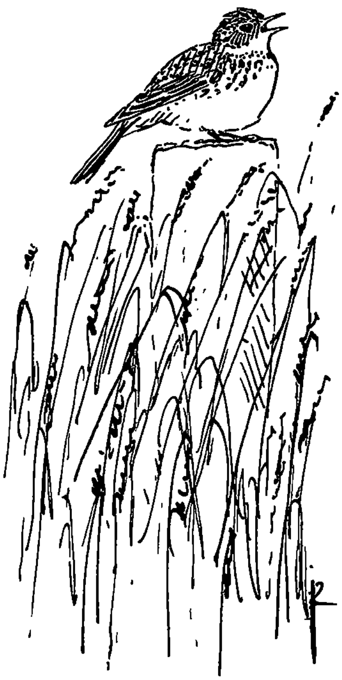
SPATIAL AND TEMPORAL DISTRIBUTION OF BREEDING SKYLARKS *ALAUDA ARVENSIS* IN RELATION TO CROP TYPE IN PERIODS OF POPULATION INCREASE AND DECREASE

D.E. CHAMBERLAIN, J.A. VICKERY & S. GOUGH



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The seasonal variation in Skylark *Alauda arvensis* occurrence, in terms of both presence and abundance, was examined in relation to crop type on a number of survey sites in English lowland farmland in two periods, 1965-70 and 1990-95. These two periods were selected to coincide with periods of population increase and decline respectively. We were able to consider the effects of changes in cropping regime on the length of the breeding season for Skylarks, a factor implicated in the cause of the Skylark population decline. The overall occurrence of Skylarks was significantly lower in the 1990-95 period, in accord with national trends. At the farm level, Skylark abundance increased significantly with crop diversity. There was little difference between spring and winter cereals in occupancy rates or seasonal trend in the 1965-70 period, but in the 1990-95 period, territories were abandoned much later on spring cereals than on winter cereals. Spring cereals were abandoned later in the season in the 1990s than the 1960s whereas winter cereals were abandoned earlier. There was thus an indication that the suitability of winter cereals had decreased between the two periods. However, in the 1990-95 period, farms with spring cereals tended to have more diverse cropping than those without, so the results for this crop may be confounded by farm-level effects. Set-aside, which only occurred in the 1990-95 period, had the highest rates of Skylark occurrence, but showed no seasonal trends. These results broadly support the suggestion that increases in winter cereals and loss of farm habitat diversity have contributed to the Skylark decline.

Key words: *Alauda arvensis* - farmland - winter cereal - spring cereal - cropping - territory

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK; E-mail: Dan.Chamberlain@bto.org

INTRODUCTION

The Skylark *Alauda arvensis*, in common with many other farmland birds, has shown large population declines in northern Europe (Hustings 1992; Tucker & Heath 1994; Fuller *et al.* 1995; Siriwardena *et al.* 1998). These declines have coincided with a period of great change in agricultural management, including changes in cereal sowing dates and crop rotations, changes in grassland management, increases in inputs of pesticides and fertilizers and changes in livestock densities (Chamberlain *et al.* 1999a) and growing evidence now exists to link the decline of the Skylark with this agricultural intensification (Wilson *et al.* 1997; Chamberlain & Crick 1999). Two changes within arable systems may have had a particularly detrimental effect on Skylarks: changes in crop type and loss of traditional short-term rotations with subsequent loss of habitat diversity.

A number of studies have considered the distribution of Skylark territories in relation to crop type and in particular to cereals, the most commonly used nesting habitat (with the possible exception of set-aside). Schläpfer (1988), working in Switzerland, found that there was seasonal variation in nesting habitat, with winter cereals being most commonly used for early nesting attempts, but spring cereals being preferred late in the breeding season. This was attributed to the seasonal development of cereal swards, tall dense vegetation being avoided by Skylarks. Wilson *et al.* (1997) also found an effect of sward height on the use of cereals as a nesting habitat in England, Skylarks abandoning crops over 50cm in height. Similar effects of vegetation height and density were found by Odderskær *et al.* (1997) in Denmark. A range of crop types available with differing sward heights is therefore required if a Skylark is to maximise the number of breeding attempts over a season (Schläpfer 1988). There is also evidence that diverse farmland provides better feeding habitat for Skylarks, particularly as the best Skylark foraging habitats, such as short-grass meadows (Jenny 1990), are not necessarily good nesting habitats (Schläpfer 1988; Wilson *et al.* 1997). Agricultural intensification has lead to a decrease in the diversity of farmland as a result of a simplification of rotations and a polarization of agriculture into either solely arable or pastoral enterprises (O'Connor & Shrubb 1986; Chamberlain *et al.* 1999a). In addition, changes in sowing regimes have meant that spring cereals have been replaced by winter-sown cereals, particularly winter wheat. Winter wheat becomes unsuitable nesting habitat comparatively early in the breeding season, and the loss of diversity may mean that suitable alternative habitats are not available. The population decline may therefore have been driven by a reduction in the number of breeding attempts possible within a season (Wilson *et al.* 1997; Chamberlain *et al.* 1999b).

