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Effects of habitat type and management on the abundance of skylarks in the breeding season

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Summary

1. There is increasing evidence to link major declines in skylark populations in Britain to agricultural intensification. However, whether causal mechanisms identified through localized studies can be generalized to the national scale remains unknown. The abundance of breeding skylarks was determined by surveying singing males in over 600 randomly selected 1-km squares throughout Britain, in which skylarks recorded were assigned to homogeneous habitat patches. A more intensive survey of skylarks was carried out on lowland farmland sites in England. Singing males were assigned to specific crop types, and data on crop height and field boundary features were recorded.
2. Skylark occupancy (presence/absence) and density where birds were present (i.e. omitting zero counts) were analysed in relation to habitat type, habitat diversity and time of year, using generalized linear modelling.
3. Set-aside, moorland and winter cereals had high rates of skylark occupancy at the national scale. Set-aside had consistently high rates of occupancy and high densities across the breeding season at different spatial scales. Apart from set-aside, there was little difference in density between habitats in the early half (March to mid-May) of the breeding season. In the later half of the breeding season (mid-May to July), density declined significantly on winter cereals, which showed significantly lower density than a number of habitats at this time, including spring cereals, legumes and moorland.
4. Within lowland farmland, there were significant effects of crop height on skylark occupancy, with crops of greater than 30 cm in height being occupied at relatively low rates. Winter cereals reached this height significantly earlier in the breeding season than a number of other crops, including spring cereals and legumes.
5. Skylark density increased with increasing habitat diversity across the whole sample of 1-km squares and in lowland 1-km squares in England. However, within the lowland farmland plots in England, skylark density showed a significant decrease with increasing habitat diversity. These conflicting results suggest that crop type rather than habitat diversity *per se* is important.
6. The effects of vegetation height on skylark abundance support the hypothesis that increases in winter cereal, and simultaneous loss of spring cereal, have had an adverse effect on skylark populations by reducing the number of breeding attempts made per year. These results support findings from smaller scale studies showing the generality of these habitat effects at different spatial scales. The extent of the British skylark population associated with agricultural land suggests that sympathetic changes in farming practice are likely to provide the best mechanism for improving the status of this species. The inclusion of options, such as spring cereal or fallow land (an equivalent to set-aside), in agri-environment schemes is likely to benefit skylarks breeding on farmland by providing suitable nesting habitat throughout the breeding season. In addition, reductions in the intensity with which

cereals are managed, such as reduced pesticide and fertilizer input under approaches such as precision farming, and the creation of sparser patches of cereal sward, are also likely to increase the suitability of winter cereals for nesting skylarks.

Key-words: generalized linear models, habitat diversity, set-aside, vegetation height, winter cereals.

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Introduction

The skylark *Alauda arvensis* L. occurs commonly in most open habitats throughout northern Europe (Cramp 1988). Vegetation structure appears to be an important determinant of habitat preference; consequently, skylarks are sensitive to land management practices such as changes in crop type and grazing regime. Skylarks will not breed in particularly tall or dense vegetation, the optimum height range for nesting in arable crops being 20–60 cm (Wilson *et al.* 1997). Seasonal changes in the height of crops appear to cause shifts in nesting habitat during the course of the breeding season (Schläpfer 1988), and consequently skylarks seem to benefit from a mosaic of different crop types (Jenny 1990; Chamberlain & Gregory 1999). Skylarks will avoid areas with a high density of hedgerows and trees (Wilson *et al.* 1997) and intensively grazed areas (Wakeham-Dawson *et al.* 1998). Set-aside, where land is left fallow, is particularly preferred, supporting high breeding densities (Henderson, Cooper & Fuller 1998) and tending to have higher reproductive success than other crops (Poulsen, Sotherton & Aebischer 1998).

Skylark populations have declined in northern Europe over the past three decades (Tucker & Heath 1994; Fuller *et al.* 1995). While there is evidence of declines in a number of habitats in the UK, the farmland population has shown the steepest decline (Chamberlain & Crick 1999). Changes in agricultural management have been identified as the most probable cause (Fuller *et al.* 1995). Sowing regimes have changed, with winter cereals replacing spring-sown cereals as the predominant arable crop during the 1970s (Grigg 1989). The sward structure of winter cereals is too dense for skylarks, particularly late in the breeding season (Wilson *et al.* 1997). Other changes in farm management, including the increase of other unsuitable crops such as oilseed rape, the increased frequency of mowing silage grass, increases in grazing pressure (Fuller & Gough 1999) and a general decrease in habitat diversity within farmland (O'Connor & Shrubbs 1986), may mean that there are fewer suitable alternative habitats. Consequently, breeding may be curtailed relatively early in the breeding season, leading to fewer breeding attempts and reduced reproductive output

per season. A further potential impact of the increase in winter cereals is that cereal stubbles, an important feeding habitat outside the breeding season (Wilson, Taylor & Muirhead 1996), have been greatly reduced since the early 1970s. This may have had particular effects on seed-eating passerines, including the skylark which is largely granivorous in winter. Skylark reproductive success may also have been affected by increases in pesticide use (Campbell *et al.* 1997). However, there is no evidence to suggest that changes in reproductive success per nesting attempt underlie the population decline. Indeed, at a national scale, reproductive success of individual nesting attempts has increased over the past 30 years (Chamberlain & Crick 1999). Therefore, reductions in the number of nesting attempts per breeding season or changes in survival outside the breeding season seem to be the more probable potential mechanisms driving the population change.

Although skylark populations on farmland appear to have undergone the steepest declines, there is also evidence that upland populations are declining (Hancock & Avery 1998). The pattern of decline in this habitat is different from that in farmland and appears to have happened somewhat later (Chamberlain & Crick 1999), implying a different cause. There have been a number of changes in upland habitats that may have affected skylark populations adversely, including increasing grazing pressure (Fuller & Gough 1999), changes in moorland management and afforestation (Hancock & Avery 1998). As upland birds tend to move to lowlands in the winter, there is a possibility that agricultural changes are having consequences for upland populations as well. However, skylarks in uplands remain little studied and relatively little is known about habitat associations within upland landscapes.

Habitat associations of skylarks have previously been described at national (Chamberlain & Gregory 1999) and local (Schläpfer 1988; Jenny 1990; Wilson *et al.* 1997; Poulsen, Sotherton & Aebischer 1998; Wakeham-Dawson *et al.* 1998) scales. The national-scale study analysed skylark density in relation to broad classes of habitat in a large number of randomly selected 1-km squares throughout the UK, where sections of predominant habitat type were classified according to the methods of Crick (1992).

Local-scale intensive studies have considered habitat associations and nesting success in relation to specific crop types, vegetation structure and other management features, but the intensity of these studies necessitated coverage of only a small number of study sites, and the extent to which results can be generalized throughout the UK remains unknown.

