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Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland

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This paper analyses data from 995 Skylark *Alauda arvensis* nests found on lowland farms in southern England from 1996 to 1998. The majority of recorded nest failures were caused by predation except in agricultural grass, where trampling and agricultural operations were equally important. Nest survival rates varied between crop types, nests in cereals being around twice as likely to succeed as nests in grass or set-aside. In cereals, nest survival rates increased with increasing distance from the nearest tramline and declined over the course of the breeding season. Predator control also had a significant independent effect on nest survival rates. On one farm where many other factors were held constant, a highly significant increase in nest survival rates from 12.3% to 40.7% coincided with the introduction of intensive predator control, which also appeared to bring forward mean laying dates. Most environmental factors explaining significant variation in nest survival rates did so only at the chick stage. The mean number of chicks produced per nesting attempt was 1.26 in cereals, 0.78 in set-aside and 0.63 in grass, the differences being due primarily to variation in nest survival rates. Low densities of Skylark territories in cereal crops are not therefore the consequence of low breeding success at the scale of the individual nest and probably reflect limitations on the number of attempts made in a season. Measures taken to improve the attractiveness of cereal crops as a nesting habitat for Skylarks, and beneficial changes in grassland management, are likely to increase overall productivity.

The Skylark *Alauda arvensis* is a familiar bird of open habitats throughout much of the Palearctic. In recent years its population, in common with many other farmland species, has declined in Britain (Chamberlain & Crick 1999) and across much of mainland Europe (Tucker & Heath 1994). In Britain, declines were particularly severe in intensively farmed arable areas (Chamberlain & Crick 1999), although severe declines have also been recorded in some apparently unchanged non-farmland habitats (Hancock & Avery 1998). Declines in farmland bird populations have coincided temporally and spatially with a rapid intensification in agriculture (Chamberlain *et al.* 2000a, Donald *et al.* 2001a). Over 70% of Britain's estimated Skylark breeding population of one million pairs occurs on farmland, with a high proportion nesting in cereals (Donald & Vickery 2000).

Previous studies of Skylarks suggest that a number of factors could have contributed to population declines. In particular, Jenny (1990a), Wilson *et al.* (1997), Chamberlain *et al.* (1999, 2000b) and Donald and Vickery (2000) all recorded low and seasonally declining densities of Skylarks in cereals and suggested that this was at least partly due to the effects of changing vegetation structure. Many of the same studies, and others (e.g. Henderson *et al.* 1998, Vickery & Buckingham 2001, Donald *et al.* 2001b) have also pointed to the high densities of breeding Skylarks on set-aside relative to other field use types. Reforms to the Common Agricultural Policy (CAP) led to the widespread introduction of set-aside in 1992 as a way of reducing agricultural surpluses. Although set-aside seems generally to hold high densities of declining farmland bird species (Evans *et al.* 1997), doubts have been raised about its effectiveness as a palliative to general agricultural intensification as it covers too small an area and its introduction has not slowed farmland bird declines (Sotherton 1998).

In assessing the importance of any habitat to breeding birds, it is necessary to determine not only the number of birds present but also the contribution

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it makes to overall recruitment of new birds to the population, since territory density may not reflect habitat quality as defined by productivity (van Horne 1983, Vickery *et al.* 1992). In fields managed through the Conservation Reserve Program (CRP, a scheme similar to set-aside) in the USA, there was evidence that, although such fields attracted high densities of breeding birds, they acted as sinks for some species, productivity failing to balance mortality (McCoy *et al.* 1999). The same authors noted that the introduction of the CRP had not been reflected in population increases in the species using such habitats. Similarly, in Britain, farmland bird declines were not reversed by the introduction of set-aside.

The most important determinant of the number of chicks produced by a nesting attempt is nest survival rate (Martin 1993, Newton 1993). The commonest cause of nest failure is predation, which one estimate suggests accounts for an average of 80% of nest failures across a wide range of species and habitats (Martin 1993). Changes in nest survival rates have been shown to have the ability to drive population trends. For example, an increase in the nest survival rates of Grey Partridges *Perdix perdix* through the experimental introduction of nest predator control was found to result in greatly increased populations (Tapper *et al.* 1996).

As farmland Skylarks nest solely in open fields, the species is likely to be particularly susceptible to agricultural change. Earlier harvesting of winter cereals (particularly barley *Hordeum*), the increasingly frequent and early cutting of silage crops and increased livestock densities are all recent changes in agricultural practice that may have reduced Skylark nest survival. The increased use of pesticides may have had an impact by reducing food availability, and has been shown to have a negative effect on nesting success in other species (e.g. Fluetsch & Sparling 1994). Chamberlain and Crick (1999) demonstrated some significant regional differences in Skylark nest survival rates across Britain and showed that nest losses were higher in agricultural (particularly grassland) than in coastal or upland habitats. However, the factors influencing these differences could not be examined with the data available.