The preference of nesting Skylarks for certain crop types and the effects of sward development on territory abandonment have been well studied (Schläpfer 1999; Wilson *et al.* 1997; Chamberlain *et al.* 1999b). However, each of these studies has considered post-intensification farmland populations during a period of population decline. No study to date has considered the seasonal changes in Skylark abundance in relation to crop type in a pre-intensification population. In this study, we compare the seasonal distribution of breeding Skylarks in different crop types from a number of separate farmland sites in two periods, 1965-70 when the population was increasing, and 1990-95 when the population was undergoing a shallow decline, after the severe decreases of the early 1980s (Chamberlain & Crick 1999). We use these data to examine whether the length of the breeding season has changed over time and how this may have been affected by changes in cropping regime. Specifically we test the hypothesis that the Skylarks breeding season has been shortened as a result of modern cropping practices.

METHODS

Bird survey

Data were derived from the Common Birds Census (CBC), an annual survey run by the BTO which was instigated in 1961 to monitor changes in the size of breeding bird populations. It involves volunteer observers visiting census sites between six and twelve times during the breeding season and recording the location of all individual birds seen onto plot maps. These individual registrations are used to determine the number and approximate size of all bird territories using mapping techniques to identify clusters of registrations (Bibby *et al.* 1992). In addition, habitat data are also collected. This includes noting the crop or grass type in each field and the predominant field boundary, defined into one of five categories; no hedge, tall hedge (>2m) with trees, tall hedge without trees, short hedge with trees and short hedge without trees. However, the quality of this habitat data varied from site to site and boundary type in particular was often not recorded by some observers. Full survey methods can be found in Marchant *et al.* (1990).

For this study, data were derived from two periods, 1965-70 and 1990-95, which were respectively before and after the substantial population declines which occurred in the late-1970s and early 1980s (Chamberlain & Crick 1999). Within each period, a subset of farmland CBC sites was selected which had the most comprehensive habitat data, with a total of 21 sites in the 1965-70 period and 23 sites in the 1990-95 period. CBC sites are not randomly distributed over UK, but show a bias towards lowland farmland in England (Fuller *et al.* 1985), hence CBC population indices are only truly representative of southern and eastern England. All sites used were within this region. Note that the sample of CBC sites is not constant, but varies from year to year as observers drop out and are replaced by new volunteers and new sites, thus (with the exception of a single site) the 1965-70 and 1990-95 periods have different individual sites. For each site, one year within the five year period in question was selected (at random) for data extraction, and the number of territories per site across the whole season was determined. The date of each visit was recorded when known, but sometimes the original observers did not note down the actual date, only the visit number. In these cases, visits were assigned a letter (where A = first visit, B = second visit and so on to visit L).

Statistical analysis

Individual crop and grass types were combined into eleven broad crop types (Table 1). The change in the proportion of farms where each crop type occurred between 1965-70 and 1990-95 periods was analysed with G-tests where expected values were greater than five (Sokal & Rohlf 1981). The mean area per farm for each crop was also compared between periods using unpaired *t*-tests. The Shannon diversity index (Krebs 1980) was used to calculate crop diversity based on the categories defined in Table 1. This index incorporates both the numbers of crops per farm and the proportion of each farm covered by each crop. The number of crop types per farm was also determined. These measures were analysed with respect to the two time periods.

The representativeness of farms in terms of crop area was considered in order to determine the validity of extrapolating the results to explain declines at a national level. This was done using agricultural statistics derived from Ministry of Agriculture Fisheries and Food (MAFF) June Census (MAFF unpublished) data for England and Wales. Four categories of crop were considered, spring cereals, winter cereals, improved grass (both permanent and temporary) and root crops (and the proportion of total farmland area covered by each was determined). It was neces-

Table 1. Crop categories considered in the analyses and the number of fields of each (1965-70, 1990-95) in the sample.

Category	Components	*n*
Brassicas	Cabbage, cauliflower, kale, oilseed rape.	10, 11
Legumes	Beans, peas	7, 15
Miscellaneous	Maize, mustard, linseed, leeks, radish, lettuce, scrub, flowers, unknown crops	5, 1
Permanent pasture	Improved grass > 5 years old	67, 51
Root crops	Carrots, onions, potatoes, sugar beet	32, 5
Rough grazing	Unimproved pasture	2, 1
Set-aside	Rotational and non-rotational not distinguished	0, 15
Spring cereals	Spring sown barley, oats and wheat	22, 18
Temporary grass	Improved grass < 5 years old (silage and hay), fallow, clover	27, 29
Other cereals	Rye, barley, oats and wheat where the sowing period is unknown	117, 28
Winter cereals	Winter sown barley, oats and wheat	19, 64

sary to combine the two grass categories as the definition used in the June Census changed between periods. Further categories were not considered in this analysis as the changes in the way crops were recorded over time and the many omissions in the June Census data (Chamberlain *et al.* 1999a) meant that other comparisons would be inaccurate.