In this study, we use two data sets to provide the most detailed and extensive assessment of habitat use by skylarks throughout Britain to date. Most previous studies have focused on lowland farmland. This study gives data that are representative of the whole of Britain, allowing habitat associations on lowland farmland to be placed in a national context. Two separate surveys were carried out. The first, referred to as the extensive survey, was carried out at the level of the 1-km square and was designed to cover a wide range of habitats throughout Britain. Squares were randomly selected within broad-scale landscape types and the data were analysed to assess broad-scale habitat associations, and the generalities of these relationships at national and regional scales. The survey design permitted a more accurate assessment of habitat use than was possible with the data used by Chamberlain & Gregory (1999), because of more precise habitat data collection. The second survey, referred to as the intensive survey, was carried out on a relatively small number of lowland farmland study plots of variable size, and involved collecting more detailed data, both on bird distributions and habitat structure, including crop height and field boundary structure and size. Determination of detailed habitat associations in this survey enabled an assessment of the generalities of habitat relationships determined from previous farm-level studies with relatively small sample size, particularly that of Wilson *et al.* (1997). It is hoped that ultimately the findings of this paper will help to contribute to future conservation strategies for skylarks in Britain over a range of habitats and spatial scales.

Methods

BIRD AND HABITAT SURVEYS

The extensive survey was carried out by volunteer field workers in a randomized stratified sample of 1-km squares in Britain in 1997. One thousand squares were selected, stratified by landscape type as defined by the Institute of Terrestrial Ecology's (ITE) Landscape Classification (Bunce *et al.* 1993, 1996). There were four landscape strata: arable, pastoral, marginal upland and upland. These were defined on the basis of a number of features, including topography, climate, geology and predominant vegetation types (Bunce *et al.* 1993, 1996). Survey squares were selected in direct proportion to the national occurrence of these landscape types (the

geographical distribution of sample squares is presented in Browne, Vickery & Chamberlain, 1999). This approach ensured that all habitat types were represented in the sample and that fieldworker effort was targeted more effectively. In total, 207 squares were surveyed in arable landscapes, 197 in pastoral, 104 in marginal upland and 100 in upland, a total of 608 1-km squares.

Each square was visited four times between mid-April and mid-June, visits commencing within 2 h of sunrise. The observers were asked to walk a route through the square, ensuring complete coverage, and were recommended to spend a minimum of 2 h in each square. The locations of singing male skylarks (i.e. territory holders) were plotted on to maps of the square that were attached to the survey forms. Each 1-km square was divided into fieldworker-defined habitat patches within each square using the system developed by Crick (1992). Habitat patches were areas of homogeneous land use (minimum size 20×20 m), for example individual fields or woods. Full methods are given in Browne, Vickery & Chamberlain (1999). Altitude was derived from ITE Land Characteristics data (Ball, Radford & Williams 1983). This was available only as a median value at the 10-km square level, so in using this information we assume that the median altitude of 10-km squares provides a reasonable measure of the altitude of 1-km squares contained within them.

For the intensive survey, field methods as adopted for the Common Birds Census (CBC; Marchant *et al.* 1990) were used to gather data on territorial skylarks on 59 farmland survey plots in lowland England (Fig. 1). Most of these were ongoing CBC plots, with the remainder taken up specifically for the skylark survey in 1997. All plots were chosen by the observer and so did not constitute a random sample. The survey areas, averaging 72 ha in size, were visited during the morning approximately 10 times between late March and early July and all singing skylarks seen or heard were plotted on to large-scale (1:2500) maps using standard notation (Marchant *et al.* 1990). Skylarks were assigned to individual fields. Crop heights were recorded for each visit, classified in to one of five categories: bare ground, < 10 cm, 10–30 cm, 30–50 cm and > 50 cm. The predominant field boundary type per field was also recorded in to one of five categories: no hedge or trees (but including other boundaries such as fences or ditches), tall hedge and trees, tall hedge no trees, short hedge with trees, and short hedge no trees.

STATISTICAL METHODS

For the extensive survey, habitats were grouped into 24 independent habitat types for analysis (Table 1) based on the habitat coding system of Crick (1992).

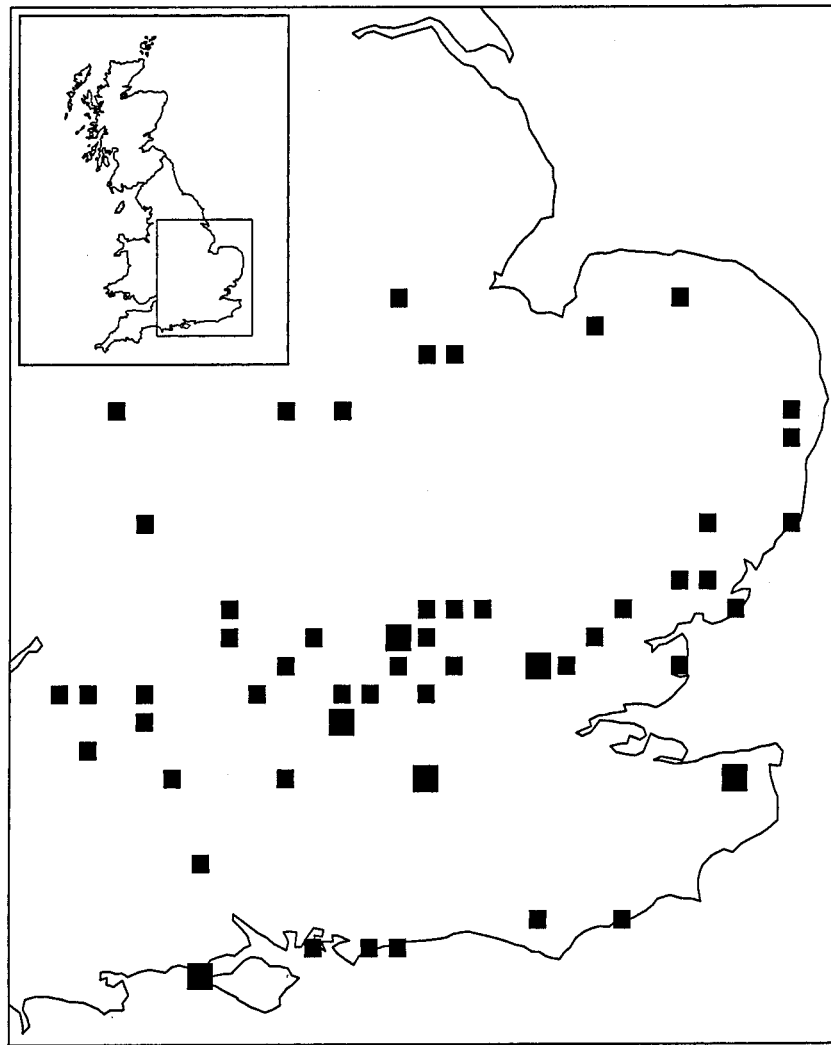


Fig. 1. The distribution of intensive survey plots per 10-km square in southern England. Large squares indicate two plots per 10-km square.

For the intensive survey, which was carried out in predominantly lowland arable landscapes, eight habitat categories were defined (Table 1). In the intensive survey, date was considered as a categorical variable (each category of half a calendar month duration, between 16 March and 31 July).

Seasonal analysis

For the extensive survey, effects of date were considered by dividing the data into early and late periods, taking 15 May as the mid-point of the breeding season, and comparing mean densities per habitat patch between periods with paired *t*-tests, omitting cases where no birds were recorded in either period. This was done over the whole data set, by landscape type, and by habitat type. The dividing point between early and late periods was chosen as 15

May because it occurs at approximately the mid-point of the breeding season, and Wilson *et al.* (1997) have previously shown that skylark habitat preferences vary seasonally, with conventional winter cereals in particular showing little usage by skylarks after this date. Where more than one visit occurred to the same square within any period, the maximum count per habitat was taken as the analysis variable. For the intensive survey, effects of date were considered in tandem with effects of habitat type (see below).