This paper identifies environmental factors explaining variation in Skylark nest survival rates and combines estimates of nest survival rates with previously published estimates (Donald *et al.* 2001c), taken from the same sample of nests, of the other parameters determining productivity at the scale of the individual nest. We aim to assess whether recent agricultural changes could have adversely affected productivity at this scale and thereby contributed to this species' recent population decline. In particular, we assess whether the observed low densities of territories in cereal crops reflect low rates of productivity there and whether the converse is true in set-aside. A detailed understanding of the factors affecting nest survival rates and therefore productivity is necessary to determine the likely impacts of future agricultural changes on Skylark populations, to determine more objectively the relative importance of different land use types as breeding habitats and to suggest measures which could improve farmland as a breeding habitat for this species.

METHODS

Selection of study sites

Farms were chosen to cover as wide a range of lowland farming types as possible and varied from intensive arable (with and without set-aside) through mixed arable and grass to intensive pastoral systems (Table 1). Farms were selected on the basis of the results of questionnaires sent to over 200 farmers asking for information on land-use types, cropping patterns and likely future changes, and without prior knowledge of their Skylark populations. All farms selected from the responses, with the exception of one organic hay system (Farm E in Table 1) and one set-aside and grazing marsh site covered only in 1998 (Farm Q), were conventionally managed, with input levels in terms of fertilizers and pesticides typical for their regions and farming types. The considerable differences in farming types across an east–west axis in southern Britain necessitated the selection of study sites from geographically widely separated areas. In 1996 and 1997, 13 farms were included in the study; four in eastern England (Norfolk and Suffolk), five in southern central England (Berkshire and Oxfordshire) and four in south-west England (Dorset) (Table 1). In 1998, nests were found on four additional farms in eastern England, four in southern central England and one more farm in south-west England. The selection of these farms followed as closely as possible the selection of the original 13.

Collection of data

Fieldwork was undertaken from the beginning of the breeding season at the start of April and continued until all nesting activity had ceased in early August.

Table 1. Distribution of nests geographically and by field type, with brief descriptions of farms and years of coverage. Predator control classes are also given (1 = no control, 2 = occasional or light control, 3 = heavy control). Predator control classes at farm A differed between years (see text). Regions: EA = East Anglia (Norfolk, Suffolk, Cambridgeshire), OX = Oxfordshire (plus 1, farm N, in Berkshire), SW = South-West (Dorset). Four farms in Oxfordshire covered only in 1998 where small numbers of nests were found are grouped.

			Nests found in:					
Farm	Region	Years	Cereals	Set-aside	Grass	Other	Control	Description
A	EA	96–98	35	383		4	1–3	arable with set-aside
B	EA	96–98	5		26	1	2	mixed arable/grass, no set-aside
C	EA	96–98	3				3	arable, no set-aside
D	EA	96–98	7	1		4	2	arable, little set-aside
E	OX	96–98			47		2	organic grass
F	OX	96–98	19	2	37	1	1	mixed arable/grass
G	OX	96–98	5	1	4		2	mostly winter cereals
H	OX	96–98	21		2		2	spring and winter cereals
J	SW	96–98	12	12	9	8	1	mixed arable/grass
K	SW	96–98		2			3	grass and fodder crops
L	SW	96–98	31	6		20	2	arable with set-aside
M	SW	96–98	5	53	20		2	mixed grass, some arable
N	OX	96–98	19	27	35	5	1	mixed arable/grass, set-aside
P	EA	98	4	12	4	1	1	arable, set-aside
Q	EA	98		30	12	3	1	set-aside, grazing marsh
R	EA	98	13	2		12	1	arable with set-aside
S	EA	98	8	4		1	1	arable with set-aside
T	SW	98	1	8			2	mixed arable/grass, set-aside
Others	OX	98	3	2		2	1/2	
Total nests			192	545	196	62		

Most nests were found by direct observation of nest-building, incubating or food-carrying adults, often made from a car or hide, although a small proportion was also found by the accidental flushing of incubating birds or cold searching areas which were repeatedly visited by birds. The number of nests found in each crop type was approximately proportional to the number of territories in each (Donald 1999). Subsequent visits were usually at least 2 days apart to avoid excessive disturbance. If the nest was found to be empty and previous visits suggested that any chicks would have been too young to leave, predation was assumed. The youngest age at which chicks were known to have successfully left the nest (in a sample of 95 nests for which leaving age was known exactly) was 6 days (mean = 7.9), so the disappearance of chicks aged 5 days or younger was recorded as predation. In fact, a high proportion of predations, particularly of older chicks, was accompanied by visible damage to the structure of the nest and, sometimes, remains of eggshells or chicks, allowing confident diagnosis of nest outcome. Most failures ascribed to agricultural operations or to starvation were based upon the observation of crushed eggs or chicks following such operations or to undamaged, underdeveloped dead chicks, respectively. Where an empty nest was thought to indicate that young had successfully left the nest, additional evidence was looked for, the most reliable indicators being fresh faecal sacs around the entrance to the nest, a well-flattened and undisturbed nest lining with feather scale present and adults carrying food or giving alarm calls nearby. Once the chicks had left the nest, they could not be followed, so the results of this work relate only to laying, incubation and the first 8 days post-hatch.