The modelling procedure adopted to analyse the effects of crop type, period and date on Skylark occurrence per field, using all registrations, followed the recommendations of Crawley (1993) in selecting the 'minimal adequate model' where non-significant terms are omitted successively, so long as there is no significant change in the model deviance. In most cases, including all interaction terms in the model meant that convergence was not reached after 20 iterations and the validity of the model fit was therefore questionable. In these cases, higher order interactions were successively omitted until convergence was achieved. Model selection then proceeded as normal. The probability that a Skylark would be present in a field was modelled in relation to crop type, date and period using binomial logistic regression. Thus Skylarks were recorded only as present (1) or absent (0) per field regardless of how many separate registrations were made in a given visit. Skylark occurrence is likely to increase with field size, which may be due both to preferences for territories away from field boundaries (Chamberlain & Gregory 1999) and also to chance (the larger a field is, the more likely a bird is to settle there even under a random settlement model). As we were not interested in the effects of field size *per se* in this analysis, field area (log-transformed) was used as an offset in the model, which adjusts for effects of field size on the probability of Skylark occurrence. This necessitated the use of a complementary log-log link function rather than the more conventional logit link which is inappropriate when an offset term is used in a binomial model (S.N. Freeman, pers. comm.). Farm number was also considered as a categorical variable nested within period (because, with the exception of a single farm, the 1965-70 and 1990-95 periods had no farms in common), and thus acts as a random 'subject' factor in this model.

Date was initially considered as a continuous variable. However, this meant that some data (mostly from the 1965-70 period) could not be considered, as visit number only, rather than the actual date of the visit, was recorded by a number of observers. The model was also repeated using visit number as a categorical variable in place of date. For those farms where the date was known, the average dates of each visit were for the most part well spaced and in the correct order. However, there was some overlap in the date of different visits across different sites. This was particularly marked in later visits. To reduce this variation, visits H and I and visits J, K and L were combined. Even so, the overlap in dates between successive visits meant that this variable could only be crudely measured in this analysis. The date at which each territory was last known to be occupied in a season was compared between crops within each period and between each period using *t*-tests. This analysis used registrations to estimate the location of each territory using standard criteria (Marchant *et al.* 1990) and meant that a number of registrations that did not meet these criteria were not included in these analyses.

The effects of habitat diversity on the probability of Skylark presence per farm in relation to date/visit and period was considered using binomial regression as above. As habitat diversity was considered at the level of the farm, this meant that the distribution of counts was less biased by a large number of zero counts, so Poisson regression with a log link was also used to model Skylark territory count in relation to habitat diversity. For binomial and Poisson models, results refer to the partial significance of a variable, determined from likelihood ratio tests (distributed as χ^2). In all cases, means and parameter estimates are presented ± 1 SE.

RESULTS

Representativeness of farms

The proportion of total farm area occupied by each of the four main crop types in each period for the CBC sites and national June Census data is shown in Table 2. Spring cereals occupied similar areas on CBC sites in both periods, which meant that they were under-represented in the 1965-70 period and over-represented in the 1990-95 period relative to the national trends. There was closer agreement in the proportion of area covered by winter cereals. Grass was over-represented in the sample of farms in the 1965-70 period. There were less striking differences in the proportions covered at different scales in root crops.

Changes in crops

The frequency of occurrence of eleven crop types in each period is shown in Fig. 1. The single largest decrease in frequency of occurrence was for other cereals, which were present in 81% of farms in the 1965-70 period, but only 22% of farms in the 1990-95 period. This does not necessarily show any real change in cropping pattern as this category included cereals where the sowing date was unknown (Table 1). Rather, this reveals that habitat data tended to be recorded more accurately in the 1990-95 period. The biggest declines were in root crops, which were present on 52% of farms in the 1965-70 period and 17% of farms in the 1990-95 period, and temporary grass which occurred on 62% and 30% of farms for the two periods respectively. Significant increases were

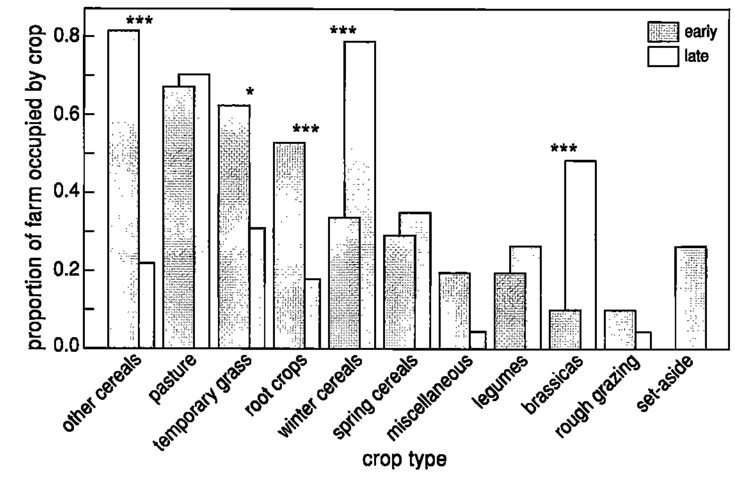

Fig. 1. The frequency of occurrence of eleven crop types in two periods, 1965-70 and 1990-95. Respective sample sizes for 1965-70 and 1990-95 periods were 21 and 23 farms. $*P < 0.05$, $***P < 0.001$ (G-test). No analysis was carried out for miscellaneous crops, rough grazing or set-aside due to low expected frequencies.

