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Population declines and reproductive performance of Skylarks *Alauda arvensis* in different regions and habitats of the United Kingdom

DAN E. CHAMBERLAIN* & HUMPHREY Q.P. CRICK

British Trust for Ornithology, The Nunnery, Thetford, Norfolk IP24 2PU, UK

Declines in the number of breeding Skylarks *Alauda arvensis* and changes in their reproductive performance were analysed using data from two long-running surveys co-ordinated by the British Trust for Ornithology: the Common Birds Census and the Nest Record Scheme. In the UK, the number of breeding Skylarks declined by approximately 55% between 1975 and 1994. This decline was steepest in agricultural habitats and in regions associated with intensive agriculture. In contrast, Skylark reproductive performance per nest, in terms of clutch size, brood size and post-hatching survival rate of nests, showed a general improvement over time. This improvement was greatest in intensively farmed agricultural habitats. Therefore changes in reproductive performance per nesting attempt were probably not responsible for the decline in numbers. It is inferred that possible causes of the decline of the Skylark are: reductions in the number of breeding attempts per pair per season, reductions in the proportion of birds attempting to breed, and increased mortality outside the breeding season.

Skylarks *Alauda arvensis*, in common with a number of other bird species, have shown large declines on farmland in northern Europe (Hustings 1992, Tucker & Heath 1994, Fuller *et al.* 1995). Over the last few decades, major changes have occurred in the management of agricultural land which have been implicated as a cause in the decline of farmland birds (O'Connor & Shrubbs 1986). These changes include the following: (1) increased specialization of land-use, (2) a switch from spring to autumn-sown cereals, resulting in a reduction of food-rich winter stubbles and a faster developing and a denser sward, (3) intensification of grassland management and loss of traditional rotational systems, (4) an increase in the diversity and amount of pesticides applied (O'Connor & Shrubbs 1986, Potts 1986).

Skylark breeding density has been shown to increase with crop diversity (Schlöpfer 1988, Jenny 1990a, 1990b) and with the proportion of ley grass used as part of a rotation (O'Connor & Shrubbs 1986, Petersen 1996), which provides a beneficial mix of habitats for nesting and feeding. However, the diversity of field use and the amount of temporary grass leys have decreased

in the UK since the early 1970s, both of which may have adversely affected the Skylarks in the UK (O'Connor & Shrubbs 1986). Stubbles are rich in weeds and probably hold very important food supplies for seed-eating birds over the winter, and their reduction has been implicated in the decline of the Cirl Bunting *Emberiza cirlus* (Evans & Smith 1994) and the Corn Bunting *Miliaria calandra* (Donald & Evans 1994). The widespread introduction of autumn-sown cereals may also have affected Skylarks in the breeding season by providing a dense sward which is less attractive as a nesting habitat than spring-sown cereals (Schlöpfer 1988, Evans *et al.* 1995). Increased pesticide application has been shown to be a major factor in the decline of the Grey Partridge *Perdix perdix* (Potts 1986) due to a reduction in their chicks' invertebrate food sources, which are affected both directly via insecticides and indirectly through the action of herbicides on important host plants (Sotherton 1991). Skylarks and other bird species, which are dependent on invertebrate food sources for rearing nestlings, may have been similarly affected.

Other hypotheses for the decline of farmland birds have received less attention than those dealing with changes in agricultural management. These include the possible effects of climate change, disease and

*Corresponding author.

predation (Fuller *et al.* 1995). However, it is likely that these would only become apparent if other factors (e.g. food abundance) make the birds weaker. A further possible factor, which may be related to farming practices, is the impact of increasing numbers of predators. Corvids are frequent predators of Skylark nests (Delius 1965). Magpies *Pica pica* and Carrion Crows *Corvus corone* have increased in number on farmland since the 1960s (Gregory & Marchant 1996) and might be expected to have caused an increase in rates of nest failure. This was studied for a number of species, including Skylark, in relation to Magpie population density but no evidence of an effect was found (Gooch *et al.* 1991).

Raptor numbers have increased steadily since the early 1970s after the catastrophic declines caused by the use of organochlorine pesticides (Newton 1979). These increases have been most evident in intensively farmed areas of eastern England where Sparrowhawks *Accipiter nisus*, the main avian predators of farmland passerines, were almost totally wiped out by the early 1960s (Newton 1986). Any impact of increases in Sparrowhawk predation may therefore be more evident in eastern England than elsewhere in the UK. The effect of predators on prey numbers is a contentious issue, but previous work has suggested that, at least in the case of the Sparrowhawk, increased numbers are unlikely to affect breeding numbers of their prey (Newton 1993).

We compare changes in population size and measures of breeding performance (clutch size, brood size, lay date, and mortality rates of eggs and nestlings) of the Skylark in different habitats and regions of the UK using data from two long-running surveys co-ordinated by the British Trust for Ornithology (BTO): The Common Birds Census (CBC) and the Nest Record Scheme (NRS). The aim of the study was to determine whether declines in Skylarks were associated with agriculture and whether these declines could be explained by variations in breeding success.

METHODS

Common Birds Census

The CBC is an annual survey which was started in 1961 to monitor changes in breeding bird numbers in the UK. It involves volunteer observers visiting census plots between six and ten times during the breeding season to map the number and position of all territorial birds. These maps are analysed by trained BTO staff to estimate the number of breeding territories of

each species according to predefined criteria. Full survey methods can be found in Marchant *et al.* (1990). Currently, there are 230 plots covered under the CBC, the majority of which are in farmland or woodland habitats, although there are a smaller number which cover a variety of other 'special' habitats, including heathland, moorland and chalk downland. The data are primarily used to calculate indices which reveal relative changes in bird numbers through time and which are directly proportional to density because the area of plots is constant between any two adjacent years. The index does not provide a measure of change in range.

A potential bias of the CBC is that plots are not randomly distributed over the UK, but are chosen by the volunteer surveyors who live mainly in southern England. Data from the CBC may therefore be unrepresentative of the UK as a whole, but it has been found to be representative for most of lowland England south of the River Humber and east of the River Severn (Fuller *et al.* 1985). For this reason, indices have been determined on a regional basis, dividing the data into north, southeast and southwest Britain (shown in Fig. 1). Northern Ireland was excluded in the regional analysis because of insufficient samples. Plots were also analysed at a finer scale according to the surrounding habitat, being grouped into agricultural, upland and coastal habitats (the latter two being mainly 'special' CBC plots), defined using the Institute of Terrestrial Ecology land classification of each 10-km square of the national grid in Britain (Bunce *et al.* 1996). Finally, individual farmland plots were classified as predominantly arable or pasture according to habitat data collected as part of the CBC. Farms defined as mixed actually encompass a wide range of farm types with variable proportions of arable land and pasture. The comparison was therefore limited to those plots which comprised close to 100% arable or 100% pasture.