Habitat associations in the extensive survey

The effects of habitat type on skylark occupancy per patch were considered using two different error models, binomial and Poisson, with the GENMOD procedure in SAS (SAS Institute 1996). This two-

Table 1. Habitat types considered and habitat codes used in the analysis. Habitat codes adapted from Crick (1992)

Habitat	Code
Cattle pasture, lightly grazed	CAT1
Cattle pasture, heavily grazed	CAT2
Chalk downland	DRYG
Dry heathland (including lowland heath)	DRYH
Hay meadows and other unintensified grassland (ungrazed)	UGRS
Hay meadows and other unintensified grassland (recently grazed or unspecified grazers)	UGRZ
Legumes (including peas and beans)*	LEGU
Mixed heathland/grass	MIXH
Moorland	MOOR
Oilseed rape (and other brassicas) *	RAPE
Other semi-natural grassland	NATG
Root crops*	ROOT
Spring-sown cereals*	SCER
Scrubland	SCRU
Set-aside*	SETA
Sheep pasture (lightly grazed)	SHE1
Sheep pasture (heavily grazed)	SHE2
Silage and other intensified grassland (ungrazed)	IGRS
Silage and other intensified grassland (recently grazed or unspecified grazers)	IGRZ
Suburban land	SUBU
Autumn-sown cereals*	WCER
Wet heathland and grassland	WETH
Other crops*	OTHC
Other habitats, including bare rock, water bodies	OTHH
All agricultural grassland (CAT1 + CAT2 + IGRS + IGRZ + SHE1 + SHE2 + UGRS + UGRZ) †	GRAS
All heathland (DRYH + MIXH + WETH) ‡	HEAT

*Used in analysis of intensive data set only. All variables used in analysis of extensive data set, except † which was used in the intensive analysis only and ‡ which was used in landscape-specific models only.

level approach was necessary as the distribution of the data contained a large number of zero counts, which meant that no reliable model could be fitted that incorporated all data. Therefore, the factors affecting the probability that skylarks would be present in a given habitat patch were initially analysed using the binomial model. Then the factors affecting the abundance of skylarks where they did occur (i.e. omitting zero counts) were considered separately using the Poisson model.

The probability (P) that a skylark would be present in a patch was analysed in relation to habitat type using binomial errors and a complementary log–log link function with the model:

$$P(\text{skylark presence}) = \beta[i + \text{environment} + \text{altitude} + \text{easting} + \text{northing} + \ln(\text{area})]$$

where β = the inverse link function, i = intercept term, and area = patch area fitted as an offset term (thus we were controlling for effects of patch area on the probability of skylark presence). The environment term encompasses all habitat categories in Table 1. Altitude and grid easting and northing are continuous variables that were included to account for the variation between sampling locations caused by factors other than habitat. The probability that a skylark would be present in a patch was expressed

as the proportion of visits in which a skylark was recorded per patch (i.e. using an events/trials model syntax; SAS Institute 1996). The form of the model meant that visits over the whole season were included, so we were unable to take into account any effect of seasonal change in presence/absence in this analysis.

Skylark abundance in relation to habitat was considered using a similar model, but the dependent variable was the maximum frequency of singing skylarks per patch over a given period, and models were fitted with a log-link function and Poisson error term. Zero counts were not modelled with this approach as the data conformed to the Poisson distribution only after the large number of zero counts had been removed. Use of patch area as an offset in the model meant that we were effectively modelling skylark density. In the Poisson model, square was used as a categorical variable in place of altitude, grid easting and grid northing. This was preferable because there will be many unmeasured variables (including variation between observers) that affect skylark abundance, in addition to geographical location and altitude. Using square as a categorical variable enabled the variation caused by these unidentified factors to be modelled with a single variable. (It was not possible to fit reliable models

to other data sets in this way.) When interaction terms were included, few models converged on a solution, so categories were considered separately. Seasonal variation in density in the Poisson model was taken into account by dividing the data into early and late periods. Both Poisson and binomial models were run on all relevant data, and then separately by landscape type, where marginal upland and upland types were combined due to low sample sizes.

With the GENMOD procedure, inclusion of an intercept term necessitates that comparisons within categorical variables are relative to a given category level, which we will term the null level. For habitat categories, the null level was usually winter cereal as this was the most commonly occurring crop type (and the second most common habitat overall after woodland), and also there is evidence that this crop type is neither preferred nor avoided but used in proportion to its area (Browne, Vickery & Chamberlain 1999). The exception to this was for upland landscape models, where the null level was taken to be moorland. Parameter estimates for null levels were set at zero, but were presented as back-transformed values and tests between parameter estimates were set relative to one. Intercepts and continuous variables were not transformed and the latter can be considered to be analogous to slope in a standard regression model. The models produced a deviance statistic (which is distributed as χ^2), where a significant result indicates that the model is over- or underdispersed. All deviances were adjusted relative to the dispersion parameter (deviance/degrees of freedom), which adjusts for the dispersion of the data. The overall significance of variables was determined using likelihood ratio tests. Parameter estimates of individual levels within categorical variables were compared to the null level using likelihood ratio tests (e.g. for habitat type, all habitats were tested against winter cereal).

Habitat associations in the intensive survey

Skylark occupancy (presence/absence) and density were modelled with respect to habitat using binomial and Poisson models as described for the extensive survey data, but the dependent variable used in the former model was a binomial response where skylarks were either present (1) or absent (0) in a patch for a given visit. The environment term included vegetation height, boundary type and date as categorical variables in addition to habitat categories for both models. The null level for date was the final date category (16–31 July), the null level for vegetation height was the highest crop (> 50 cm), and for boundary type the null level was no hedgerow present. Inclusion of interaction terms

was possible for the Poisson models using this data set.

Habitat diversity

Habitat diversity was calculated per square in the extensive survey using the Shannon diversity index (Krebs 1980). Maximum skylark count from the extensive survey was modelled in relation to habitat diversity index as a continuous variable, initially over all squares, and then in lowland squares (arable and pastoral landscapes) and upland squares (upland and marginal upland landscapes). Squares in which the majority of habitats were defined as lowland farmland (at least 95% of the area) were also identified. Differing effects of habitat diversity on skylark abundance between upland, lowland and predominantly farmland land classes have been reported previously (Chamberlain & Gregory 1999). Data were divided into early and late periods. Habitats with very low skylark abundance, as revealed by Poisson and binomial models, were not considered in the calculation of the index. The effects of habitat diversity on skylark abundance were considered using Poisson regression. No offset term was necessary as all squares were of equal area. For the intensive survey, diversity was calculated in the same way, but using fewer habitats (Table 1), and date and boundary type were included in the model. Plot size varied, so plot area was used as an offset in this model. For both intensive and extensive surveys, the data were at the level of the whole square or plot, so the skew of the data caused by many zero values was not as extreme as the previous analysis, and all counts could be included.