Table 2. The percentage of total farm area covered by four crop types in the sample of CBC plots and at a national (England and Wales) scale derived from MAFF June Census data.

	CBC sites		MAFF June Census	
	1965-70	1990-95	1965-70	1990-95
Grass	17.2	21.0	6.0	22.0
Root crops	9.5	2.3	5.9	6.1
Spring cereals	9.5	8.0	21.0	3.0
Winter cereals	9.1	33.6	7.6	21.6

recorded in brassicas (especially oilseed rape), increasing from 10% to 48% occurrence, and winter cereals which increased from 33% to 78% occurrence. No other crop types showed significant changes in frequency of occurrence, but set-aside only occurred on 1990-95 period farms, having been introduced in 1988 and made compulsory in 1992 (Firbank 1998). The difference in the area occupied by each crop was also analysed by comparing total crop area per farm with an unpaired t-test (omitting farms where the particular crop was not present). Only root crops showed a significant change, with the 1990-95 sample of farms having significantly larger mean area per farm than the early sample of farms, although the frequency of occurrence of root crops had decreased (t_{13} = 2.21, $P < 0.047$; mean ± SE 1965-70 = 3.99 ± 0.55 ha, n = 11; 1990-95 = 6.51 ±1.15 ha, n = 4).

There was no significant difference in crop diversity between periods (t_{42} = 0.15, n.s.; mean 1965-70 = 1.06 ± 0.10, n = 21, mean 1990-95 = 1.07 ± 0.08, n = 23). However, there was a significant difference in the mean number of field types per farm between periods (t_{42} = 2.24, $P < 0.031$), with farms in the 1965-70 period having almost four more crops per farm on average than farms in the 1990-95 period (mean 1965-70 = 14.48 ± 0.98, n = 21), mean 1990-95 = 10.83 ± 1.27, n = 23). Thus a greater variety of crops were grown in the early period, but the results imply that these additional crops only made up a small proportion of total farm area as there were no significant differences in diversity index which takes into account both the number of crops and the area that they occupy.

Factors affecting Skylark occurrence

When date was considered as a continuous variable, there were significant effects of crop type and farm on the probability of Skylark occurrence determined from individual registrations (likelihood ratio tests: crop χ^2_{10} = 32.57, $P <$ 0.001; farm χ^2_{34} = 681, $P < 0.001$). Winter cereals, brassicas and spring cereals had the highest probability of occurrence and rough grazing, permanent pasture, root crops and miscellaneous crops (mainly vegetables) had the lowest probability of occurrence, but many of these estimates had very wide confidence intervals (Table 3). There was no significant difference in the probability of occurrence between periods. The interactions between date and crop and period and crop also had significant effects (likelihood ratio tests: crop x date χ^2_{11} = 27.55, $P < 0.003$; crop x period χ^2_9 = 40.55, $P < 0.001$). This is because Skylarks showed different patterns of abundance within seasons and between time periods depending on crop type. When boundary type was added to the models (which reduced the sample size by 56% (n = 44), as boundary type was often not recorded), there were again significant effects of farm, crop type and date (crop χ^2_8 = 35.46, $P <$ 0.001, $P < 0.001$; farm χ^2_{16} = 209, $P < 0.001$; date χ^2_1 =19.27, $P < 0.001$) and parameter estimates were similar to those in Table 3, with spring cereals, set-aside, other cereals and winter cereals having the highest estimates (in that order) and permanent pasture the lowest. There was, however, no significant effect of boundary type (χ^2_4 = 5.50, n.s.).

When the effect of date was considered by using visit number as a categorical variable (and thus including more data), only the effects of crop and farm were significant (likelihood ratio tests: crop χ^2_{10} = 131.2, $P < 0.001$; farm χ^2_{43} = 769, $P <$ 0.001). Parameter estimates of the probability of occurrence in different crop types were mostly lower than those using date as a continuous variable and confidence intervals were narrower. This was because the farms that didn't have date recorded as a continuous variable happened to have a lower occupancy rate. Out of the total number of visits on all fields, Skylarks were present in 36.5% (n = 4000) of visits for farms where date was recorded as continuous, but were present only in 24.2% (n = 1021) of visits on the subset of farms where date was recorded only as categorical. The relative ranks of the parameter estimates were similar to those in the continuous date model, except that set-aside and spring cereals had the highest estimates (Table 3). Again, there was no

Table 3. The probability of Skylark occurrence in different crop types modelled using a binomial error structure with date expressed in two ways, as a continuous variable and as a categorical variable. Probabilities were determined from back-transformed parameter estimates derived from binomial logistic regression. Model deviance for date as a continuous variable = 3554, *df* = 3961, dispersal = 0.90. Model deviance for date as a categorical variable = 4162, *df* = 4414, dispersal = 0.94.