Modern indexing methods such as log-linear Poisson regression (McCullagh & Nelder 1989) model a matrix of site counts by years, with site and year effects (ter Braak *et al.* 1994). The year effect is an index of change in numbers; the site effect describes how each site deviates from the overall trend where the first of a run of years is set at an index of 1 and units of change are arbitrary. We implemented this technique by using TRIM (Trends and Indices for Monitoring data) software (ter Braak *et al.* 1994). Following the methods of Peach and Baillie (1994), a run of data from a single plot was divided into sections. These were treated separately if a discontinuity occurred due to changes in observers or if the plot was not surveyed fully in a particular year.



Figure 1. Regions of Britain used in Common Birds Census and Nest Record Card analysis of Skylarks. For Common Birds Census analysis: north = Scotland + north, southeast = midlands + southeast + East Anglia.

Log-linear Poisson regression can fit models to the data to incorporate covariates (e.g. habitat type) if required. A χ^2 goodness-of-fit test and a Wald test were carried out on each model. A significant result in the former test showed that there was heterogeneity in the data and that the model did not provide a good fit. The Wald test is analogous to a homogeneity of slopes test between covariate levels and significance indicates differing slopes between levels. An assumption of the modelling procedure is that the count data are not overdispersed with respect to the mean (i.e. that the variance/mean ratio should equal unity); the coefficient of dispersion for the Skylark data was 0.96, sufficiently close to unity for the assumption not to be violated.

Two types of model were fitted to the data. The first

incorporated individual plot and year effects to reveal the detailed pattern of changes in population size in different covariate levels over time. However, a Wald test for this model tells us nothing about the nature of the differences between levels, only that a difference exists. A second model which fits linear trends was therefore used to compare covariate levels using a Wald test, providing the model fitted (i.e. non-significant χ^2 test). The modelling program (TRIM) limited the number of covariate and year combinations which could be incorporated into the models, thereby reducing the maximum number of levels in this analysis to three.

Nest Record Scheme

The Nest Record Scheme (NRS) was set up in 1939 and monitors the annual breeding performance of a wide range of species. Sample sizes in early years were typically small, so our analyses only consider data from 1950 onwards. (For a complete review of the NRS, see Crick & Baillie, 1996). Data collection is made by volunteer ornithologists who complete Nest Record Cards (NRCs) for each nest found. Information recorded on the NRC includes: (1) details of nest site, (2) habitat, (3) the contents of the nest at each visit and (4) evidence of success or failure. The number of breeding attempts per pair per season cannot be estimated from NRS data.

In the following analyses, Skylark NRCs were analysed at increasingly fine levels of region (shown in Fig. 1) and habitat in order to determine: (1) how measures of productivity and reproductive success of individual nesting attempts vary across regions and habitats defined at different scales, (2) whether these measures have changed over time and (3) whether annual changes have been consistent across regions and habitats. These analyses were designed to give an insight into whether reproductive success per nesting attempt has contributed to the decline of the Skylark and whether different levels of reproductive performance are associated with particular regions or habitats. Six different variables were analysed: (1) lay date of the first egg in a clutch (where day 121 = 1 May), (2) clutch size, (3) brood size, (4) partial hatching loss, which is a measure of brood reduction (and includes early nestling mortality and partial hatching failure), calculated as the difference between the clutch size and brood size of individual attempts, $1 - (\text{brood size}/\text{clutch size})$, (5) daily failure rates of whole nests at egg stage and (6) daily failure rates of whole nests at nestling stage. These last two are

referred to as daily clutch and brood mortality rates respectively, and were calculated from the methods of Mayfield (1961, 1975) and Johnson (1979). Partial hatching loss was transformed using the arcsine square-root function before analyses.

Mayfield's methods were used to determine nest failure rates because nests monitored by the NRS are not usually found before egg-laying and may not be watched to conclusion. If early losses are not taken into account, then calculation of nest success as the proportion of nests found that were successful will overestimate success. Similarly, if nests that are not watched to outcome are discounted, failure rates increase unrepresentatively because nests which fail quickly are included in the sample while those that existed longer than the observations (and which were likely to include some successes) are excluded. If the unknown outcomes are included, then nest success will be artificially inflated because of the omission of subsequent failures. Mayfield's method overcomes these problems and makes maximum use of available data. All nests are included, so long as they have been revisited at least once to allow the calculation of daily failure rates of nests. There are 11 assumptions associated with the Mayfield method (Crick & Baillie 1996), the majority of which are clearly met by NRS data. One of the critical assumptions is that daily survival rates are constant over the period of calculation. We have assumed that nest failure rates are constant over the egg period and over the nestling period. Although this is unlikely to be true, the values calculated are useful for comparative purposes, assuming that observer behaviour has not changed appreciably over the years, and are used as such in this paper.

Calculations of average lay date only included cases where estimation by back-calculation was within ± 5 days. Clutch sizes were not accepted if egg-laying could have continued after the last visit. Brood size was taken as the maximum recorded. A minimum of two nest visits was required to calculate each variable, apart from brood size. As these criteria were different for each variable, sample sizes differ. A possible source of bias in the data was that large numbers of cards were sometimes submitted from intensive surveys from a single study site and nest recorder. An attempt was made to minimize this bias by only analysing one NRC (selected at random) per observer per year.

The productivity data (lay date, clutch size and brood size) were analysed in three different ways: (1) with respect to year with linear, quadratic and cubic regressions, (2) with respect to region and habitat with

ANOVA and (3) with a general linear model (GLM) incorporating year effects and the year \times habitat interaction to test for homogeneity of slopes. All regression and GLM analyses used annual means weighted by sample size in order to reduce the influence of means with small sample sizes. We analysed nest mortality rates using pair-wise comparisons with z-tests for the difference between two means (Hensler & Nichols 1981).

RESULTS

Changes in the abundance of breeding Skylarks

Indices of the change in numbers of Skylarks on CBC plots in the UK (omitting woodland plots) between 1962 and 1994 are shown in Figure 2. Numbers increased steeply at first and then levelled off in the late 1960s. This pattern has been observed in many passerines, and is indicative of population recovery after the severe winter of 1962/63 (Marchant *et al.* 1990). The CBC index was then stable until the mid-1970s when there was a marked decline, with a particularly severe decrease between 1981 and 1982. Analyses below were restricted to the period from the start of the decline in 1975. A linear trend fitted the data from 1975 onwards (goodness-of-fit test: $\chi^2_{1497} = 1392$, $P = 0.97$) and estimated a decline in Skylark numbers of $55 \pm 3.6\%$ (95% confidence limits) up to 1994. A linear trend also fitted the data from 1982 onwards ($\chi^2_{902} = 700$, $P = 1.0$) showing that Skylarks continued to decline after the severe 1981–82 fall (slope \pm se = -0.019 ± 0.004).