At each nest, the following were recorded: crop type, height of vegetation at the nest site, vertical density of vegetation at the nest site, distance of the nest to the nearest field boundary, distance of the nest to the nearest hedge or tree-line, and, in the case of nests in cereals, distance of the nest to the nearest tramline (the bare, unplanted tractor tracks found in modern cereal crops). Approximate first egg dates were back-calculated assuming laying at one egg per day and an incubation period of 10 days. Vegetation height and density were measured using a double sward stick, which measured the heights at which two discs, free to move up and down a 2-m central graduated wooden pole, were arrested by the vegetation when gently lowered onto it. The smaller lower disc had a diameter of 60 mm and weight of 107 g, the larger upper disc a diameter of 200 mm and weight of 83 g. Vegetation height was measured as the height at which the larger upper disc was arrested; density was calculated as the percentage of the height of the upper disc reached by the lower, smaller disc. The extent of predator control on each farm was assessed by questioning farmers and gamekeepers and was classified as absent, light or heavy (involving a professional gamekeeper).

Statistical analysis

Generalized Linear Models were used to model a binary nest outcome variable (failure or success) in terms of exposure (the number of days over which a particular nest was observed, Mayfield 1975) to derive an estimate of the daily nest survival rate (Aebischer 1999). As nest failure was very rarely witnessed as it happened, it was assumed to have occurred half-way between the last two visits. In cases where successful nests were revisited after the young had left the nest, we assumed that young left the nest 8 days after hatching and calculated exposure accordingly.

Analyses were carried out using GLIM (Aitken *et al.* 1989, Crawley 1993). Models assumed a binomial error distribution and a logistic link function was used to relate the binary dependent variable to the assumed error structure. The exposure period in days was entered as the binomial denominator. The reduction in residual deviance caused by entering an explanatory variable was treated as a likelihood ratio test and its significance assessed by comparing it with the χ^2 distribution with the appropriate number of degrees of freedom. In all cases the ratio of the residual deviance to the remaining degrees of freedom was lower than 2, and data were not overdispersed (Aebischer 1999).

Categorical variables entered into the models were crop type (a four-level factor of cereals, set-aside, grass and 'other'), region (three levels: East Anglia, Oxfordshire and Dorset), year (three levels: 1996, 1997, 1998) and predator control (three levels). The single farm in Berkshire was assigned to the region Oxfordshire for these analyses, since it was geographically closest to that region. Continuous variables entered were first egg date (measured as days from 1 April), distance from field edge and distance from nearest hedge or tree-line (both measured in m), height of vegetation at the nest (cm), density of vegetation at the nest and, for a subset of the data comprising nests in cereals only, distance in centimetres to the nearest tramline.

Not all nests contributed data to all the continuous variables. Consequently, a two-stage modelling process was adopted. All the categorical variables and the continuous variable relating to first egg date were available for 941 nests. Univariate and multivariate models related nest survival rates to the categorical variables and first egg date. In multivariate models, maximal models were fitted and each variable removed and replaced sequentially. At the end of each iteration, that explaining the least variance was removed. This process was repeated for egg-stage and chick-stage nests separately to assess whether factors affecting nest survival rates operated equally across the nesting period. Once the best multivariate model using the full data set had been determined, separate data sets containing only cases for which each of the other continuous variables was not missing were built. Univariate analyses were then carried out as before and the effects of each on nest survival rates assessed. Each was then added in turn to a model into which the categorical variables identified by the main analysis as being the most important had already been entered, to assess whether the continuous variable being tested added significantly to the model.

Since nests in the same field are likely to show some degree of autocorrelation in both their response and explanatory variables, there is a possible problem in nest-level analyses with pseudoreplication. Although the distribution of nests, with at least 10 and up to 16 farms contributing nests in each crop type (Table 1), from a large number of individual field/year combinations ($n = 290$) is likely to reduce this problem, a second set of analyses was carried out using fields rather than nests as replicates in Mayfield analyses. The response variable became the total number of failures in each field in each year, with the total number of exposure days in that field in that year (failures and successes combined) being entered as the binomial denominator. Since data from all nests within each field were combined, the subsequent analyses could only assess the effects of field-level factors (crop type, predator control, region, year) on nest survival rates.

The effects of predator control on nest survival rates were assessed in two ways. First, all nests were assigned a predator control value of 1 (nest on a farm with no predator control), 2 (nest on a farm with light or occasional control) or 3 (nest on a farm with intensive control by a gamekeeper) and this was entered as a three-level categorical variable in the models described above. However, the great majority of nests assigned a value of 3 (heavy control) were found on one particular farm in 1998 (Table 1), and a high proportion of these were in set-aside. A second approach arose fortuitously from the introduction of intensive predator control on one farm (Farm A in Table 1) where a large number of nests was found in set-aside ($n = 46$, 175 and 161 in 1996, 1997 and 1998, respectively). In 1996 there was no predator control on this farm (all nests assigned a control value of 1), in 1997 half of the farm was lightly controlled (control value 2) and the other half not controlled (control value 1) and in 1998 the whole farm was heavily controlled (all nests assigned a control value of 3). Predator control was targeted at mammalian predators, particularly mustellids, Hedgehogs *Erinaceus europaeus* and Red Foxes *Vulpes vulpes*. This analysis had the advantage of controlling many site and habitat factors, since all nests were found in the same 10 fields of the same habitat type (well-established, non-rotational set-aside) in all three years. Mayfield models were fitted using the same rationale as the full sample models described above.