Date variable	Continuous		Categorical	
Category	Probability of occurrence	Confidence limits	Probability of occurrence	Confidence limits
Brassicas	0.28	0.09 - 0.67	0.08	0.04 - 0.16
Legumes	0.17	0.03 - 0.64	0.04	0.02 - 0.10
Miscellaneous	0.00	-	0.10	0.04 - 0.23
Permanent pasture	0.03	0.01 - 0.08	0.04	0.02 - 0.08
Root crops	0.04	0.01 - 0.14	0.08	0.04 - 0.17
Rough grazing	0.01	0.00 - 0.99	0.07	0.03 - 0.21
Set-aside	0.13	0.03 - 0.48	0.16	0.07 - 0.33
Spring cereals	0.23	0.09 - 0.51	0.12	0.06 - 0.23
Temporary grass	0.09	0.03 - 0.24	0.08	0.04 - 0.17
Other cereals	0.20	0.08 - 0.46	0.09	0.04 - 0.18
Winter cereals	0.25	0.11 - 0.51	0.08	0.04 - 0.18

Table 4. Parameter estimates for the seasonal variation in the probability of Skylark occurrence in different crop types in two periods, 1965-70 and 1990-95. Estimates were derived from binomial logistic regression of Skylark occurrence per field modelled with respect to date as a continuous variable. n/a = crop not recorded in sufficient number for parameter estimation. **P* < 0.05, ***P* < 0.01, ****P* < 0.001 (likelihood ratio tests).

Crop type	1965-70	1990-95
Brassicas	0.008 ± 0.012 n.s.	-0.011 ± 0.004**
Legumes	-0.006 ± 0.013 n.s.	-0.006 ± 0.004 n.s.
Miscellaneous	-0.007 ± 0.008 n.s.	n/a
Permanent pasture	0.010 ± 0.005*	0.002 ± 0.004 n.s.
Root crops	0.002 ± 0.004 n.s.	0.013 ± 0.008*
Rough grazing	0.006 ± 0.041 n.s.	0.044 ± 0.032 n.s.
Set-aside	n/a	0.003 ± 0.005 n.s.
Spring cereals	-0.004 ± 0.003 n.s.	-0.001 ± 0.003 n.s.
Temporary grass	0.001 ± 0.006 n.s.	-0.001 ± 0.004 n.s.
Other cereals	0.002 ± 0.002	-0.008 ± 0.004*
Winter cereals	-0.007 ± 0.004*	-0.008 ± 0.002***

significant effect of period. When boundary type was added to the model, crop effects were significant with parameter estimates that were similar to those from previous models, but there was once again no significant effect of boundary type (χ^2_4 = 5.98, n.s.).

Significant interactions in the continuous date model were investigated further by running the model on separate periods. There was no significant interaction between date and crop in the 1965-70 period (χ^2_9 = 8.85, n.s.) indicating relatively little variation in the seasonal pattern of Skylark occurrence between crop types in this period. In the 1990-95 period, this interaction was significant (χ^2_{10} =27.19, P < 0.001). When the effects of date were analysed for each crop type and period individually, the probability of Skylark occurrence declined significantly as the season progressed in winter cereals and increased in permanent pasture in the 1965-70 period (Table 4). In the 1990-95 period, Skylark occurrence declined in brassicas, winter cereals and other cereals as the season progressed, but for winter cereals the effect was at a much higher significance level than the earlier period (Table 4). Parameter estimates for spring and winter cereals were comparable in the 1965-70 period (spring cereal = 0.88, 95% confidence interval = 0.67 - 0.98; winter cereal = 0.86, 95% confidence interval = 0.62 - 0.98) but spring cereals were more likely to hold Skylarks in the 1990-95 period (spring cereal = 0.91, 95% confidence interval = 0.67 - 0.99; winter cereal = 0.79, 95% confidence interval = 0.52 - 0.96). The crop to show the greatest change between periods was root crops, where probability of occurrence had declined from 0.91 (95% confidence interval = 0.77 - 0.98) in 1965-70 to 0.53 (95% confidence interval = 0.26 - 0.86) by 1990-95.

Effects of crop diversity

The probability that Skylarks would be present at the whole farm level significantly increased with crop diversity, using a model with date as a continuous variable (χ^2_1 = 7.00, P < 0.009, parameter estimate = 0.38 ± 0.15). There was a significant decrease in the probability of occurrence with increasing date (χ^2_1 = 10.67, P < 0.002, parameter estimate = -0.007 ± 0.002), and the probability of occurrence at the farm level was, surprisingly, lower in the 1965-70 period (χ^2_1 = 90.09, P < 0.0001; parameter estimates, 1965-70 period = -2.99 ± 0.31, 1990-95 period = -2.70 ± 0.31). When visit was considered as a categorical variable, very similar results were obtained. When Skylark count (rather than occurrence) was analysed in relation to period, date and crop diversity using Poisson regression, there was no significant effect of crop diversity on Skylark count (χ^2_1 = 0.10, n.s.). There was no significant effect of date, but there was a significant effect of period, with counts in the 1965-70 period being greater than counts in the 1990-95 period (χ^2_2 = 125, P < 0.001; parameter estimates, 1965-70 period = -1.63 ± 0.24, 1990-95 period = -2.34 ± 0.24). When visit category was considered instead of date as a continuous variable, there was a weakly significant effect of crop diversity on Skylark count (χ^2_1 = 4.22, P < 0.04, parameter estimate = 0.24 ± 0.11). Once again, counts in the 1965-70 period were significantly higher than counts in the 1990-95 period. For both Poisson models (using either continuous date or visit category), dispersion was relatively high (6.49 and 6.79) indicating that these models were not a good fit compared to binomial models (0.63 and 0.66 respectively) and the latter can be considered to more be more reliable.