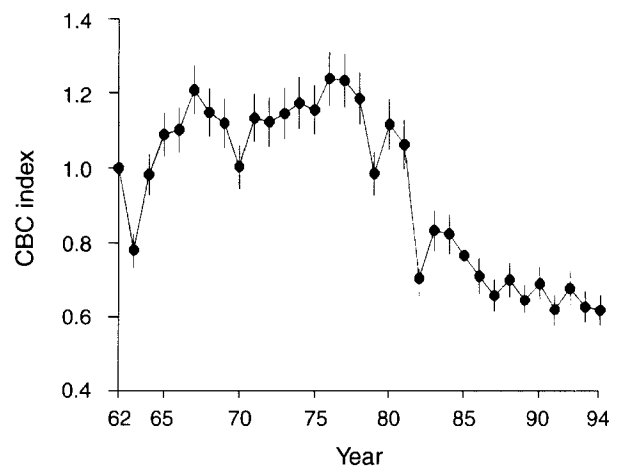


Figure 2. CBC indices of Skylarks between 1962–1994, combining farmland and 'special' plots. Results are means \pm se.

Further analyses were conducted to see if the declines were associated with particular regions or habitat types. CBC indices were determined for Skylarks from 1970 to 1994 in three regions of Britain: north, southwest and southeast (Fig. 1). Linear trends fitted the data from 1975 onwards ($\chi^2_{1408} = 1300$, $P = 0.98$). There was no significant difference in trend between regions (Wald test: $\chi^2_2 = 3.20$, ns; slopes \pm se: north -0.034 ± 0.003 , southwest -0.024 ± 0.006 , southeast -0.029 ± 0.004).

Next, analyses were carried out after grouping plots into agricultural, upland or coastal habitat defined at the 10-km square level. The trend of changes in Skylark numbers in agricultural habitats (Fig. 3a) was very similar to that in combined habitats (Fig. 2), reflecting the fact that the majority of CBC plots in the latter were farmland. There were decreases in the other two habitats (Fig. 3b & 3c), although not as steep as that in agricultural habitats. Linear trends fitted the data from 1975 (goodness-of-fit: $\chi^2_{1455} = 1323$, $P = 0.99$) and slopes differed significantly between habitat types (Wald test: $\chi^2_2 = 33.2$, $P < 0.0001$) with agricultural habitats showing a steeper decline than coastal or upland habitats (respective slopes \pm se were -0.049 ± 0.003 , -0.016 ± 0.006 and -0.035 ± 0.006). The detailed patterns of decline were different across the three habitats. The farmland CBC index showed a sharp decline in the late 1970s and early 1980s followed by a less steep decline thereafter. The trend in coastal habitat showed a shallow decline in the late 1970s and early 1980s followed by stability. Skylark CBC indices from upland habitat showed the opposite trend to these, with a period of stability followed by a progressive decline from about 1980. The difference in linear trend between habitats was significantly different when considered from 1980 onwards ($\chi^2_2 = 15.3$, $P < 0.001$), with agricultural and upland habitats showing similar rates of decline, respective slopes (\pm se) being -0.038 ± 0.030 and -0.043 ± 0.078 , but the decline in the coastal habitat was at a significantly slower rate of -0.009 ± 0.009 per year.

Agricultural plots were further divided into predominantly arable and predominantly pasture using habitat data collected as part of the CBC. The trends in the CBC index on both types of farmland were generally very similar and showed the large drop in index between 1981 and 1982. Although the decline in CBC index was less steep on pasture than arable farmland, it was not significant from 1975 onwards (Wald test: $\chi^2_1 = 3.00$, ns, slopes \pm se arable -0.046 ± 0.006 , pasture -0.021 ± 0.014).

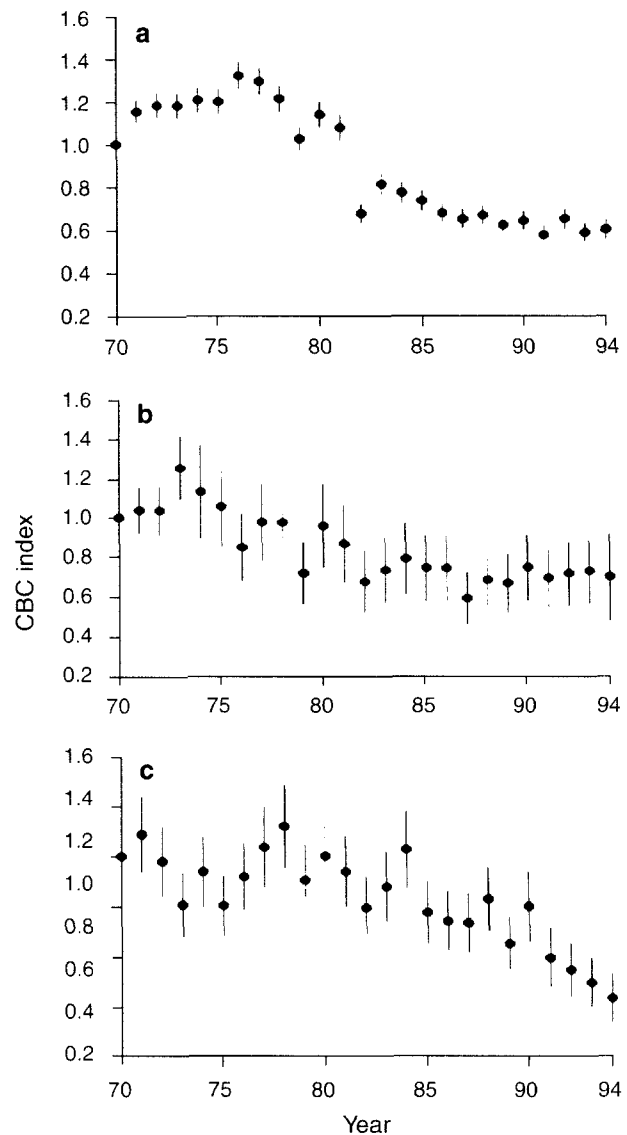


Figure 3. CBC indices of Skylarks between 1970 and 1994 in three broadly defined habitat types: (a) agricultural; (b) coastal; (c) upland. Results are means \pm se.