Results

SEASONAL VARIATION IN DENSITY (EXTENSIVE SURVEY)

There was no change in density between early and late periods for all habitats combined (paired $t_{708} = 0.31$; NS). Similarly, there was no significant difference between early and late periods when landscape types were considered separately. Of 24 individual habitat types recorded in the extensive survey, winter cereal showed a significantly higher density in the early period (early = 0.12 ± 0.23 birds ha^{-1} , late = 0.09 ± 0.17 birds ha^{-1} ; paired $t_{132} = 2.68$; $P < 0.008$) and grazed hay meadow showed a significantly higher density in the late period (early = 0.06 ± 0.08 birds ha^{-1} , late = 0.15 ± 0.17 birds ha^{-1} ; paired $t_6 = 2.60$; $P < 0.02$). No other habitat showed a significant difference in skylark density between periods.

HABITAT ASSOCIATIONS (EXTENSIVE
SURVEY)

The relationship between skylark occupancy and habitat was explored using binomial regression with the GENMOD procedure in SAS (SAS Institute 1996). To avoid small sample sizes, chalk downland (DRYG) and semi-natural grassland (NATG) were combined, as were grazed hay meadow (UGRZ) and grazed silage (IGRZ). The back-transformed parameter estimates (where values above 1 indicate higher probability of occurrence relative to winter cereal) and significance levels from χ^2 tests are shown in Table 2. The majority of habitats showed a parameter estimate of less than 1, indicating a lower probability of skylark occupancy compared with winter cereal. This was because this crop had one of the highest occupancy rates, with 47% ($n = 731$ patches) of all winter cereal habitat patches having skylarks recorded. Only set-aside and moorland

Table 2. Parameter estimates and 95% confidence limits from log-linear models derived from binomial regression, where the dependent variable is the number of visits where skylarks were present out of the total number of visits per habitat patch over a given period. Habitat patch area was used as an offset in the model. The number of habitat patches is given in parentheses. All parameter estimates of class variables are relative to winter cereal. Habitat codes are given in Table 1

Variable	Parameter estimate	Confidence limits
CAT1	0.41*** (213)	0.31–0.54
CAT2	0.57*** (350)	0.48–0.68
DRYH	0.93 NS (144)	0.76–1.10
IGRS	0.60*** (676)	0.52–0.68
IGRZ + UGRZ	0.23*** (249)	0.15–0.34
LEGU	1.01 NS (88)	0.85–0.85
MIXH	0.89 NS (75)	0.69–1.10
MOOR	1.31*** (104)	1.16–1.43
NATG + DRYG	0.88 NS (99)	0.70–1.06
OTHC	0.77* (223)	0.66–0.90
OTHH	0.50*** (131)	0.35–0.68
RAPE	0.73*** (153)	0.61–0.87
ROOT	0.92 NS (125)	0.78–1.07
SCER	1.08 NS (223)	0.96–1.19
SCRU	0.37*** (234)	0.26–0.51
SETA	1.40*** (74)	1.30–1.49
SHE1	0.52*** (171)	0.38–0.69
SHE2	0.41*** (486)	0.33–0.50
SUBU	0.12*** (615)	0.09–0.17
UGRS	0.52*** (207)	0.40–0.67
WETH	0.60** (51)	0.37–0.90
WOOD	0.05*** (734)	0.03–0.09
WCER	1.00 (731)	
Easting	0.0008***	0.0004–0.0011
Northing	0.0005***	0.0003–0.0007
Altitude	–0.0014***	–0.0020 to –0.0008
Intercept		–2.18

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, not significant (likelihood ratio tests).

showed significantly higher parameter estimates, with respective occupancy rates of 61% ($n = 74$) and 52% ($n = 104$). There was no significant difference in the probability of skylark occupancy between winter cereals and dry heathland, legumes, mixed heathland, semi-natural grassland, root crops and spring cereals. Many habitats showed significantly lower estimates than winter cereal, the lowest being woodland, suburban land, grazed silage and scrub. There were significant positive effects of grid easting and northing on the probability of skylark presence per habitat patch and a significant negative effect of altitude.

Poisson regression was used to analyse maximum skylark density (i.e. count offset by habitat patch area) in relation to habitat and season relative to winter cereal. Habitats that had a low rate of occupancy (taken as over 75% of the sample having zero counts) were not included in the analysis, leaving a total of 16 habitat types in the model. Both habitat and square had highly significant ($P < 0.0001$) overall effects when considering data from the whole breeding season. Skylark density was significantly higher on moorland, dry heathland, legumes and set-aside relative to winter cereal (Table 3). Density was significantly lower relative to winter cereal in root crops only. No further parameter estimates were significantly different from zero. When divided into early and late periods, there were significantly higher densities of skylarks in set-aside and wet heathland in the early period, although the latter habitat had a small sample size (Table 3). No other habitats showed a significant effect in the early period, and the overall effect of habitat was weak compared to other models ($\chi^2_{15} = 30.25$; $P < 0.015$). In the later period, there were positive associations with dry heathland, moorland, legumes, spring cereals and set-aside. There were no habitats showing significantly lower densities relative to winter cereal.

HABITAT ASSOCIATIONS IN DIFFERENT
LANDSCAPE TYPES (EXTENSIVE SURVEY)

Binomial models for each landscape type had poor fits, each showing a dispersion parameter significantly different from 1 (likelihood ratio tests), and so here we will only consider the effects of habitat on density, omitting zero counts. Model details and parameter estimates differing significantly from the null variable for arable, pastoral and upland landscapes are shown in Table 4. Due to small sample sizes, certain habitats were combined with similar habitats, or omitted when $n < 5$. In arable and pastoral landscapes, all heathland habitats were combined (HCRY + HMIX + HWET), and in pastoral landscapes, moorland was omitted. In upland landscapes, all cereals were combined (WCER + SCER + OTHC), and set-aside and

Table 3. Habitat parameter estimates and 95% confidence limits from log-linear models derived from Poisson regression, where the dependent variable is maximum skylark count per habitat patch over a given period. Habitat patch area was used as an offset in the model. The number of habitat patches is given in parentheses. All parameter estimates of class variables are relative to winter cereal. The overall effect of both habitat and square was significant ($P < 0.05$) for each model. Habitat codes are given in Table 1

	All data		Early period (before 16 May)		Late period (after 15 May)	
Model dispersion	0.47		0.40		0.49	
Total squares	376		306		320	
CAT1	0.96 NS (30)	0.76–1.21	0.81 NS (18)	0.61–1.09	1.07 NS (25)	0.82–1.40
CAT2	1.00 NS (69)	0.82–1.22	0.96 NS (47)	0.76–1.20	1.24 NS (56)	0.97–1.59
DRYH	1.56*** (59)	1.20–2.03	1.07 NS (39)	0.78–1.47	2.45*** (40)	1.71–3.50
IGRS	1.07 NS (144)	0.93–1.23	1.05 NS (100)	0.90–1.22	1.17 NS (110)	0.99–1.39
LEGU	1.22* (40)	1.02–1.45	1.21 NS (29)	0.98–1.49	1.33** (36)	1.10–1.60
MIXH	1.00 NS (38)	0.71–1.43	0.76 NS (21)	0.51–1.14	1.65 NS (28)	0.98–2.76
MOOR	1.70*** (54)	1.29–2.24	1.22 NS (30)	0.88–1.69	2.58*** (44)	1.77–3.74
NATG	1.16 NS (27)	0.91–1.49	1.07 NS (19)	0.79–1.44	1.22 NS (24)	0.93–1.60
OTHC	0.94 NS (73)	0.79–1.12	0.94 NS (53)	0.76–1.16	1.01 NS (58)	0.83–1.24
RAPE	0.92 NS (55)	0.76–1.11	0.90 NS (39)	0.73–1.11	1.02 NS (39)	0.81–1.29
ROOT	0.82* (51)	0.68–0.99	0.84 NS (33)	0.67–1.06	0.90 NS (44)	0.72–1.12
SCER	1.12 NS (98)	0.97–1.30	1.02 NS (71)	0.86–1.22	1.28** (80)	1.08–1.51
SETA	1.51*** (45)	1.27–1.80	1.33** (39)	1.09–1.61	1.75*** (41)	1.44–2.13
SHE2	0.87 NS (73)	0.70–1.10	0.87 NS (45)	0.66–1.15	0.89 NS (56)	0.66–1.19
WETH	1.44 NS (14)	0.98–2.10	1.57* (10)	1.02–2.41	1.27 NS (9)	0.75–2.14
WCER	1.00 (340)	1.00 (276)	1.00 (263)			
Intercept	–0.05		–0.29		–0.24	