The parameters of the GLIM models were used to derive daily nest failure rates, f, expressed as a proportion. Percentage nest survival rates over the whole of the nesting period, a more readily interpreted value, were calculated as $100[(1 - f)^{22}]$ where 22 is the approximate nesting period in days determined by observation (usually 4 days of laying, 10 days of incubation and chicks in the nest for 8 days).

RESULTS

The distribution of nests by farm and crop type is given in Table 1.

Causes of nest failure

Of the 995 nests found, the outcome of 964 could be assessed. Of these, 544 (56.4%) were successful (defined as at least one chick leaving the nest), 324 (33.6%) were predated and 96 (10%) failed due to other or to unknown causes. Other causes of nest failure included abandonment or starvation of eggs or chicks ($n = 56$, 13.3% of all failures), destruction of nests by agricultural operations ($n = 27$, 6.4% of all failures) and trampling by livestock ($n = 9$, 2.1% of all failures). There was a significant difference between six main crop types in the proportion of nest failures to predation and to all other causes of failure combined (Table 2). Examination of adjusted standardized residuals, which were treated as close approximations to z-scores, suggested that the difference arose from a higher than expected proportion of nest failures in set-aside being due to predation and a higher than expected proportion of nests in both grassland categories failing through causes other than predation. The identity of the predator was generally unknown, although it was considered that a wide range of taxa was involved.

Table 2. Causes of nest failure in six main crop types. 'Cropped grass' is defined as grass cut for silage or hay, 'Non-cropped grass' as grass used primarily for grazing or as an uncut ley. 'Other' comprises mainly nests on grass tracks or grassy field margins, with very small numbers each (< 10) in sugar beet, peas, rape, carrots and linseed. There was a significant difference between crop types in the proportion of failures due to predation and to other causes ($\chi^2 = 41.8$, $df = 5$, $P < 0.0001$).

	Type of failure	
Crop type	Predation	Other
Winter cereals	25	11
Spring cereals	9	6
Set-aside	199	25
Cropped grass	37	27
Non-cropped grass	11	9
Other	21	5

Nest survival rates

The overall daily nest survival rate (all crops, years and regions combined) was 0.938, equating to an overall nest survival rate over the whole nesting period of 24.2%. Daily failure rates calculated for the egg and nestling stages separately did not differ significantly. The results of univariate models are presented in Table 3. Of these the three having the greatest effect were the categorical variables representing crop type, the level of predator control and year. First egg date, vegetation height and distance to the nearest tramline (cereal nests only) also had significant effects, although α was not adjusted for multiple testing. In no cases did the addition of quadratic or higher order terms significantly improve the fit of the model. In a subset of the data relating to nests in cereals, the distance to the nearest tramline was found to have a highly significant effect on nest survival at the egg stage but no discernible effect at the chick stage (Table 3). Nests were significantly more likely to fail the closer they were to the nearest tramline.

Table 3. Univariate models of nest failure rate incorporating categorical and continuous variables. Other than first egg date and distance from field boundary, measurements of all continuous variables were available from 1997 and 1998 only. Results are given for the whole nesting period ('all') and for chick and egg stages separately.

Independent variable	*n*	*df*	χ^2 (all)	χ^2 (chicks)	χ^2 (eggs)
Categorical					
crop type	941	3	11.88**	14.62**	ns
predator control	941	2	15.23***	11.11**	ns
year	941	2	15.02***	21.44***	ns
region	941	2	ns	ns	ns
Continuous					
first egg date	941	1	4.86*	ns	ns
vegetation height	575	1	4.20*	ns	5.66*
vegetation density	575	1	ns	ns	ns
distance from field boundary	845	1	ns	ns	ns
distance from hedge/trees	665	1	ns	ns	ns
distance to nearest tramline[a]	141	1	4.06*	ns	14.6***

[a] Nests in cereals only.
*0.01 < P < 0.05; **0.001 < P < 0.01; ***P < 0.001.

Table 4. Multivariate models of nest failure rates using categorical variables and first egg dates for the whole nesting period and for the chick stage only. All other variables were deleted from maximal models. All variables were deleted for models of nest failure rates at the egg stage only. Values shown are the increases in deviance caused by deletion of each variable from the minimum adequate model.

Variable	*df*	All	Chicks
Crop type	3	17.6***	10.4*
Year	2	7.8*	10.5**
Predator control	2	7.6*	8.2*
Crop type*first egg date	4	14.3**	11.0*

*0.01 < P < 0.05; **0.001 < P < 0.01; ***P < 0.001.

Results of multivariate models are given in Table 4. For the whole nest period and for nests at the chick stage only, the minimum adequate models retained the crop type, predator control and year terms and the interaction between crop type and first egg date. All terms were deleted from the model relating to egg stage only.

Daily nest failure rates across the whole of the nesting period, estimated from the parameters of the GLIM model, are given in Table 5 for each of the three categorical variables selected separately by the multivariate model. Survival estimates for nests in set-aside at Farm A (which accounted for 70% of all set-aside nests) and for all other set-aside nests combined did not differ significantly ($\chi^2 = 0.13$, $df = 1$, $P = 0.7$) so all set-aside nests were combined in further analyses. *Post hoc* pair-wise tests were used to identify significant differences between levels in each of the three categorical variables. Nest survival rates did not differ significantly between farms where there was no predator control (group 1) and those where there was light or occasional control (group 2) ($\chi^2 = 3.28$, $df = 1$, $P = 0.07$), but survival rates were significantly higher in areas of heavy control (group 3) than in areas of no control ($\chi^2 = 13.3$, $df = 1$, $P = 0.0003$) and areas of light control ($\chi^2 = 4.03$, $df = 1$, $P = 0.045$). Nests in cereals had significantly higher survival rates than each of the other three field types, which did not differ significantly from each other. Nest survival rates were lower in 1997 than in 1996 or 1998 ($\chi^2 > 10.0$, $df = 1$, $P < 0.002$ in both cases).