Nest record analysis

Annual mean lay date, clutch size, brood size, partial hatching loss, clutch mortality rate and brood mortality rate were analysed with linear, quadratic and cubic regressions from 1950 onwards (Figs 4 & 5). Lay date did not show any significant trend over the years (Fig. 4a). Both brood size and clutch size increased linearly and significantly between 1950 and 1994 (Fig. 4b & 4c), but there was no effect of year on partial hatching loss (Fig. 4d). Quadratic and cubic terms did not provide significant improvement in fit

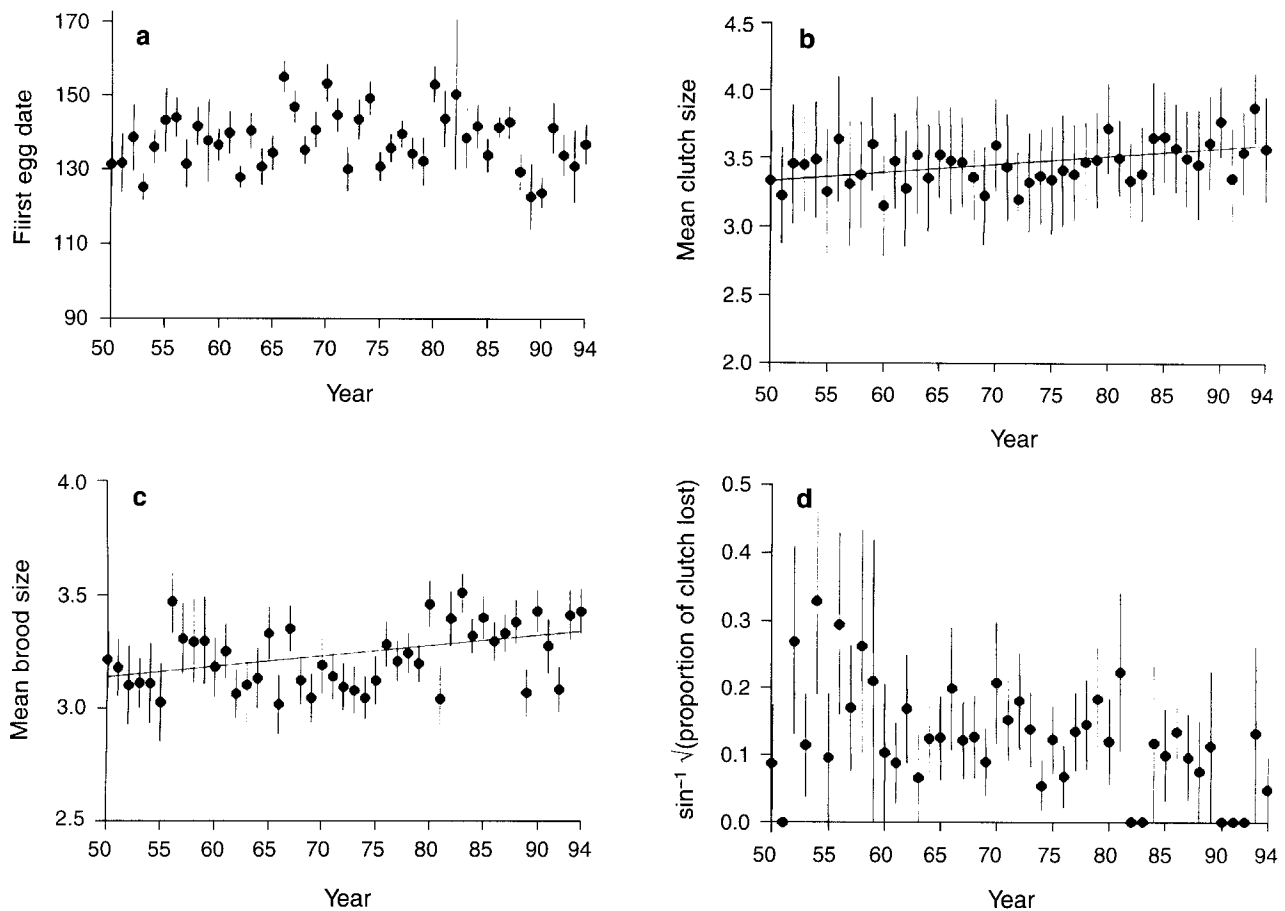


Figure 4. Annual variation in lay date (a), clutch size (b), brood size (c) and partial hatching loss (d) of Skylark nests. Lay date (where 121 = 1 May), clutch size and brood size are expressed as mean \pm se, partial hatching loss as arcsine square-root-transformed. Regression: (a) $F_{1,43} = 0.01$ n.s., $r^2 = 0.0002$; (b) $F_{1,43} = 7.16$ $P < 0.01$ $r^2 = 0.14$, clutch size = $3.01 + (0.0063 \times \text{year})$, se of slope = 0.0024; (c) $F_{1,43} = 4.68$ $P < 0.04$ $r^2 = 0.10$, brood size = $2.91 + (0.0046 \times \text{year})$, se of slope = 0.0021; (d) $F_{1,43} = 2.89$ n.s., $r^2 = 0.03$. Regressions were weighted by sample size. Points with no error bars indicate all samples had the same value for a given year (se = 0).

when added to these models.

There were no significant long-term trends in clutch or brood mortality rates (Fig. 5). In order to overcome problems of small sample sizes in subsequent analyses of regional and habitat differences, mortality estimates were divided into an early period (1962–74) when Skylark numbers were increasing or stable, and a late period (1975–94) when numbers were declining (Fig. 2). There was no significant difference in clutch mortality rates between the two periods over the whole country (mean \pm se (n) daily mortality rates ($\times 100$): early period 3.76 ± 0.32 (543), late period 3.89 ± 0.31 (596), $z = -0.29$ ns). However, brood mortality rates were significantly higher in the early period, indicating that there has been an overall increase in nesting success per attempt since 1975 (mean \pm se (n) daily

mortality rates ($\times 100$): early period 5.99 ± 0.53 (383), late period 4.63 ± 0.39 (537), $z = 2.07$, $P < 0.05$).