Table 4. Habitat parameter estimates in different landscape types from log-linear models derived from Poisson regression, where the dependent variable is maximum skylark count per habitat patch over a given period. Only parameter estimates differing significantly from the null level are shown. Habitat patch area was used as an offset in the model. The number of habitat patches is given in parentheses. The overall effect of square was significant ($P < 0.0001$) for each model. Habitat codes are given in Table 1

	All data		Early period (before 16 May)		Late period (after 15 May)	
Arable						
Dispersion	0.45		0.40		0.48	
Total squares	155		138		145	
Habitat effect	$\chi^2_{12} = 44.25***$		$\chi^2_{12} = 28.39**$		$\chi^2_{12} = 48.96***$	
	HEAT	0.27* (7)	HEAT	0.27* (5)	CAT2	1.45* (29)
	IGRS	1.20* (72)	LEGU	1.26* (24)	HEAT	0.28* (6)
	LEGU	1.22* (33)	SETA	1.47*** (26)	IGRS	1.33** (59)
	ROOT	0.76* (38)			LEGU	1.32** (30)
	SETA	1.58*** (31)			SETA	1.79*** (28)
Null habitat	WCER	1.00 (255)	WCER	1.00 (209)	WCER	1.00 (202)
Intercept	–0.05		–0.32		–0.24	
Pastoral						
Dispersion	0.51		0.41		0.48	
Total squares	111		97		90	
Habitat effect	$\chi^2_{12} = 36.78***$		$\chi^2_{12} = 11.13$ NS		$\chi^2_{12} = 61.49***$	
	HEAT	1.87* (13)			HEAT	3.11*** (6)
					SCER	1.74** (27)
					SETA	1.58* (11)
Null habitat	WCER	1.00 (81)	WCER	1.00 (63)	WCER	1.00 (58)
Intercept	–1.01		–1.01		–1.01	
Upland						
Dispersion	0.45		0.38		0.43	
Total squares	109		71		84	
Habitat effect	$\chi^2_7 = 6.61$ NS		$\chi^2_7 = 11.70$ NS		$\chi^2_7 = 2.01$ NS	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, not significant (likelihood ratio tests).

semi-natural grassland habitats were omitted. In arable landscapes, set-aside showed consistent significant positive effects on skylark density (Table 4). Legumes showed positive associations and combined heathland showed negative associations in each period. There was an indication that winter cereals became relatively less preferred later in the season, with a greater number of habitats showing a significantly higher parameter estimate. In pastoral landscapes, there were overall (i.e. periods combined) positive effects of heathland. However, habitat associations varied seasonally, with no significant effect of habitat in the early period, but in the late period, heathland, spring cereal and set-aside all showed significantly higher parameter estimates than winter cereal. In upland landscapes, there was no significant effect of habitat in any period (Table 4).

HABITAT ASSOCIATIONS ON INDIVIDUAL FARMS (INTENSIVE SURVEY)

Parameter estimates derived from Poisson and binomial models for the effects of crop type, boundary features, altitude and geographical location on skylark abundance on lowland farmland (intensive survey) are shown in Table 5. Parameter estimates for vegetation height and date (i.e. continuous variables reduced to categories) are shown in Figs 2 and 3. The probability of skylark presence on habitat

patches was significantly affected by crop type ($\chi^2_7 = 64.70$; $P < 0.0001$). Set-aside, spring cereals and legumes had a significantly higher probability of skylark occupancy than winter cereals (Table 5). Skylarks tended to avoid all fields with hedgerow boundaries, especially those with trees (Table 5). There were no significant effects of grid easting, grid northing or altitude on skylark occupancy (Table 5). This was not surprising, as intensive survey plots were restricted to lowland farmland in south-east England (Fig. 1). There was little difference in skylark occupancy rates between different date categories ($\chi^2_8 = 11.43$; NS), only the earliest category showing a significant difference ($P < 0.02$) in parameter estimate compared with the latest category (Fig. 2a). There was a significant overall effect of vegetation height ($\chi^2_4 = 30.16$; $P < 0.0001$), with significantly higher parameter estimates for crops lower than 30 cm in height, relative to the tallest crops (Fig. 2b).

There was a significant overall effect of crop type on skylark density ($\chi^2_7 = 48.19$; $P < 0.0001$). Parameter estimates for the effects of individual crop type on skylark density were similar to those effects on skylark occupancy, with the highest densities occurring in set-aside and legumes, but there was no significant difference between winter- and spring-sown cereals (Table 5). There was a significant effect of boundary type ($\chi^2_4 = 30.21$;

Table 5. Parameter estimates for the effects of crop type, boundary type (defined as categorical variables) altitude, easting and northing (defined as continuous variables) derived from generalized linear models, considering only intensive survey plots from lowland arable farmland. The binomial model considers the probability of skylark occupancy using a complementary log-log link function. The Poisson model considers the density of skylarks in patches where they were present (i.e. zero counts are omitted) using a log-link function. The models also included effects of date and vegetation height, which are shown in Figs 2 and 3. Each model was based on 59 plots, n = number of habitat patches. Habitat codes are given in Table 1

Variable	Category	n	Binomial model (skylark occupancy)		Poisson model (skylark density)	
			Dispersion = 1.06		Dispersion = 0.46	
Crop	GRAS	218	0.99 NS	0.88–1.10	1.26 NS	0.99–1.59
	LEGU	14	1.32***	1.14–1.46	2.91*	1.16–7.29
	OTHC	51	1.15 NS	0.99–1.30	0.76 NS	0.25–2.30
	RAPE	16	1.05 NS	0.84–1.24	0.84 NS	0.48–1.46
	ROOT	12	1.18 NS	0.94–1.39	0.78 NS	0.27–2.26
	SETA	31	1.51***	1.41–1.56	3.98***	2.83–5.59
	SCER	22	1.29***	1.10–1.44	0.81 NS	0.47–1.40
	WCER	179	1.00	1.00		
Boundary	Short hedge no trees	72	0.86*	0.74–0.92	0.76**	0.64–0.90
	Short hedge with trees	65	0.51***	0.41–0.63	0.88 NS	0.72–1.08
	Tall hedge no trees	28	0.86 NS	0.71–1.02	1.13 NS	0.92–1.40
	Tall hedge with trees	167	0.66***	0.58–0.75	0.94 NS	0.81–1.09
	No boundary vegetation	211	1.00	1.00		
Easting†			–0.0101 NS	–0.0021–0.0012	0.0045 NS	–0.0020–0.0110
Northing†			0.0048 NS	–0.0058–0.0181	–0.0259***	–0.0330 to –0.0188
Altitude†			–0.0003 NS	–0.0019–0.0013	–0.0007 NS	–0.0017–0.0003
Intercept			–2.71		–0.95	

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, not significant (likelihood ratio tests); †parameter estimates presented $\times 10^2$.