The retention of the interaction of crop and first egg date (Table 4) indicated significant seasonal effects varying between crops. In cereals and set-aside, survival rates fell over the course of the season, whereas in grass crops survival rates increased. Height of vegetation at the nest-site and the distance of the nest from the edge of the field or from the nearest hedge or tree-line did not have an effect on nest survival rates in any case. There were no significant differences in nest survival rates between spring sown and winter sown cereals ($\chi^2 = 1.73$, $df = 1$, $P = 0.2$), nor between rotational and non-rotational set-aside ($\chi^2 = 1.1$, $df = 1$, $P > 0.2$).

The 941 individual nests were grouped into a total of 286 field/year combinations. Numbers of individual nests within these field/year combinations varied from

Table 5. Daily nest failure estimates (*f*) from GLIM models for each of the three categorical variables shown to have a significant effect on nest failure rates. *n* = sample size. The daily failure estimates are also expressed as overall nest survival rates (%). Results are presented from nest-level analyses (combined *n* = 941 for each factor) and from combined field-level analyses (combined *n* = 287) (see Methods).

		Nest-level analysis			Field-level analysis		
Factor	Level	*f*	*n*	(%)	*f*	*n*	(%)
Crop type	Cereals	0.0428	183	38.2	0.0419	99	39.0
	Grass	0.0722	173	19.2	0.0698	72	20.4
	Set-aside	0.0668	525	21.8	0.0673	83	21.6
	Other	0.0555	60	28.5	0.0555	33	28.5
Predator control	None	0.0720	463	19.3	0.0720	132	19.3
	Light	0.0596	305	25.9	0.0588	134	26.4
	Heavy	0.0411	173	39.7	0.0408	21	40.0
Year	1996	0.0542	199	29.3	0.0550	66	28.8
	1997	0.0794	348	16.2	0.0791	107	16.3
	1998	0.0537	394	29.7	0.0529	144	30.2

1 to 43 (mean = 3.3, se = ±0.3). The field-level analyses, which control for within-year spatial autocorrelation of nests from the same fields, produced virtually the same results as the nest-level analyses. Crop type, year and predator control again retained significant independent effects, with resulting daily failure rates virtually identical to those derived from nest-level analyses (Table 5). The number of nests found in each field/year combination had no significant effect on parameter estimates ($\chi^2 = 0.15$, $df = 1$, $P = 0.7$).

Predator control

On the north Norfolk farm where large numbers of nests were found in non-rotational set-aside and predator control levels changed over the course of the study, the effects of predator control could be investigated in more detail, since many other variables were held constant. There was a significant difference between the three years in the estimates of daily nest survival rates, with survival rates lower in 1997 than in 1996 or 1998 (Table 6). *Post hoc* pairwise tests showed that survival rates were significantly higher in 1998 than in the previous two years but that the observed difference between 1996 and 1997 was not significant. When predator control was fitted rather than the annual term, a rather different pattern emerged (Table 6), with survival rates appearing to rise over the three years of the study, although once again *post hoc* pairwise testing showed the only significant difference to be between 1998 and the other two years. As there was no variation between nests in predator control in 1996 and 1998, the difference between the annual and predator control models shown in Table 6 lay in variation between nests in levels of predator control in 1997. Previous analysis of the main data set showed that survival rates were significantly lower in 1997 than in the other two years of the study, but the predator control factor appeared to somewhat reverse the year factor at this site. A further model was fitted to the data from 1997 alone to assess whether control level (levels 1 or 2) had an effect. The addition of a predator control term approached significance ($\chi^2 = 3.41$, $df = 1$, $P = 0.06$), although since the half of the farm on which predator control was carried out in that year contained only two set-aside fields, sample sizes in this group were low ($n = 41$, as opposed to $n = 132$ on the other, uncontrolled, half of the farm).

Table 6. Daily failure rates (*f*) in nests in set-aside, 1996–98, on one farm in north Norfolk. There was a significant difference between years ($\chi^2 = 21.28$, $df = 2$, $P < 0.0001$) and between predator control classes ($\chi^2 = 23.48$, $df = 2$, $P < 0.0001$) in failure rates (see text for interpretation). Overall nest survival rates are also given.

	f	*n*	Overall survival rate (%)
Year			
1996	0.078	54	16.8
1997	0.086	189	13.8
1998	0.040	168	40.7
Predator control			
None	0.091	192	12.3
Light	0.064	51	23.3
Heavy	0.040	168	40.7