Regional variation in reproductive performance

Great Britain was divided into six regions: Scotland, north England, Midlands, Wales with southwest and west England (referred to as southwest), East Anglia and southeast England (Fig. 1). Lay date, clutch size, brood size and partial hatching loss were analysed with a generalized linear model (GLM) incorporating region, year, and the interaction between the two as factors (means are shown in Table 1). There was no evidence of any trend in lay date between 1950 and 1994 (GLM: $F_{1,191} = 0.09$, ns). Trends with year varied between regions ($F_{3,191} = 3.21$, $P < 0.01$) and, when lay dates

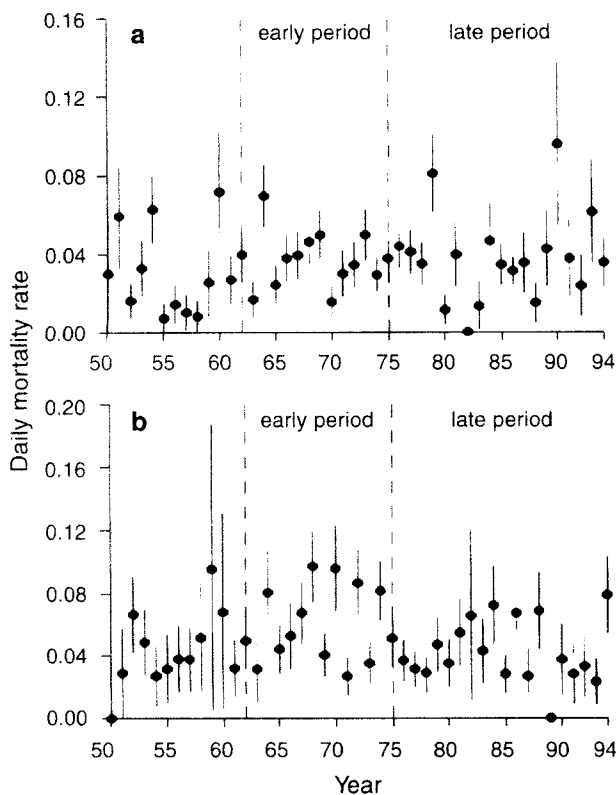


Figure 5. Annual variation in daily mortality rates of Skylark nests: (a) clutch mortality, (b) brood mortality. Results are mean \pm se. Broken vertical lines represent early and late periods used in regional and habitat analyses. Linear regression: (a) clutch mortality $F_{1,43} = 0.60$ n.s. $r^2 = 0.014$; (b) brood mortality $F_{1,43} = 0.04$ n.s. $r^2 = 0.0008$. Regressions were weighted by sample size. Points with no error bars indicate all samples had the same value for a given year (se = 0).

were compared between regions over all years, there was a significant difference (ANOVA: $F_{5,518} = 3.21$ $P < 0.01$), with East Anglia and the southeast having later lay dates than Scotland or the north (Table 1). This result could have arisen due to there being a greater number of second or late clutches laid in lowland or more southerly regions, thus increasing the overall mean lay date for these areas. Indeed, the frequency

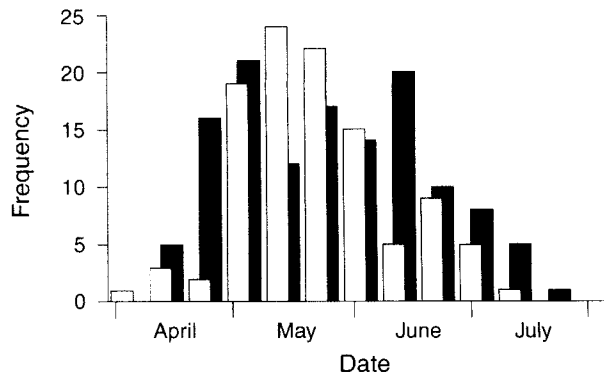


Figure 6. The frequency distribution of lay dates (first egg) of Skylarks in Scotland (\square) and southeast England (\blacksquare) divided into 10-day periods.

distribution of lay dates through the year (Fig. 6) shows that the frequency distribution of lay date in Scotland is relatively compressed into a short period, whereas in southeast England, laying activity, while starting at around the same time, continued for longer, with evidence of a bi-modal distribution, implying a greater proportion of second clutches.

There was no significant effect of region on clutch size ($F_{5,223} = 1.25$, ns) nor a significant interaction between year and region ($F_{5,223} = 0.41$, ns) but, as in the regression analysis (Fig. 4b), there was an overall significant increase in clutch size over the years ($F_{1,223} = 5.74$, $P < 0.01$). Brood size increased linearly from 1950 ($F_{1,244} = 7.47$, $P < 0.01$), but there was no evidence of a difference between regions when the yearly trend was taken into account ($F_{5,244} = 1.47$, ns). There were no significant differences in partial hatching loss between regions ($F_{5,187} = 0.76$, ns) nor any trend across years ($F_{1,187} = 1.62$ ns).

Mean daily clutch and brood mortality rates and z scores for regional comparisons are shown in Table 2. In the early period, there was only one significant difference in clutch survival between regions, with the southeast showing a higher mortality rate than

Table 1. Mean \pm se measures of Skylark productivity in the period 1950–94. For lay date, date 121 = 1 May. Partial hatching loss is calculated as clutch size minus brood size. Sample sizes are in parentheses.

Region	Lay date	Clutch size	Brood size	Partial hatching loss
Scotland	139.2 \pm 2.0 (103)	3.41 \pm 0.05 (149)	3.36 \pm 0.05 (215)	0.05 \pm 0.01 (77)
North	131.3 \pm 1.8 (120)	3.40 \pm 0.05 (236)	3.18 \pm 0.05 (340)	0.08 \pm 0.02 (43)
Southwest	139.5 \pm 4.2 (38)	3.56 \pm 0.08 (70)	3.40 \pm 0.07 (119)	0.06 \pm 0.02 (40)
Midlands	140.0 \pm 2.5 (94)	3.49 \pm 0.05 (180)	3.17 \pm 0.05 (259)	0.09 \pm 0.02 (36)
East Anglia	143.8 \pm 4.2 (37)	3.61 \pm 0.09 (62)	3.25 \pm 0.08 (89)	0.10 \pm 0.04 (23)
Southeast	141.3 \pm 2.2 (131)	3.42 \pm 0.04 (243)	3.24 \pm 0.05 (323)	0.06 \pm 0.02 (43)

Table 2. Skylark daily clutch and brood mortality rates (nests lost per day x 100) for six British regions. Results are mean \pm se. Paired comparisons have been carried out using a z-test for the difference between two means. Sample sizes are in parentheses.

	Daily mortality rate (x 100)					
	Scotland	North	Southwest	Midlands	Southeast	East Anglia
Early period (1962–1974)						
Clutch mortality ^a	1.93 \pm 0.93 (34)	3.94 \pm 0.65 (201)	3.71 \pm 0.99 (56)	3.50 \pm 0.64 (120)	4.49 \pm 0.73 (121)	4.91 \pm 1.44 (34)
Brood mortality ^b	7.15 \pm 2.69 (21)	6.24 \pm 1.00 (106)	4.96 \pm 1.49 (37)	5.53 \pm 1.05 (90)	5.50 \pm 1.06 (81)	4.77 \pm 2.44 (18)
Late period (1975–1994)						
Clutch mortality ^c	2.93 \pm 0.57 (134)	5.37 \pm 0.69 (144)	5.54 \pm 1.33 (53)	3.87 \pm 0.73 (110)	3.43 \pm 0.65 (116)	1.87 \pm 0.78 (42)
Brood mortality ^d	5.36 \pm 0.88 (118)	3.27 \pm 0.63 (152)	2.22 \pm 1.20 (44)	4.07 \pm 0.85 (112)	6.49 \pm 1.04 (108)	8.88 \pm 2.31 (34)

^aSignificant pairwise comparisons: Scotland v. southeast $z = 2.17^*$.