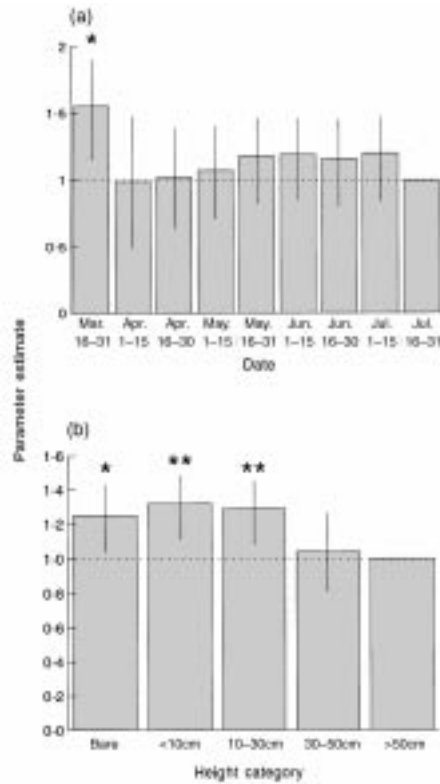


Fig. 2. Parameter estimates derived from generalized linear models for the probability of skylark occupancy per habitat patch in relation to the effects of (a) date, divided into categories of half-month duration, and (b) vegetation height, divided into categories. The model uses a binomial error structure with a complementary log–log link function. Parameter estimates and hypothesis tests ($*P < 0.05$, $**P < 0.01$) are relative to the final category in each figure, the estimate of which is set at one (dashed horizontal line). Error bars represent 95% confidence intervals.

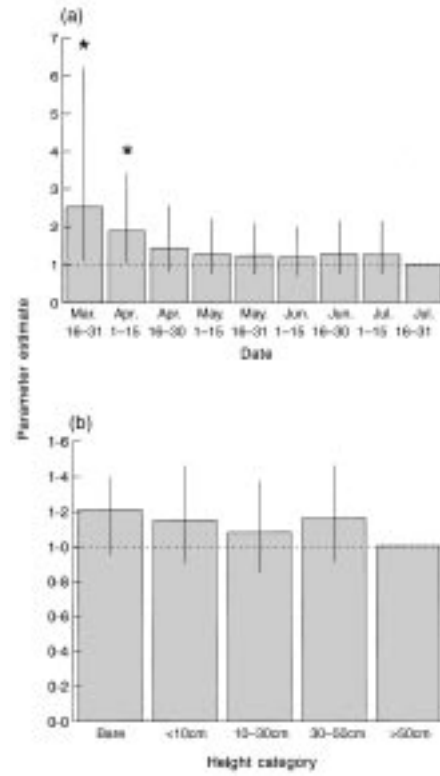


Fig. 3. Parameter estimates derived from generalized linear models for the density of skylarks per habitat patch (omitting zero values) in relation to the effects of (a) date, divided into categories of half-month duration, and (b) vegetation height, divided into categories. The model uses a Poisson error structure with a log-link function. Parameter estimates and hypothesis tests ($*P < 0.05$, $**P < 0.01$) are relative to the final category in each figure, the estimate of which is set at one (dashed horizontal line). Error bars represent 95% confidence intervals.

$P < 0.0001$), short hedges with trees showing a significantly lower density relative to that in fields without boundaries. There was no significant effect of altitude or grid easting, but there was a significant decline in abundance in more northerly plots (Table 5). There was no significant overall effect of date on skylark density ($\chi^2_7 = 12.68$; NS), although there was an indication that the highest densities occurred earliest in the breeding season (Fig. 3a), with late March and early April having significantly higher parameter estimates than the latest period (which also had the lowest density overall). There was no significant overall effect of vegetation height on skylark density ($\chi^2_4 = 4.90$; NS; Fig. 3b). There were significant interactions between crop type and boundary type ($\chi^2_{12} = 77.14$; $P < 0.0001$), indicating that certain crops are associated with particular boundary types, and there was a weakly significant interaction between date and crop type ($\chi^2_{43} = 64.83$; $P < 0.02$), indicating that the effect of crop is partly dependent on date. The unscaled deviance for this

model was low (Table 5), indicating a relatively poor model fit due to underdispersion.

It was not possible to produce a model of skylark occupancy incorporating interaction terms between categories that converged on a solution. The analysis of skylark density indicated that the effect of crop type on density may depend on date. Also, it is possible that crop preferences are associated with vegetation height, as skylarks tend to avoid tall crops (Wilson *et al.* 1997), so interactions seem likely. Figure 2b showed that the probability of skylark occupancy was significantly higher in crops shorter than 30 cm. This may be a critical height at which skylarks abandon territories. Vegetation height increased significantly with date for each of the eight crop types considered, but certain crops reached the 30–50 cm category level much quicker than others. On average, winter wheat attained a height of between 30 and 50 cm by 14 May. Spring cereals attained this height category on average 23 days later, by 6 June (Fig. 4). There was a signifi-

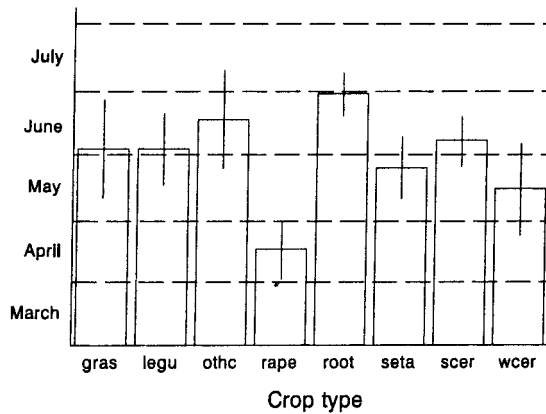


Fig. 4. The mean date (where date 1 = 1 March) on which a height category of over 30 cm was recorded for eight crop types. Error bars represent standard errors. Habitat codes are given in Table 1.

cant difference in the date at which this height category was recorded between crops (ANOVA $F_{7,732} = 37.3$; $P < 0.0001$), post-hoc Scheffe tests showing that winter cereal reached this height significantly earlier than all other crops except set-aside and oilseed rape (which had a significantly earlier date than all crops, including winter cereal). Furthermore, when considering the effects of habitat on the presence or absence of skylarks from a patch at vegetation heights over 30 cm, there was a relatively weak effect of habitat ($\chi^2_7 = 16.20$; $P < 0.025$), only grass showing a significantly different (lower) parameter estimate relative to winter cereal. There was no effect of date or altitude in this model, but there were highly significant effects of boundary type, easting and northing ($P < 0.0001$ in each case). Therefore, this result implies that differences in the probability of occupancy between crops are largely associated with vegetation height.