Factors affecting territory settlement and abandonment

The first and last date on which a registration was made for a particular territory was used to estimate dates of territory settlement and abandonment. Registrations not considered as belonging to a territory were not included. The 1965-70 period generally had a slightly later settlement date than the 1990-95 period (mean 1965-70 = 17 April ± 1.8 days, n = 128, mean 1990-95 = 13 April ± 2.0 days, n = 148), but the difference was not significant (t_{274} = 1.59, P < 0.11). However, the 1990-95 period had significantly earlier first visits overall (t_{431} =8.76, P < 0.001, mean 1965-70 = 4 April ± 1.15 days, n = 164, mean 1990-95 = 27 March ± 0.52 days, n = 249), so any differences in settlement date may have been due to a difference in early survey date between the two periods. The settlement date of Skylarks on the commonest crop types in each period are shown in Figure 2. In the 1965-70 period, winter cereal was settled on average 10 days earlier than any other crop and was significantly earlier than permanent pasture (t_{22} = 2.27, P < 0.001). In the 1990-95 period, winter cereal was second only to temporary grass in the average date of first settlement, although the former was a much more vari-

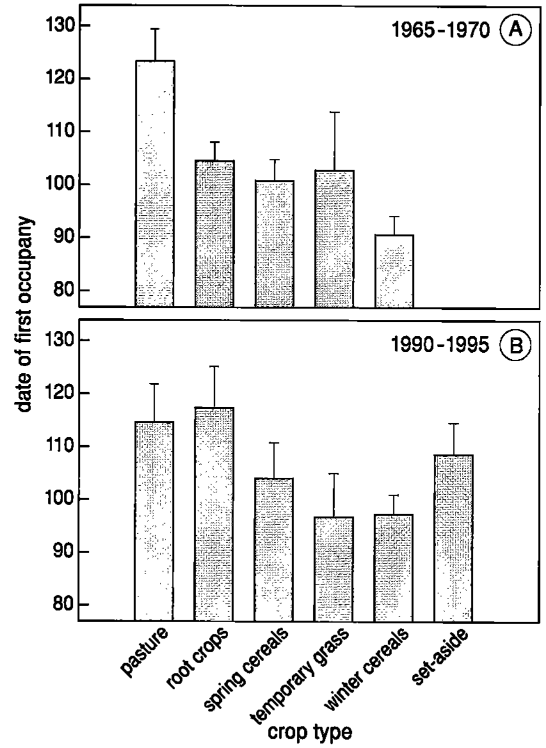

Fig. 2. Mean ± SE dates of first occupancy of Skylark territories in the commonest crop types in 1965-70 and 1990-95 periods.

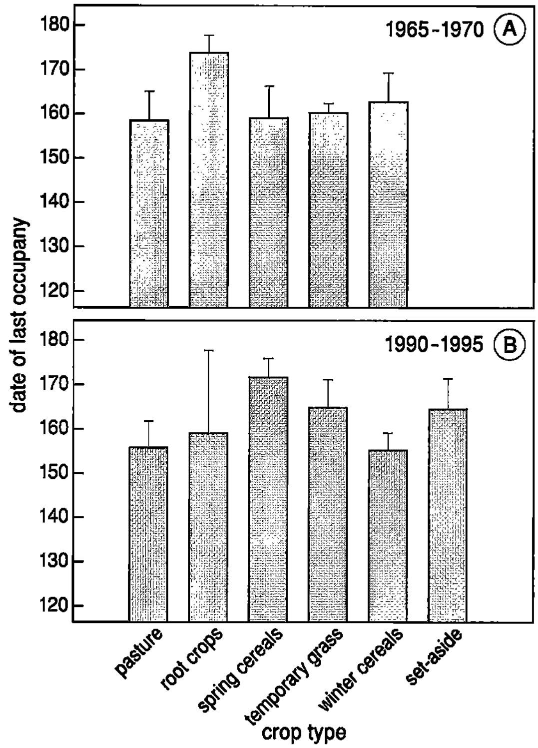

Fig. 3. Mean ± SE dates of last occupancy of Skylark territories in the commonest crop types in 1965-70 and 1990-95 periods.

able measure and no differences were significant between any crops.

The overall date of abandonment was earlier in the 1990-95 period (mean 1960-65 = 12 June ± 2.09, n = 128, mean 1990-95 = 6 June ± 2.11, n = 148), but the difference was not significant (t_{274} = 1.91, $P < 0.057$). Fig. 3, shows the mean dates of abandonment for the commonest crop types in each period. In the 1965-70 period, there is little difference between crop types, root crops being occupied the latest on average. In the 1990-95 period, spring cereals have the latest mean date of abandonment and winter cereals the earliest, a significant difference (t_{59} = 2.84, $P < 0.007$). Between the two periods, spring cereals were occupied for 12 days longer on average in the 1990-95 period, but this difference was not significant (t_{26} = 1.66, n.s.). This may have been an underestimate because there was a relatively large proportion of farms where spring cereals were occupied on the final visit, with 78% of final visits to spring cereals being occupied in the 1990-95 period, but only 36% of winter cereals (χ^2_2 = 9.94, $P < 0.01$). Respective figures for the 1965-70 period were 36% and 23% (χ^2_2 = 0.74, n.s.). Temporary grass was occupied for longer and winter cereals, root crops and permanent pasture were occupied for shorter times in the 1990-95 period, although for all of these crops the actual change in mean date is less striking than for spring cereals and no differences between periods were significant.