^bNo pairwise comparisons were significant.

^cSignificant pairwise comparisons: Scotland v. north $z = 2.73^*$; north v. southeast $z = 2.05^*$; north v. East Anglia $z = 3.36^{***}$; southwest v. East Anglia $z = 2.38^*$.

^dSignificant pairwise comparisons: north v. southeast $z = 2.65^*$; north v. East Anglia $z = 2.34^*$; southwest v. southeast $z = 2.34^*$; southwest v. East Anglia $z = 2.31^*$.

* $P < 0.05$.

Scotland. Many more significant differences occurred in the later period, notably in that East Anglia and the southeast had significantly lower clutch mortality rates than north. This trend was reversed for brood mortality, which was significantly higher in East Anglia and the southeast (the most intensively farmed regions) than the north and southwest. When comparing the two time periods, only northern England showed a significant decrease of 52% in the brood mortality rate ($z = 2.51$, $P < 0.05$).

Habitat and reproductive performance

The regional analyses indicated differences in productivity and nesting success which may be associated with differences between upland and lowland habitats, or between more or less intensively agricultural areas.

In this next set of analyses, NRCs were analysed in relation first to broad-scale habitat factors, and then to more specific habitat definitions based on the precise nature of the habitat surrounding the nest. In the latter case there were many possible categories, not all of which were relevant to this study (e.g. suburban parkland and golf courses). Thus, sample sizes became considerably smaller at the fine-scale habitat level.

Mean Skylark lay date, clutch size, brood size and partial brood loss in broadly defined habitats of agricultural, coastal and upland/heathland are shown in Table 3. There was no significant effect of year on lay date when considered by habitat type, nor any differences between overall means. Clutch size in agricultural habitat was significantly smaller than in coastal or upland habitats. When habitats were considered separately, there was a significant linear increase

Table 3. Habitat and year effects on laying date (where date 121 = 1 May), clutch size, brood size and partial hatching loss (clutch size – brood size) in Skylarks. Means \pm se are analysed for habitat and across-year trends by a general linear model incorporating the interaction term. Sample sizes are in parentheses.

Habitat	Lay date	Clutch size	Brood size	Partial hatching loss
Agricultural	134.6 \pm 1.80 (151)	3.13 \pm 0.04 (292)	3.12 \pm 0.04 (379)	0.09 \pm 0.02 (178)
Coastal	134.3 \pm 2.37 (79)	3.62 \pm 0.07 (117)	3.50 \pm 0.05 (207)	0.07 \pm 0.02 (68)
Upland/heathland	142.5 \pm 4.38 (33)	3.57 \pm 0.11 (58)	3.25 \pm 0.08 (103)	0.05 \pm 0.03 (38)
GLM:				
Habitat	$F_{2,91} = 0.57$ ns	$F_{2,108} = 3.53$ *	$F_{2,125} = 3.62$ *	$F_{2,92} = 2.77$ ns
Year	$F_{1,91} = 1.13$ ns	$F_{1,108} = 0.02$ ns	$F_{1,125} = 3.31$ ns	$F_{1,92} = 0.18$ ns
Habitat \times year	$F_{2,91} = 0.61$ ns	$F_{2,108} = 2.83$ ns	$F_{2,125} = 2.45$ ns	$F_{2,92} = 0.29$ ns

* $P < 0.05$.

Table 4. Daily clutch and brood mortality rates (nests lost per day x 100) of Skylarks in different broadly defined habitat types. Results are mean \pm se.

	Daily mortality rate (x 100)		
	Agricultural	Coastal	Upland
Clutch mortality ^a			
Early period (1962–1974)	5.04 \pm 0.63 (181)	2.28 \pm 0.80 (53)	0.71 \pm 0.60 (28)
Late period (1975–1994)	3.91 \pm 0.54 (184)	4.32 \pm 0.54 (85)	3.35 \pm 0.98 (50)
Brood mortality ^b			
Early period (1962–1974)	4.88 \pm 0.82 (120)	7.88 \pm 1.92 (39)	9.68 \pm 2.86 (19)
Late period (1975–1994)	3.70 \pm 0.64 (161)	5.13 \pm 1.05 (100)	1.88 \pm 0.86 (40)

^aSignificant pairwise comparisons: agricultural v. coastal, early $z = 2.71^{**}$; agricultural v. upland, early $z = 4.75^{***}$; early v. late upland $z = 2.23^*$.

^bSignificant pairwise comparisons: coastal v. upland, late $z = 2.39^*$; early v. late upland $z = 2.61^{**}$.

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

in clutch size with year in agricultural habitats (linear regression: $F_{1,43} = 5.80$, $r^2 = 0.12$, $P < 0.02$, slope \pm se = 0.0094 ± 0.0039), but not in the other two habitats (coast $F_{1,35} = 0.20$; upland $F_{1,25} = 0.02$, both ns). There was a significant difference in brood size between habitats, with agricultural habitat having the smallest and coastal the highest mean brood sizes (Table 3). There was no significant effect of either habitat or year on partial hatching loss.

Mean clutch and brood mortality estimates in agricultural, coastal and upland/heathland habitats for early (1962–74) and late (1975–94) periods are shown in Table 4. In the early period, clutch mortality in agricultural habitats significantly exceeded those in both coastal and upland habitats by 55% and 86%, respectively. There were no significant differences in brood mortality between habitats in the early period. In the late period, there were no significant differences in clutch mortality between habitats, but brood mortality was significantly lower in upland than coastal habitats. Comparing early and late periods, only the upland habitat showed significant differences, with an

increase in clutch mortality of 264%, but a decrease in brood mortality of 81%.

Both the regional and habitat-based analyses have so far indicated that the greatest changes in Skylark reproductive performance were associated with lowland agriculture, which also tended to be the poorest habitat in terms of some aspects of Skylark productivity and reproductive success. NRS data were analysed further in relation to more specific habitat types within the agricultural environment, first in terms of the predominant farming type and then in relation to the field type in which the nest was found.