A series of one-way ANOVAs revealed that there were no significant differences on this farm between the three years of the study in the height or density of vegetation at the nest site, the distance of the nest from the edge of the field or the distance of the nest from the nearest hedge or tree-line ($P > 0.2$ in all cases). However, there was a significant difference in first egg dates between the three years, nesting attempts being on average around 10 days earlier in 1998 than in 1997 and around 15 days earlier than in 1996 ($F_{2,373} = 8.36$, $P < 0.001$). This difference may have been due to differences in the intensity of fieldwork through the breeding season between years, or to a particularly mild early spring in 1998. However, a comparison of first egg dates of nests on all other farms except this one showed no significant difference between years ($F_{2,548} = 0.456$, $P > 0.6$), suggesting real and site-specific effects. It is possible that increased predator control actually brought the average first egg date forward by reducing the numbers of early failures and late replacement clutches. In order to assess whether this difference in first egg dates could account for the observed differences in nest survival rates, the effects of laying date were assessed by modelling. First egg date had a significant effect on nest survival rates in a univariate model ($\chi^2 = 9.5$, $df = 1$, $P = 0.002$) but did not significantly reduce residual deviance when forced into a model already containing either a year or predator control effect. Similarly, when either year or predator control were forced into a model already containing the other, there was no significant effect on residual deviance, since the two were completely intercorrelated at this site in two of the three years.

Nest productivity

A number of different parameters need to be estimated if productivity at the scale of the individual nesting attempt is to be calculated and compared between crops. The productivity *p* (defined here as the number of chicks successfully leaving the nest) of an individual Skylark nesting attempt can be estimated as:

$$p = ch(1 - l)((1 - f)^{22})$$

where *c* is clutch size, *h* is the proportion of eggs which hatch, *l* is the proportion of chicks dying before they are old enough to leave the nest (excluding whole nest failures), *f* is the daily nest failure rate and 22 is the length in days of the nesting period (from the laying of the first egg to when the chicks leave the nest). The derived estimates of nest productivity presented above were entered into this equation with estimates of the other parameters from the same sample of nests (Donald *et al.* 2001c) to estimate nest productivity (defined as the mean number of chicks produced per nesting attempt). Estimates *l* and *h* did not differ between crop types, but clutch size and nest failure rates varied significantly and separate estimates of each were entered into the equation for each crop. Mean clutch size over the whole season was entered for each crop type and the nest survival rates given in Table 5 were used. Due to the higher survival rates of nests in cereal crops, these were found to be the most productive in terms of chicks produced per nesting attempt, despite having lower clutch sizes than nests in set-aside (Fig. 1).

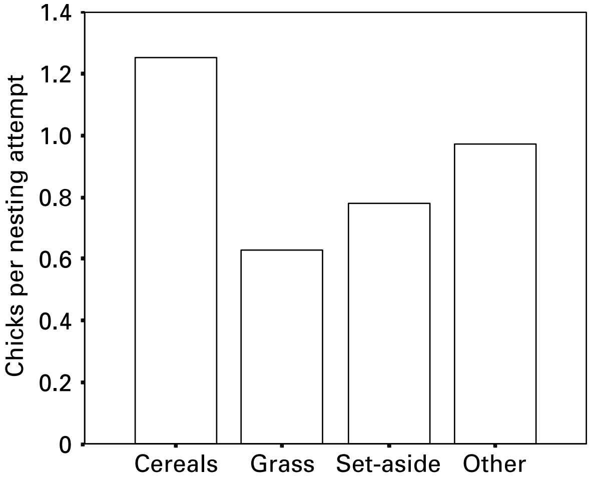

Figure 1. Estimated productivity, in terms of chicks produced per nesting attempt, of Skylark nests in four different crop types. 'Other' comprises mainly nests in grassy field margins or farm tracks and a small number of nests in various arable crops such as linseed and oil-seed rape.

DISCUSSION

Effects of nest visiting

Despite efforts to minimize disturbance of vegetation around the nest, the effects on nest survival rates of, often frequent, visiting could not be assessed. Previous studies of the effects of nest-visiting on other open nesting species were reviewed by Mayer-Gross *et al.* (1997), who concluded that any such effects are unlikely to be important. Galbraith (1987) showed that marking and visiting nests of Lapwings *Vanellus vanellus*, one of the very few other species that nest only in open fields, had no effect on nest survival rates. Several experiments with artificial nests have also tended to suggest that the effects of nest visiting are negligible. There were found to be no differences in failure rates of a sample of artificial lark nests that were visited and a sample that were not visited in Spain (Suárez *et al.* 1993), and no effects on nest survival of daily visits to artificial nests in open field habitats in the USA (Gottfried & Thompson 1978).

Limitations of the models

The models presented in this paper relate to observations made from the initiation of nest building to the chicks leaving the nest. The results therefore say nothing about the survival rates of chicks between leaving the nest at around 8 days of age and fledging at around 14–16 days. It is likely that leaving the nest well before fledging is a strategy designed to minimize predation, so it may be possible that total brood survival rates are higher after leaving the nest than before. The rapid tarsal development of this species indicates such a strategy (Donald *et al.* 2001d). Delius (1965) suggested that around 50% of chicks leaving nests on his non-farmland study site were still alive at 16 days and around 20% at 30 days, representing considerably higher survival rates than estimates for the nest stage calculated for the current study.