DISCUSSION

In terms of probability of occurrence, there was little difference between 1965-70 and 1990-95 periods when considering individual fields. At the whole-site level there was a significantly higher probability of occurrence in the 1990-95 period, although this was not very striking, as there were few CBC sites where no Skylarks were recorded on a given visit. Over all visits, Skylarks were present at the farm level in 89% ($n = 159$) of visits in the 1965-70 period and in 91% ($n = 205$) of visits in the 1990-95 period. More interesting was the significantly higher Skylark counts in the 1965-70 period at the site level. These contrasting results show that considering a simple measure such as occurrence may be misleading. The changes in abundance were more evident than changes in occurrence as Skylarks still occur over much of the countryside, but they are less numerous. A similar pattern is evident at a larger geographic scale, where Skylark abundance has declined by over 50% over 25 years (Chamberlain & Crick 1999), but change in the number of occupied 10 km squares has been negligible over a similar period (Gibbons *et al.* 1993).

The probability of a Skylark being present on a field was highest on spring cereals, set-aside, winter cereals and brassicas. These crops have previously been shown to be the most commonly used nesting habitats when considering the season as a whole (Wilson *et al.* 1997; Poulsen *et al.* 1998; Browne *et al.* 2000; Chamberlain *et al.* 1999b). However, crop use varies throughout the course of the breeding season, with winter cereals being occupied early on, but being abandoned later in the season when sward development results in it becoming unsuitable nesting habitat. Other crops, particularly spring cereals, that have less dense vegetation tend to be more extensively used later in the season (Wilson *et al.* 1997). Seasonal declines in the use of winter cereals, other cereals and brassicas were evident in this study, but there was no evidence of increasing use of spring cereals as the season progressed. In the 1965-70 period, there was little difference in either the seasonal trend in occurrence between spring and winter cereals, both showing a seasonal decrease, or in the date of territory abandonment between the two crops. However, in the 1990-95 period, spring cereals had a consistently higher probability of Skylark occurrence, and they were also abandoned later in the season, supporting breeding Skylarks an average of 16 days after territories on winter cereals had been abandoned (Fig. 3). Differences in non-cereal crops were less striking, although Skylark occurrence had declined in root crops between 1965-70 and 1990-95. This may have been because in the 1965-70 period, these crops would have been relatively low intensity fodder roots which were fairly widespread at the time, but in the later period most would have been more intensively produced potatoes or sugar beet.

There was a higher probability of Skylark occurrence on sites with a higher crop diversity, and a weak association between Skylark count and crop diversity. Similar relationships have been detected in other studies (Schläpfer 1988; Chamberlain & Gregory 1999; Chamberlain *et al.* 1999b). Such relationships are expected given that a range of crops may be exploited over the course of a breeding season (Schläpfer 1988). However, it should be noted that diversity *per se* may be less important than the actual crop types available (Chamberlain *et al.* 1999b). A farm with permanent pasture, rough grazing and temporary grass will be less suitable to Skylarks than a farm with equivalent areas of set-aside, spring cereals and winter cereals, yet the diversity will be the same.

Cropping changes and population declines

Whilst there are a number of possible (and not mutually exclusive) causes of the Skylark decline in Britain, much evidence to date suggests the switch from spring to winter sown cereals has had a major effect by reducing the number of breeding attempts which may be made in a season (Wilson *et al.* 1997). In this study, the overall higher Skylark occurrence on spring cereals and the later occupancy of spring cereals compared to winter cereals lends further support to this idea. The differences between the date of abandonment of cereals between periods imply that the relative suitability of winter cereals has decreased and the suitability of spring cereals has increased later in the breeding season between the late 1960s and early 1990s. There are a number of explanations for the differences between the date of abandonment of cereals between periods. Firstly, the difference may be due to a decrease in the suitability of winter cereals. Pesticide and fertiliser inputs have increased greatly since the late 1960s (Chamberlain *et al.* 1999a) which is likely to have lead to dense, faster growing crops which become unsuitable for nesting relatively early in the breeding season. This should apply to both types of cereals, so the fact that spring cereals have not shown the same decrease in the date of abandonment indicates that these may not have been managed in the same way. Pre-emergent herbicides are more likely to be used on winter cereals (Chamberlain *et al.* 1999a) and these had only just become commercially available in the late 1960s (O'Connor & Shrubb 1986). Also, use of growth regulators such as Cyclocel on winter cereals, which increase the density of cereal swards, has increased greatly since the 1960s (P.N. Watts, pers. comm.). A further explanation, not mutually exclusive with respect to that above, is that the difference between cereal types may arise due to farm level effects if the farms on which spring cereals are grown are for some reason less intensive than those farms with winter cereals. The pattern of change in spring cereals between periods was not representative of the national change, indicating that the sample of farms was atypical. Crop diversity was higher on farms where spring cereals were present in the 1990-95 period (t_{21} = 2.77, $P < 0.012$, spring cereals present: diversity = 1.32 ± 0.08 n = 8; spring cereals absent: diversity = 0.94 ± 0.09 n = 15), but there was no significant difference in the 1965-70 period (t_{19} = 0.81 n.s., spring cereals present: diversity = 1.19 ± 0.20, n = 6; spring cereals absent: diversity = 1.00 ± 0.11, n = 15). The effects of spring cereal in the 1990-95 period could therefore be confounded by habitat suitability at the site level.