HABITAT DIVERSITY AND SKYLARK ABUNDANCE

The diversity index was determined for each square in the extensive survey using all habitats in Table 2 except those that were occupied at very low rates, all habitats with a parameter estimate lower than 0.5 being omitted. These were: lightly grazed cattle pasture (CAT1), grazed silage and hay (IGRZ + UGRZ), scrub (SCRU), heavily grazed sheep pasture (SHE2), suburban land (SUBU) and woodland (WOOD). There were significant positive relationships between habitat diversity and maximum skylark count over all visits and in early and late periods separately over all squares and in lowland squares only (Table 6). There were no significant effects in upland squares or predominantly farmland squares. Unscaled model deviance was high in each

case, indicating poor model fits for this analysis. For the intensive survey of lowland farmland, there was a significant effect of habitat diversity on skylark density, but higher diversity was associated with a lower skylark density (parameter estimate = -0.78 ± 0.16 ; $n = 342$ patches; $\chi^2_1 = 23.16$; $P < 0.0001$). There was no significant effect of date ($\chi^2_9 = 8.67$; NS) or boundary type ($\chi^2_4 = 8.88$; NS) on skylark density in the intensive survey. There were no significant interactions between diversity index and either date ($\chi^2_8 = 2.70$; NS) or boundary type ($\chi^2_4 = 1.94$; NS).

Discussion and conclusions

SKYLARK HABITAT ASSOCIATIONS

The highest rates of skylark occupancy occurred in set-aside, winter cereals, spring cereals, legumes, root crops, mixed and dry heathland, semi-natural grassland and moorland. When skylark density was considered in habitat patches where they were present, the highest densities were in set-aside, dry heathland, moorland and legumes, and lowest in root crops. Set-aside was consistently associated with the highest densities and the highest probabilities of occupancy in the whole extensive data set, in arable landscapes (extensive survey) and in lowland arable farms (intensive survey). There was also a significant, although relatively weak effect, of set-aside in the late period in pastoral landscapes (extensive survey). A number of studies have indicated that set-aside is strongly favoured by skylarks (Wilson *et al.* 1997; Poulsen, Sotherton & Aebischer 1998), which may be due both to the vegetation structure and the food sources available (Poulsen 1996). The two different types of set-aside, rotational and non-rotational, were not differentiated in the present study, but there is evidence that the abundance of skylarks is highest in rotational set-aside (Henderson, Cooper & Fuller 1998) and it seems likely that the high parameter estimates for set-aside in the present study were mostly due to the influence of rotational set-aside. Skylarks tended to occur rarely in woodland, scrub and suburban land, which have very little suitable nesting habitat, but also in poorly drained habitats (wet heath) and heavily grazed habitats. Generally, the level of disturbance and the sward structure caused by heavy grazing create unsuitable skylark nesting habitat and may also have a detrimental effect on food abundance (Wakeham-Dawson *et al.* 1998). There has been some suggestion that light levels of grazing, especially by cattle, will provide a patchy sward that may offer suitable nesting habitat (Shrubbs 1990). Skylarks also tended to be absent from fields bounded by hedgerows, especially those containing trees. This preference for open habitats has been demonstrated previously, and may be associated

Table 6. Habitat parameter estimates (\pm SE) for the effect of habitat diversity (Shannon index) on maximum skylark count from the extensive survey over a given period in squares of differing landscape type derived from Poisson regression. n = number of 1-km squares

	All data			Early period			Late period		
	Parameter estimate	Dispersion	n	Parameter estimate	Dispersion	n	Parameter estimate	Dispersion	n
All squares	0.91 \pm 0.12***	5.90	601	0.89 \pm 0.13***	5.22	514	0.83 \pm 0.13***	5.86	513
Lowland squares	1.08 \pm 0.15***	5.82	399	1.16 \pm 0.16***	4.87	370	0.92 \pm 0.17***	6.13	365
Upland squares	0.41 \pm 0.27 NS	5.97	202	0.14 \pm 0.32 NS	5.84	144	0.43 \pm 0.31 NS	5.20	148
Farmland squares	0.18 \pm 0.23 NS	5.81	127	0.28 \pm 0.25 NS	5.06	116	0.11 \pm 0.25 NS	6.22	124

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, not significant (likelihood ratio tests).

with predator avoidance (Schlöpfer 1988; Wilson *et al.* 1997; Chamberlain & Gregory 1999).

The highest parameter estimates for skylark density across all landscape types were in the non-agricultural habitats of moorland and dry heathland. This was only evident in the later period, and was partly a consequence of the decreasing suitability of developing arable crops (see below). Heathland also showed significantly higher parameter estimates than winter cereal in pastoral landscapes, although there was a negative effect of heathland relative to winter cereals in arable landscapes, so the relative suitability of heathland varies according to landscape type. Semi-natural habitats such as these may hold higher numbers of skylarks because of lower disturbance, less uniform vegetation (and hence more suitable nesting habitat) and higher prey availabilities due to lack of pesticide input, compared with farmland habitats. In a previous study of skylark habitat associations (Chamberlain & Gregory 1999), semi-natural grassland habitats held the highest overall mean densities, but they were also the most variable, thus indicating a wide variation in skylark abundance within habitat types. In this study, we omitted zero counts when analysing skylark density, which may have selected the best semi-natural sites. There were, respectively, 52% ($n = 104$) and 41% ($n = 144$) of moorland and heathland habitat patches that had no skylarks. However, when considering habitat associations within upland landscapes, no significant differences between habitats were detected, implying that differences at the national level are merely reflecting a more general upland–lowland contrast. The results here are in contrast to those found by Brown & Stillman (1993) in upland habitats, who found positive associations between skylark abundance and grass and bracken and negative associations with heather moorland. Clearly, there is a need for more detailed understanding of the factors affecting sky-

lark abundance in uplands and what causes the wide variation within semi-natural habitats in general used by skylarks.

EFFECTS OF VEGETATIONAL DEVELOPMENT

There was some evidence that both skylark occupancy and density were higher early in the breeding season. This may have been either because of a lowering of song activity when young were in the nest (although this seems less likely given that skylarks are multibrooded), or because of rapid abandonment of habitats that were unsuitable from a relatively early stage of the breeding season. There was a significant decrease in the density of skylarks in winter cereal in the later part of the season. In terms of habitat associations, winter cereals and spring cereals were not significantly different in density in the early season, and there was generally little difference in density between habitats. However, by the late period, spring cereals supported significantly higher densities of skylarks than winter cereals, as did a number of other habitats. This pattern was also evident in arable and pastoral landscape types separately. These results imply that the suitability of winter cereals to skylarks in arable and pastoral landscapes declines as the breeding season progresses.

In lowland arable landscapes, vegetation height had significant effects on the probability of the occupancy of skylarks in a crop. The greatest rates of occupancy occurred where vegetation was present at heights of under 30 cm. Wilson *et al.* (1997) found that the number of nesting attempts decreased in winter cereals, but increased in spring cereals as the season progressed, a result also found by Schlöpfer (1988). The higher densities on spring cereals in the late period in our study may have been due to

sward structure, as winter cereals reached a height category of 30–50 cm tall significantly earlier than a number of other crops, including spring cereals. On average, winter cereals became unsuitable by 14 May. This result is in close agreement with Wilson *et al.* (1997), who found that there were very few nesting attempts on conventionally managed winter cereals after mid-May, although they reported that skylarks tolerated a slightly taller crop, preferring a height of between 20 and 60 cm. This difference may have arisen because of differences in methodology between the two studies [as Wilson *et al.* (1997) based their analysis of vegetation height on nests actually found], or variations in birds' responses to vegetation caused by differences in weather between years (Evans, Wilson & Browne 1995). Nevertheless, our estimate was within the range of Wilson *et al.* (1997).