Causes of nest failure

The majority of nest failures were caused by predation, although there were significant differences between crop types in the numbers failing through predation and through other causes. In particular, losses of nests in grassland to trampling by livestock (particularly cows) and cutting of silage and hay crops were found to almost equal losses to predation. In contrast, few nests were lost to factors other than predation in cereals or set-aside. Schläpfer (1988), Jenny (1990a) and Wilson *et al.* (1997) also found that cutting of grass crops was the only agricultural activity to cause significant levels of nest failure. Jenny (1990a) recorded a significantly higher rate of loss to grass cutting than to predation on his largely grassland study site, with 95 out of 98 nests found in grass meadows failing to mowing, and low predation rates in cereals. None of these studies suggested that agricultural operations in non-grassland habitats were important causes of nest failure. On non-farmland sites the great majority of nest failures were ascribed to predation by Delius (1965) and Suárez *et al.* (1993). Long-term changes in the causes of nest failure of Skylarks are unknown, but data for the Corn Bunting *Miliaria calandra*, a farmland passerine similar to the Skylark in terms of nest-site selection, suggest that the proportion of nests lost to agricultural activity has increased since 1970 (Crick *et al.* 1994). It seems likely that changes in grassland management are also likely to have adversely affected Skylark productivity in this habitat.

Factors affecting nest survival rates

The results of this study suggest that significant variation in Skylark nest survival rates can be explained by several factors that act independently. The three main factors identified were crop type, the level of predator control and an additional annual effect that probably reflects an unmeasured variable, of which likely possibilities include weather effects and predator population levels or behaviour (the significantly higher proportion of failures due to predation in 1997 suggesting the latter). Although nest survival rates at the egg and chick stages did not differ significantly, the variables found best to explain variation in nest survival rates appeared to have an effect only at the chick stage, with survival rates at the egg stage appearing to be unaffected by any of the measured variables. The exception to this was in cereal crops, where a factor strongly affecting nest survival rates at the egg stage only was the positioning of the nest in relation to tramlines. The seasonal decline in nest survival rates in cereals is likely to be linked to the seasonal increase in the number of nests built next to tramlines (Donald & Vickery 2000), although harvesting also causes some very late nests to fail.

The lack of a significant effect of geographical region in any model suggests that the results obtained have some generality and are not the result of local factors. It also suggests that there were no systematic differences between fieldwork teams in the recording of exposure or nest outcome.

Despite the intensive nature of cereal management, skylark nests in cereals had significantly higher survival rates than those in untreated set-aside, a finding supported by Weibel (1999). This is in contrast to the results of Wilson *et al.* (1997), who found that survival rates in cereals were lower than in set-aside (due largely to higher rates of whole brood starvation). However, their sample sizes were considerably smaller and their analyses did not take account of other factors such as annual effects or predator control. The low nest survival rates in set-aside mirror those of another field nesting species,

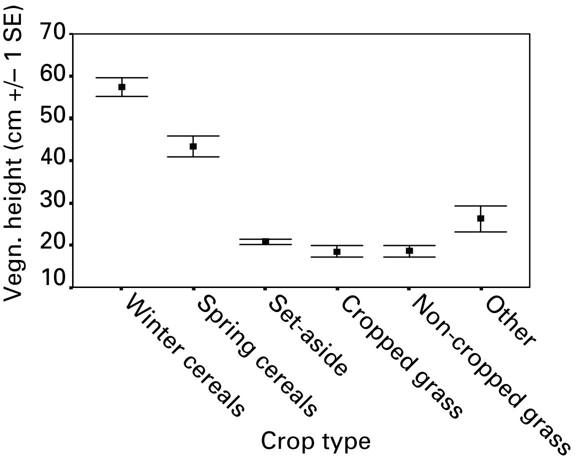

Figure 2. Height of vegetation at nest-site in six field types. There was a significant difference between groups ($F_{5,594}$ = 105.7, $P < 0.0001$). *Post hoc* testing (Tukey's Studentized range test) showed that winter and spring cereals differed significantly from each other and from the other four field types, and cropped grass differed from 'other' (grassy field margins, tracks and mixed arable crops).

the Dickcissel *Spiza americana*, in CRP fields in the USA (Hughes *et al.* 1999).

The scale of the difference suggested by the current study was unexpected, nests being around twice as likely to fail in grass or set-aside as they were in cereals, since previous work has suggested that predation risk is important in determining nest-site selection by this species (Suhonen *et al.* 1994) and since there is some evidence that pesticide applications can reduce nest survival rates (Fluetsch & Sparling 1994). Martin (1993) suggests that nest-site selection is made largely on the basis of avoiding nest predation and that this selectivity is important enough to explain many of the observed patterns of habitat selection and bird community structure that have traditionally been attributed to food availability and competition.