In conclusion, Skylarks are associated with high crop diversity, spring cereals, set-aside and winter cereals. The suitability of the latter crop decreases through the breeding season. Winter cereals have declined in overall suitability between periods, being less likely to hold Skylarks and being abandoned earlier in the 1990s than in the 1960s, which may be due to increased growth rates brought about by increases in pesticide and fertiliser applications. Skylarks may now only be able to make a single early nesting attempt in winter cereals, but the great increase in the area of this crop since the 1960s and the general decrease in crop diversity may mean that alternative nesting habitats are unavailable. The possibility that the national population decline has been largely driven by increases in winter cereals and consequent reductions in the number of breeding attempts per season, by decreasing suitability of winter cereals, and by reduction in farm diversity was broadly supported by this work. Cereals are a particularly important habitat in terms of the UK population (Donald & Vickery *in press*), so their management may be an effective way to enhance the Skylark population by increasing the area of spring cereals, reducing inputs to winter cereals and increasing crop diversity.

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SAMENVATTING

De Veldleeuwerik *Alauda arvensis* is in grote delen van Noord-Europa sterk in aantal achteruitgegaan. Deze afname viel samen met perioden waarin de landbouw aan grote veranderingen onderhevig is geweest, zoals bijvoorbeeld een intensiever graslandbeheer, veranderingen van de tot dan toe gangbare wisselingen van gewassen in de akkerbouw, een toegenomen gebruik van kunstmest en bestrijdingsmiddelen en een hogere begrazingsdichtheid. De afname van de Veldleeuwerik wordt dan ook meestal in verband gebracht met de intensivering van landbouw en veeteelt en Europa. Het verlies van habitatdiversiteit, door grootschaligheid en door een vermindering van het aantal verbouwde gewassen in de landbouw, is voor de Veldleeuwerik waarschijnlijk van doorslaggevende betekenis geweest. In veel onderzoek naar de achteruitgang van de Veldleeuwerik werd de dichtheid en verspreiding van broedterritoria bekeken in relatie tot het type gewas (vooral graansoorten; het meest door deze soort gebruikte type bouwland om in te nestelen). Het naast elkaar verbouwen van winter- en zomergranen, met de daarmee

samenhangende veranderingen door het seizoen heen van bouwland met verschillende gewashoogtes, bleek van grote betekenis te zijn voor de mogelijkheden om per jaar meer dan één legsel groot te brengen. Ofschoon jong, opgroeiend graan voor Veldleeuweriken uitermate geschikt is om in te nestelen, is bijvoorbeeld kort grasland het meest geschikte terrein om op te foerageren. Kleinschalige landbouw, met veel kleine percelen en een grote verscheidenheid aan gewassen, is voor de Veldleeuwerik dan ook veruit het meest geschikt. De intensivering van de landbouw heeft niet alleen tot een verminderde diversiteit geleid, maar ook zijn de zaai- en maairegimes van graan zodanig veranderd dat bouwland met wintergraan tegenwoordig meestal ongeschikt wordt als broedterrein op het moment dat de voorjaars- en zomergranen nog geen alternatief bieden. De afname in de populatie wordt dan ook waarschijnlijk vooral veroorzaakt doordat er per jaar minder broedpogingen kunnen worden ondernomen.

Het meeste onderzoek aan Veldleeuweriken werd uitgevoerd nadat de afname in de populatie al goed merkbaar was, dus op een moment dat de landbouw al geïntensiveerd was. In dit artikel wordt getracht een vergelijking te maken van de veranderingen in talrijkheid van Veldleeuweriken gedurende het seizoen in relatie tot de veranderende gewassen voor- en nadat de landbouw geïntensiveerd raakte. Hiertoe werden gegevens uit de jaren 1965-70 (toen het aantal Veldleeuweriken toenam) vergeleken met materiaal uit de jaren 1990-95 (een periode met een geringe teruggang in de populatie na de drastische afname begin jaren tachtig). Over het algemeen waren de dichtheden Veldleeuweriken in de laatste periode aanmerkelijk lager dan in de eerste periode. De dichtheden Veldleeuweriken waren het hoogst in gebieden met een grote variatie aan gewastypen. Er werden duidelijke aanwijzingen gevonden dat de geschiktheid van bouwland met wintergraan in de laatste periode geringer was dan in de jaren zestig. Dit onderzoek ondersteunt de suggestie dat een afname van diversiteit in de landbouwgewassen heeft bijgedragen tot de afname van Veldleeuweriken. (CJC)

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