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Changes in corn bunting distribution on the South Downs in relation to agricultural land use and cereal invertebrates

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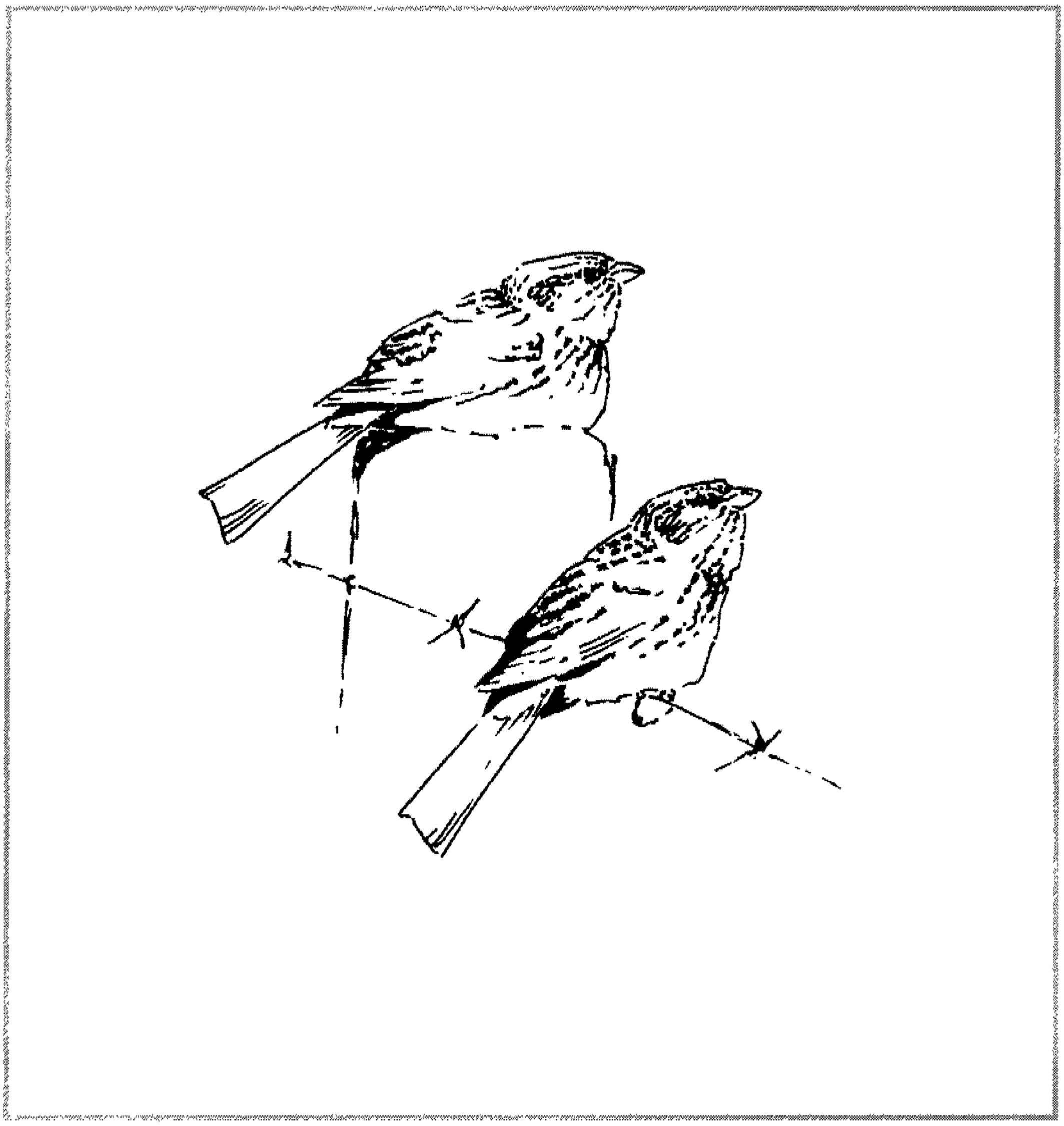

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CHANGES IN CORN BUNTING DISTRIBUTION ON THE SOUTH DOWNS IN RELATION TO AGRICULTURAL LAND USE & CEREAL INVERTEBRATES

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1. Summary

1. Corn Buntings (*Miliaria calandra*) have declined in Britain and Northern Europe over the last 100 years, and this decline has been most rapid in the last 25 years.

2. In March 1970, The Game Conservancy Trust counted singing male Corn Buntings during a spring count of Partridges in its Sussex Study Area (approximately 34 km^2), and has, since that year, kept annual records of land use and invertebrate numbers in cereals for this area. These records, in conjunction with the 1970 Corn Bunting count, created an opportunity to investigate links between agricultural change and Corn Bunting numbers.

3. During the summer of 1994, the locations of singing male Corn Buntings were mapped over the same area as in 1970. Corn Bunting nesting ecology was investigated through analysis of chick faeces and through observation of adult nesting behaviour on two farms of contrasting management type.