We found no difference between the date at which set-aside and winter cereal exceeded the 30-cm height category. However, set-aside typically has a more varied sward structure than arable crops, and is more patchy, with areas of bare ground and dense vegetation (Henderson, Cooper & Fuller 1998), thus height *per se* will be of less importance. Indeed, Wilson *et al.* (1997) found that neither vegetation height nor cover were significant predictors of skylark abundance in set-aside. There was no significant effect of vegetation height on skylark density (omitting zero counts) in the present study, but for the taller height categories occupancy would have been low for the majority of crops, and these patches would have been omitted from the analyses if no skylarks were holding territories. The majority of habitat patches left in the analysis would be ones (such as set-aside) where vegetation height was of less importance to the suitability of the habitat for skylarks.

The decline of the skylark population has been attributed to changes in agricultural practice (Fuller *et al.* 1995; Chamberlain & Crick 1999). An increasing amount of evidence suggests that a crucial factor underlying the population decline is a reduction in the number of breeding attempts made per year that has arisen due to changes in sowing regimes, changes in the growth rate and sward density of crops and, in particular, the replacement of spring cereals with winter cereals (Wilson *et al.* 1997). In the present study, the mean difference in the date at which crops reached the 30–50 cm height category between spring and winter cereals was 23 days. The nesting period for skylarks is around 14 days from egg-laying to hatching, and females may make a subsequent attempt when young are 17–18 days old (Delius 1965). The difference in date between the two cereal types is thus almost equivalent to the duration of the period between successful nesting attempts.

HABITAT DIVERSITY

It is common for skylarks to make nesting attempts in more than one crop within a breeding season, as vegetation structure becomes suitable at different times of year in different crops (Schläpfer 1988; Jenny 1990; Wilson *et al.* 1997). There is some evidence that skylark densities are higher in more diverse upland habitats and on lowland farmland with a greater diversity of field types (Chamberlain & Gregory 1999). In the present study, there was evidence from the extensive survey that skylark abundance was higher across all squares and higher in lowland landscapes with a high habitat diversity. There was, however, no effect of habitat diversity on density in upland landscapes or predominantly farmland squares. Furthermore, the results from the intensive survey showed a significant decrease in skylark density with increasing habitat diversity. This result may have been affected by the relatively small number of habitats from which the diversity index was calculated, and the fact that the definitions of grassland were not sufficiently detailed. However, the lack of consistency at different scales, both within this study and in comparison to Chamberlain & Gregory (1999) must call into question whether the result is ecologically meaningful. A problem with considering habitat diversity is that all habitats are given equal weight, so a square with set-aside, winter cereals and spring cereals has the same diversity as a square with equivalent areas of oilseed rape, grazed pasture and root crops, yet from our analysis we know that the former group of habitats is likely to be far more suitable for skylarks than the latter group. While a diversity of habitats is likely to be beneficial to skylarks under certain circumstances, the actual components of diversity are likely to be important as well, and we feel that measures of habitat diversity should be used with caution.

METHODOLOGICAL CONSIDERATIONS

This survey has sought to determine habitat associations of skylarks by surveying territory-holding males, but a proportion of these are likely to be non-breeders. Delius (1965) estimated that approximately 10% of males (mostly first years) in his coastal population were non-breeders. Also, Wilson, Taylor & Muirhead (1996) found certain habitats that had territory-holding males but showed no evidence of actual breeding. An example was legumes, a crop that supported high densities of singing males in this study. For some habitats, therefore, the density of singing males may not be a good indication of habitat quality in terms of reproductive success. If non-breeders are overrepresented in particular habitats, then the habitat preferences of the breeding population may be poorly estimated

in this study (for example, non-breeders may be excluded from the better territories). Previous studies have found that density and nesting success both tend to be high in a given habitat where an estimate of actual nesting attempts is made, particularly in set-aside and spring cereals (Wilson *et al.* 1997; Poulsen, Sotherton & Aebischer 1998). However, winter cereal, which tends to have a high abundance of skylarks in the first half of the breeding season, is unlikely to be a very productive habitat. Therefore, skylark abundance is not likely to be related to habitat quality in winter cereals or legumes.

A further potential problem is that a skylark that was seen directly over a given habitat type was assigned to that habitat only. If skylarks favour territories with a diversity of habitats, then this may lead to inaccurate results as neighbouring habitats are also part of the territory. Wilson *et al.* (1997) reported that skylarks did hold territories over two fields, but no territory included significant parts of three fields. Poulsen, Sotherton & Aebischer (1998) found the mean territory size across all fields on farmland to be 2.62 ha and the highest mean per habitat was 5.2 territories per hectare on set-aside. The mean (\pm SD) habitat patch size over the whole of this survey was 9.95 ± 14.68 ha ($n = 6155$), and in farmland only 7.05 ± 8.99 ha ($n = 4099$). Given that on average the habitat patch size is large relative to the likely territory size, it seems reasonable to assume that the recorded habitat will occupy a large proportion of a given skylark's territory in the majority of cases. Repeat analyses were carried out using patches of minimum size found by Poulsen, Sotherton & Aebischer (1998), but this made little difference to the results (D.E. Chamberlain, unpublished data).

CONCLUSIONS

This study has shown that skylarks exhibit habitat associations that vary seasonally. In farmland this is because vegetational development of certain crops makes them less suitable for nesting as the season progresses. Where there is little or no suitable alternative nesting habitat, skylarks may curtail their breeding attempts relatively early. These results strongly support the findings of Wilson *et al.* (1997), who looked at similar habitat associations and nesting success in a more intensive survey but covering only a small number of survey sites, thus showing that their findings have general applicability to lowland farmland at wider geographical scales. However, the results presented here are less informative about skylark habitat associations in the uplands due to the resolution of the habitat data, and given the evidence for upland population declines (Hancock & Avery 1998; Chamberlain &

Crick 1999 we suggest that further research is needed in upland habitats.

The extent of the British skylark population associated with agricultural land (Browne, Vickery & Chamberlain 1999) suggests that sympathetic changes in farming practice are likely to provide the best mechanism for improving the status of this species. The clear preferences by skylarks, shown in this study, for set-aside and spring cereal suggest that the inclusion of these or their equivalent (e.g. fallow land rather than set-aside) in agri-environment schemes is likely to benefit the species by increasing habitat diversity and providing suitable nesting habitat throughout the breeding season. Set-aside is likely to be a more productive habitat than other crops (Poulsen 1996), but it is unclear whether its widespread introduction in 1992 has had any effect in terms of slowing, or reversing, the skylark population decline. It is possible that set-aside, of the type suitable for skylarks, has not been in place long enough at high enough levels to have had an effect at the population level. Similarly, agri-environment schemes may not result in the creation of sufficient areas of new habitat to halt the population decline of widespread farmland birds such as skylarks. These schemes should be promoted alongside measures designed to reduce the intensity with which winter cereals, in particular, are managed. Reduction of pesticide and fertilizer inputs, for example, through approaches such as precision farming, may benefit skylarks by increasing food supply. However, the results of this study suggest crop structure is a more important factor than food availability and the creation of areas of sparse cereal sward, or even bare ground within cereal fields (Odeskær *et al.* 1997), may enhance nest site availability for skylarks.

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