There were no significant differences in either lay date, clutch size, brood size or partial hatching loss between farms which were predominantly arable and those which were predominantly pasture nor any evidence of trends with year (Table 5). Clutch mortality in arable farmland showed a significant reduction of 80% between periods, while mortality in pasture land did not change significantly (Table 6). As a consequence, clutch mortality was significantly lower in arable than pasture land in the later period. There was

Table 5. Farmland type and year effects on laying date (date 121 = 1 May), clutch size, brood size and partial hatching loss (clutch size – brood size) in Skylarks between 1950 and 1994. Mean \pm se are analysed for farmland type and across-year trends by a general linear model incorporating the interaction term. Sample sizes are in parentheses.

Farm type	Lay date	Clutch size	Brood size	Partial hatching loss
Arable	139.4 \pm 3.71 (43)	3.45 \pm 0.09 (73)	3.06 \pm 0.10 (85)	0.10 \pm 0.02 (77)
Pasture	131.6 \pm 4.25 (30)	3.41 \pm 0.07 (69)	3.09 \pm 0.08 (108)	0.06 \pm 0.11 (26)
GLM:				
Habitat	$F_{1,40} = 0.82$ n.s.	$F_{1,62} = 1.92$ n.s.	$F_{1,69} = 0.34$ n.s.	$F_{1,49} = 0.03$ n.s.
Year	$F_{1,40} = 0.29$ n.s.	$F_{1,62} = 1.60$ n.s.	$F_{1,69} = 0.41$ n.s.	$F_{1,49} = 0.41$ n.s.
Habitat \times year	$F_{2,40} = 0.49$ n.s.	$F_{1,62} = 1.49$ n.s.	$F_{1,69} = 0.39$ n.s.	$F_{1,49} = 0.23$ n.s.

Table 6. Daily clutch and brood mortality rates (nests lost per day x100) of Skylarks in arable and pasture farmland types. Results are mean \pm se. Sample sizes are in parentheses.

	Daily mortality rate (x 100)		
	Arable	Pasture	z (arable v. pasture)
Clutch mortality			
Early period (1962–74)	5.04 \pm 1.16 (48)	6.84 \pm 1.48 (45)	-0.96
Late period (1975–94)	1.67 \pm 0.79 (36)	6.38 \pm 1.28 (53)	-3.13**
z (early v. late)	2.40*	0.24	
Brood mortality			
Early period (1962–74)	3.32 \pm 1.35 (32)	6.04 \pm 1.92 (28)	-1.16
Late period (1975–94)	4.96 \pm 1.72 (32)	2.94 \pm 1.09 (44)	0.99
z (early v. late)	-0.75	1.40	

* $P < 0.05$, ** $P < 0.01$.

no significant difference in brood mortality between farmland types or between early and late periods within farmland type (Table 6).

Field types were defined as cereals, grazed pasture, ungrazed (agricultural) grassland and vegetables. In addition to information on the immediate habitat surrounding the nest, NRCs also contain information on the nature of other habitats in close proximity to the nest. Thus in the following analyses it was possible to omit any records which had two or more of the selected habitats in close proximity. In this way, the records used are much more likely to be representative of any possible effect of the nesting field types, rather than field types in close proximity. Due to small sample sizes, lay date, partial brood loss and nest mortality rates were not analysed. In addition, data were split into early and late periods as in the analysis of nest mortality estimates above. There was no significant difference in clutch size either between field types (ANOVA: $F_{3,87} = 0.07$ ns), between periods ($F_{1,87} = 2.19$, ns) or in brood size between field types ($F_{3,144} = 0.36$, ns) or early and late periods ($F_{1,144} = 3.54$, ns).

DISCUSSION

The numbers of Skylarks in the UK have declined by approximately 55% since the mid-1970s. All regions and habitats of Britain have shown declines, although they have been steepest in agricultural land. The productivity of individual nesting attempts has, conversely, increased over time, with the greatest improvement in productivity being observed in agricultural habitat. Below we discuss various features of the decline in Skylark numbers, before considering why breeding performance per nesting attempt might have improved. We conclude with a consideration of

the factors that might have been the cause of the decline.

The overall decline included a particularly severe drop between 1981 and 1982 which may be explained by weather conditions in the 1981 summer and the 1981/82 winter. The latter was relatively cold, with heavy snowfalls which might have resulted in high Skylark mortality. The 1981 breeding season coincided with relatively high rainfall which could have reduced reproductive success due to poor foraging conditions and the chilling of chicks in open nests (Evans *et al.* 1997, M. Jenny pers. comm.). Indeed, brood size was low in 1981 (Fig. 4c) and partial hatching losses were particularly high (Fig. 4d), although whole clutch and brood mortalities were about average (Fig. 5). However, the fact that there was no recovery as followed other severe winters (e.g. 1969–70 and 1978–79) and that the CBC index continued in a significant decline indicates that weather conditions are unlikely to have been the underlying reason for the overall decline, although they may have made the situation worse for a population that was already declining.

Changes in agricultural management are the most probable cause of the overall decline – the decline was significantly steeper in agricultural habitat than in coastal and upland habitats. Changes in land use may also have occurred in the latter habitats. In the uplands, there have been increases in grazing pressure and changes in moorland management (Fuller 1996) which are likely to have had adverse effects on Skylarks as they have on other ground-nesting species (Shrubb 1990, Crick 1992). It is possible that farmland is a suboptimal 'sink' habitat and that changes in numbers might be expected to be more severe in it than in more productive habitats (Brown 1969, Fretwell & Lucas 1970). Compared to coastal and upland habitat types,

farmland was the least productive habitat (on a per nest basis), but only in the period before the decline in Skylark numbers (see below), so the different patterns of decline seem unlikely to be due to the relative productivities of habitats.

Despite the observed decline in Skylark numbers, breeding performance per nesting attempt has shown a general improvement over time. Both clutch and brood size have increased significantly over the last 25 years, mainly in agricultural habitats. Similarly, brood mortality has decreased since the early 1960s and the differences in nest losses between habitats and regions of differing agricultural intensity were more pronounced in the period before 1975 (i.e. before numbers began to decline), consistent with decreased mortality rates over time. The general improvement in reproductive performance in agricultural habitats was not anticipated, given the large-scale changes in farming practice suspected of causing Skylark declines. Reproductive success may have been expected to suffer due to lower habitat diversity – and hence less choice for food or nest sites under varying conditions throughout the breeding season – and a decrease in the amount of food available due to increases in pesticides. Similarly, decreases in food supply may affect lay date or clutch size in adults, as has been shown among the Paridae (Perrins 1996).

A potential confounding factor in the detected temporal and spatial trends in clutch and brood size is lay date. Mean clutch size increases and then falls over the course of the breeding season as would be expected for a multi-brooded species (Crick *et al.* 1993). However, there was no evidence that differences in mean lay date varied over time or between habitats. Thus trends in clutch and brood size are likely to reflect genuine changes in the productivity of nesting attempts, rather than reflecting changes in the distribution of nesting through the season. However, there was a regional difference, with southern and eastern regions having earlier lay dates, although this was not sufficient to cause differences in average clutch or brood sizes between regions.

