate was derived by multiplying the mean area of a habitat per 1-km square within a stratum of the winter range and the number of squares within that stratum, and then summing across strata. Each of the 1000 resamples was calculated by randomly resampling (with replacement) observed habitat areas per square within strata. Mean areas, stratum estimates and a total estimate were produced and the lower and upper 95% confidence limits were taken as the 25th and 975th values of the ranked 1000 estimates.

c. The randomization method determines the proportional use of each habitat type and compares this with the use expected by random settlement. This 'no selection' null model assumes that flocks of Skylarks land randomly within each square so that habitat use is equal to habitat availability. Each count of a field was randomly reassigned (with replacement) to a habitat type with a probability equal to the proportional availability of each habitat type within the same square. One thousand resamples for the entire data set were made to produce 1000 independent estimates of habitat use under the null model. The mean of the 500th and 501st ranked values was used as the expected use under the null model and the 25th and 975th values were taken as 95% confidence limits. The null hypothesis of no habitat selection is rejected if the observed use falls outside the 95% confidence limits. Following Wilson *et al*. (1996), statistical significance was calculated as follows: the two-tailed probability of observing a certain number of birds on a patch is two times the proportion of resampled values that were equal to or more extreme than the observed value.

d. The randomized test of field size selection used all squares containing at least one flock of Skylarks and only patches classified as farmland fields (level 1 codes M, N, P and Q) and falling wholly within these squares. These fields were divided into eight size classes: 0–2.5 ha; 2.6–5.0 ha; 5.1–7.5 ha; 7.6–10.0 ha; 10.1–12.5 ha; 12.6–15.0 ha; 15.1–20.0 ha; more than 20.0 ha. For each size class, observed use was defined as the proportion of the total Skylark count found in fields of the given size class. Expected use was calculated as follows. In each square, each flock was reassigned to a field at random with a probability equal to the proportional area of each field within the square. The proportion of Skylarks falling in each size class was calculated. This procedure was repeated 1000 times to produce 1000 independent estimates of the expected field size selection under the null hypothesis of random settlement. For each size class the mean of the 500th and 501st ranked values were used as the expected use and the 25th and 975th values were taken as 95% confidence limits. A field size class was selected more or less than expected by chance if the observed occupancy of that size class fell above or below the 95% confidence limits respectively.

e. This analysis was not confounded by spatial autocorrelation of field sizes within squares because all the 100 ANOVA using only one field of each habitat type drawn at random from each square recorded significant differences in field size across habitats at $P < 0.0001$.

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APPENDIX 1

Habitat coding scheme: three-level habitat classification used for the Wintering Skylark Survey. For non-agricultural habitats, a list of habitats and land uses included within each category is given. For agricultural habitats and land uses, the full coding scheme is reproduced from the fieldworkers' survey instructions. One code is selected from each level to describe the habitat or land use within a patch.

Non-agricultural habitats

Level 1		
Code	Type	Land use
A	Woodland	Deciduous, coniferous and mixed woodland
B	Scrubland	Scrub, coppice, young plantation and young clear-fell
C	Semi-natural grassland/marsh	Downland, grass moor, machair, water meadows, reed swamp
D	Heathland & bogs	Heath, bog, breck
F	Human sites	Industrial, residential, municipal grass, farm building, allotment, golf course
G	Water bodies	Pond, lake, reservoir, river
I	Inland rock	Cliff, scree, limestone pavement, rock outcrop, quarry, mine spoil, cave
J	Miscellaneous	Any other habitats not listed
R	Coastal	Marine/estuarine shore, saltmarsh, sand dune, brackish lagoon, seawall

continued

Appendix 1 continued

Agricultural habitats

Level 1		Level 2		Level 3	
Code	Type	Code	Type	Code	Type
M	Grass	01	Improved	01	Ungrazed
		02	Unimproved	02	Recently grazed, animals absent
		03	Sown (in autumn)	03	Currently cattle grazing
		04	Unknown	04	Currently sheep grazing
				05	Currently horses grazing
				06	Currently other/mixed stock grazing
N	Crops	01	Wheat	01	Crop less than 5cm tall
		02	Barley	02	Crop more than 5cm tall
		03	Unknown/other cereal	03	Straw covering field
		04	Linseed	04	Polythene covering field
		05	Beans		
		06	Oilseed rape		
		07	Unknown/other brassicas		
		08	Maize/sweetcorn		
		09	Sugar beet		
		10	Fodder roots		
		11	Potatoes		
		12	Carrots		
		13	Other vegetables/flowers		
		14	Unknown/other root crops		
		15	Unknown/other crops		
P	Stubbles	01	Wheat stubble	01	Clean stubble
		02	Barley stubble	02	Weedy stubble
		03	Unknown/other cereal stubble	03	Currently grazed
		04	Linseed stubble	04	Undersown
		05	Bean/pea stubble		
		06	Oilseed rape stubble		
		07	Maize/sweetcorn stubble		
		08	Sugar beet stubble		
		09	Potato stubble		
Q	Other	01	Pig farm	01	Plough
		02	Bare earth	02	Harrow
		03	Fallow ground		