At least three possible explanations exist for the difference in survival rates between field types. First, nests in cereal crops were built under significantly higher vegetation than were nests in other habitat types (Fig. 2), possibly providing better cover from predators. The structure of the vegetation at a nest site has been shown by several previous studies (e.g. Tuomenpuro 1991, Hughes *et al.* 1999) to have an effect on survival rates of other farmland species. Secondly, generalist predator density may be lower in cereals than in less intensively managed habitats, particularly in set-aside where high plant and invertebrate numbers (Colston & Perring 1995) may attract them or their prey. Thirdly, there may be a density-dependent effect on predation, whereby certain individual predators specialize in searching for Skylark nests in areas of high nest density, but take nests opportunistically in habitats where the density of nests is low. Evidence for such a relationship was suggested by a study of Skylarks on a non-farmland site (Delius 1965). The lower survival rates at the egg stage of nests near or actually on tramlines in cereal crops might reflect this opportunism, since tramlines are likely to be used by mammalian predators as access routes through an otherwise dense habitat. Losses of nests near tramlines to crushing by tractors were rarely observed. Elevated rates of nest failure have been described from other linear habitats (e.g. Major *et al.* 1999).

The intensive management of cereal fields in terms of pesticide applications did not result in lower nest success rates compared to untreated set-aside. However, it is possible that reduced food supplies caused by pesticide applications on conventionally managed farmland might limit the number of nesting attempts made by a pair in a season or the number of territories a unit area could support.

Whatever the reason for the differences in nest survival rates between field types, it is apparent that Skylarks do not select nest-sites solely on the basis of maximizing nest survival rates, since territory densities are highest in habitats of low nest survival and lowest in habitats of high nest survival. It is therefore likely that there are compensations to nesting in areas of low nest survival rates, the most likely of these being an increase in productivity in terms of an increase in the number of nesting attempts made per season. A further consideration is that other determinants of habitat selection may outweigh considerations of probable productivity. Previous studies (e.g. Jenny 1990b, Wilson *et al.* 1997, Weibel 1998) have suggested that Skylarks select both nesting and foraging sites at least partly on the basis of vegetation structure, preferring a height of less than 50 cm for nesting and any height below 25 cm for foraging. Most nests in cereals are constrained to be built in vegetation higher than this (Fig. 2), since increasingly rapid cereal development means that by the onset of the main breeding season crops are already higher than this. The effects of crop structure on Skylark territory density have been discussed by Wilson *et al.* (1997), Chamberlain *et al.* (1999, 2000b), Donald and Vickery (2000) and Donald *et al.* (2001b).

Predator control

Intensive predator control is carried out on British farmland primarily as a way of increasing game-bird populations for sporting purposes (Tapper 1992). Experimental studies have shown that predator control has significant effects on nest success rates and subsequent populations (e.g. Anthony *et al.* 1991, Tapper *et al.* 1996). However, a meta-analysis of a number of studies suggested that, while predator control had a positive effect on nest survival rates and post-breeding population sizes, its effect on subsequent breeding populations was often not significant (Côté & Sutherland 1997). Poor nest success rates of a number of lark species and other ground nesters on a newly designated nature reserve in Spain were related to a reduction in predator control (Suárez *et al.* 1993). However, the effects of predator control on declining non-game farmland species such as the Skylark have not been examined in detail. Although Stoate *et al.* (1998) recorded no significant increase in Yellowhammer *Emberiza citrinella* nest survival rates in central England with the introduction of predator control on their study site, they also noted that nest survival rates there were already higher than the UK national average.

The results of the present study strongly suggest that predator control significantly increases Skylark nest survival rates. Despite not following a rigorous experimental structure like the work of Tapper *et al.* (1996), the effects of the introduction of predator control at one farm, where many other variables could be held constant between years, reinforced this conclusion. The finding that nest survival rates are significantly affected by predator control requires careful interpretation. While intensive predator control might be considered in the conservation of individual populations, it is not likely to be a practical solution to addressing national population declines. Although across Britain the highest overall Skylark densities generally occur within areas of highest predator control (Tapper 1992, Gibbons *et al.* 1993), it is unlikely that declines in levels of predator control are an important factor in recent population declines. Population declines have been recorded in regions where there is no history of predator control (e.g. Hancock & Avery 1998). Furthermore, the presence of intensive predator control does not necessarily result in high subsequent breeding populations (Côté & Sutherland 1997); the lowest densities of Skylark territories found in the present study were recorded on the two farms (Farms C and K in Table 1) with the highest levels and longest history of predator control of any in the study. It is likely that habitat selection and food availability are the primary determinants of territory density but that once nesting has commenced, predator control has a significant effect on nest outcome.

Implications for conservation

This study supports previous work suggesting that nest survival rates in farmed grassland are low due to the high rates of nest loss to agricultural operations and to trampling by livestock. Measures taken to reduce the number of cuts taken from silage fields and so lengthen the gaps between such cuts to allow birds time to nest and raise chicks to independence (a total period of around 32 days) are likely to improve the species' breeding success on grassland. The promotion of lower-density stock grazing would have the double effects of raising sward heights to a level suitable for nesting attempts to be made (many pasture fields are too heavily grazed for birds to have sufficient cover to build nests) and reducing the number of nests lost to trampling.

Previous assessments of the value of cereal fields as a breeding habitat for Skylarks have typically been based only on the generally low density of territories present and the assumption that food availability is low and starvation rates therefore high. The high nest survival rates of Skylarks in cereal fields relative to other crop types suggest that this is in fact potentially a very productive breeding habitat. Measures to increase territory densities in cereal crops, such as the provision of safe nesting sites away from tramlines, are likely to be very effective in the conservation of this species since cereals hold a high proportion of the overall population (Odderskær *et al.* 1997, Donald & Vickery 2000).

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