While the amount of pesticide used on farmland has increased, the use of directly toxic pesticides, such as DDT, has not been widespread since the 1960s and the problems that pesticides now cause are more likely to be via effects on the food supply (Potts 1986, Campbell *et al.* 1997). It is possible that increases in clutch and brood size are due to a reduction in directly toxic pesticides leading to a pattern of recovery similar to that observed in raptors (Newton 1979, 1986, Crick 1994). While raptors were shown to

be highly sensitive to the toxic effects of organochlorine pesticides (Newton 1979), there is also some evidence that granivorous birds may be subject to lethal and sublethal effects (Jefferies 1973). Changes in abundance, distribution (Newton 1972, Parslow 1973) and reproductive performance (Mayer-Gross 1965, Cramp & Olney 1967) of finches and buntings in intensively farmed regions during the 1950s and 1960s were also consistent with the use of toxic pesticides. Detailed analysis of Corn Bunting NRCs has revealed similar patterns of breeding performance to that shown here for the Skylark, with declines in the 1960s followed by recovery (Crick 1997). These declines were also most evident in areas of intensive arable agriculture, suggesting a possible link to the use of organochlorine pesticides. Other types of pesticide (such as organophosphates and carbamates) may also have affected farmland birds, but their usage continued to increase throughout the period of recovery in Skylark breeding performance (O'Connor & Shrubbs 1986).

A further possible explanation for the increase in breeding performance is that reproductive success is density-dependent, a decrease in population density resulting in lower competition for resources and hence increased productivity. There is evidence for density-dependent reproductive success in a number of other bird species (Lack 1966, Perrins 1979, Arcese & Smith 1988). Although improvements in breeding success may be a density-dependent response, the continued decline after the large decrease between 1981 and 1982 suggests that other factors, such as adult survival, have not improved enough for population recovery.

Given the general increase in productivity per nesting attempt and nest survival, it seems doubtful whether factors affecting the success of individual nesting attempts could have brought about the observed decline in Skylark numbers. One factor which cannot be directly measured by NRS data is the number of attempts per pair per season. This may have decreased due to: (1) earlier harvesting operations, as has been suggested for Corn Bunting (Donald 1997); and (2) the earlier development of dense swards on autumn-sown cereal crops (Evans *et al.* 1995). The latter may be suitable for early nesting attempts, but not later in the breeding season when vegetation is more developed. If suitable alternative habitats are not available in the immediate vicinity, then further nesting attempts are unlikely to be made. Evans *et al.* (1995) found that Skylarks deserted areas of autumn-sown crops as soon as the sward reached a critical height, which occurred relatively early in the breeding season.

The substantial increase in the area under autumn-sown cereals may have rendered large areas of farmland relatively unsuitable for Skylark nesting. In pasture, changes such as increases in stocking rates and changes in grassland management could have had similar effects.

Skylarks may also be affected by factors operating outside the breeding season. One such aspect of farm management is the loss of winter stubble due to the widespread introduction of autumn-sown wheat. This is likely to have particular impacts on the survival of seed-eating species (Evans & Smith 1994, Donald & Evans 1995) including the Skylark, which has a largely granivorous diet in the winter. The widespread introduction of set-aside in the early 1990s may to some extent reverse this decreasing trend in stubble (Wilson *et al.* 1995); if this is a causal factor in the decline in Skylarks, some recovery may become evident in the near future. (But note that Government policy has changed since the mid-1990s to decrease the proportion of land under set-aside).

Increased mortality outside the breeding season may also be caused by factors operating within it. For example, although average brood size may have increased, nothing can be concluded about the health of the fledglings produced. If chicks are malnourished when they leave the nest, their chances of survival to breed in the subsequent breeding season may be reduced. Such relationships between nestling weight and subsequent juvenile survival have been found in the Great Tit *Parus major* (Perrins 1965) and Blackbird *Turdus merula* (Magrath 1991). Similarly, if adults have to increase their work rate to feed nestlings adequately during the breeding season, their subsequent survival may be reduced (Partridge 1989, Stearns 1992). So, although poor juvenile survival may be a major cause of the decline of the Skylark, the root cause could still lie in agricultural changes having effects within the breeding season.

The hypothesis that increases in corvid numbers may have led to declines in Skylark numbers due to increased nest predation are not supported by the results of this study. Most nest mortality is likely to be due to predation (Delius 1965). Only in upland habitats was a significant increase in egg mortality rate detected over time, although a contradictory result was found for nestling mortality rate in the same habitat. It seems unlikely that an increase in corvid predation would only be evident in uplands, particularly when other possible causes exist – e.g. trampling resulting from increased grazing. However, it is possible that increases in mammalian predators – e.g. foxes (Tapper

1992), mustelids and even voles (J. Coulson pers. comm.) – due to decreased keeping (Tapper 1990) and other factors might be a cause of the decline in nesting success in the uplands.

Increased predation pressure due to an increase in Sparrowhawks is likely to act particularly on inexperienced juveniles (Newton 1986) but may affect nest mortality through the predation of breeding adults. The recovery of Sparrowhawk numbers across most habitats, with the largest increases in most intensively farmed areas, reflects the declines in Skylark numbers across habitats and regions. This apparent link cannot be taken as evidence of a causal relationship because there have been many other broad-scale changes in the countryside over this period that are likely to have driven the changes. Furthermore, it is doubtful whether predation alone could account for the decreases in Skylark numbers. Certainly in Great Tits and Blue Tits *Parus caeruleus*, increased Sparrowhawk predation does not appear to have any effect on the numbers breeding (Perrins & Geer 1980, Newton *et al.* 1997), although increases in Sparrowhawks could result in a greater proportion of immigrant breeders, implying that increased predation may only have an impact on non-breeders (Newton 1993). Whether the numbers of non-breeding birds are affected by predation in a similar way is not known, but any factor which reduces their numbers (e.g. reduction in food supply) in conjunction with increased predator pressure could clearly have effects on overall population size.

The decline of the Skylark appears not to have been caused by reductions in breeding productivity of individual nesting attempts. Increased mortality outside the breeding season, a reduction in the proportion of the Skylarks attempting to breed and a reduction in the number of nesting attempts per breeding season seem the most likely factors to have caused the decline, although there is currently little direct evidence for these factors. Further research into factors affecting adult and juvenile survival outside the breeding season, particularly the importance of winter stubble as a food source and the impact of increasing predator numbers, and the factors affecting territory settlement and the number of nesting attempts per breeding season are needed to understand fully the factors underlying the decline of the Skylark.

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