4. Changes in Corn Bunting density between 1970 and 1994 were highlighted by mapping Corn Bunting distribution as contours of increasing density across the study area. Such spatial measures of density were analysed in relation to crop and invertebrate data for the area from the two years.

5. Corn Bunting range had contracted within the study area between 1970 and 1994. Analysis of Corn Bunting density in relation to crop type showed that in both years spatial distribution was densest in the areas of rotational grass and spring-sown barley. Both crop types had declined over the 25-year period.

6. Analysis of chick faeces identified four main invertebrate taxa in the diet of chicks and adults: spiders and harvestmen, caterpillars (Lepidoptera and Symphyta), large beetles and small beetles. All except large beetles had declined in abundance between 1970 and 1994.

7. The density of Corn Buntings was positively related to the number of caterpillars across the study area. This and previous work indicated that the abundance of these invertebrates was highest in spring-sown crops, particularly undersown ones.

8. The density of Corn Buntings across the study area was negatively related to the number of spiders and harvestmen in cereal crops. Spiders and harvestmen were found to be more abundant in autumn-sown crops than in spring-sown crops, and differences in abundance of these invertebrates across the study area were entirely explicable by the time of sowing.

9. Comparison of pesticide use on a modern and a traditionally-managed farm within the study area showed that the number of applications of fungicide, herbicide and insecticide between sowing and 1994 harvest were consistently higher on a modern farm than on a traditional farm. There was no relationship

between Corn Bunting density and the proportion of the cropped area treated with summer insecticide in 1994.

10. The land use and crop management with which high Corn Bunting density was most strongly associated were representative of a traditional rotational mixed farming regime which has all but disappeared in the study area and across Britain as a whole in the last 25 years.

11. The adoption of modern intensive farming methods throughout Britain, including the specialisation of livestock and arable farming with high associated inputs and reduction in landscape diversity, was identified as the most likely factor to have affected the Corn Bunting's decline in the last 25 years.

12. Future research should concentrate on confirming the connection between Corn Bunting density and farming regime through detailed studies of population dynamics (survival, philopatry, breeding success) on modern and traditional farms. Particularly relevant also are the interactions between agricultural system, pesticide use and the invertebrates eaten by adult and young Corn Buntings.

2. Introduction

The widespread population decline and considerable range contraction of the Corn Bunting (*Miliaria calandra*) that has taken place in Britain over the last 100 years, and especially the last 25 years, has been well documented and discussed (Marchant *et al.* 1990, Gibbons *et al.* 1993, Donald *et al.* 1994). Historical records suggest that the Corn Bunting suffered a dramatic decline in numbers and range throughout the British Isles during the 1930s, and disappeared from many western and northern areas at this time. Numbers apparently stabilised after this initial decline, but in the late 1960s the species again began to disappear from many areas of Britain, the areas hardest hit being those which had experienced a reduction in Corn Bunting numbers at the beginning of the century.

The Corn Bunting population index calculated from the Common Bird Census (Marchant *et al.* 1990) has decreased by over 65% between 1970 and 1992, the decline being most marked in the north and west of the country (Gibbons *et al.* 1993). Corn buntings have disappeared from northern, north-western and central England, as well as from the south-west peninsula, and gaps in their distribution are widening in East Anglia and south-eastern England (Donald *et al.* 1994). In Scotland, the range is now restricted to a much smaller section of the east coast than at any other time since 1900, and strongholds in the west coast islands are also in decline. In Ireland, Corn Buntings now occur only in a small area of the west coast, whereas they occupied around six Irish coastal areas in the middle of this century (Donald *et al.* 1994). The British decline is, moreover, part of a more widespread reduction in Corn Bunting numbers, with similar declines being reported throughout north-west Europe (Mead 1992).

Reasons suggested for the decline vary, but the underlying theme is that agricultural development, and changes in farming practices, have in some way been responsible for the range contraction and population decline of the species. This theory is supported by parallel declines in other species closely associated with the agricultural environment, including Grey Partridge (*Perdix perdix*), Skylark (*Alauda arvensis*), Tree Sparrow (*Passer montanus*) and Linnet (*Carduelis cannabina*) (Potts 1986, 1991, Marchant *et al.* 1990). The agricultural changes which have been given as likely reasons for these declines include a nationwide reduction in the total area of cereals grown during the first 40 years of this century (Grigg 1989). More recently, this decline has continued in northern and western Britain as farming has become more specialised and farming types have become more polarised across the British Isles (Donald & Evans in press). Intensification of agricultural practice has also led to a loss of overall habitat and species diversity across much of Britain's landscape (Barr *et al.* 1993), although it is not clear how this may have affected Corn Buntings.

A positive association with barley has also been suggested as a factor (Thompson & Gribbin 1986, O'Connor & Shrubb 1986), but more recent studies have shown that this is not significant (Donald & Evans, in press), and that the total area of barley grown is currently greater than between 1930 and 1960, when Corn Bunting populations increased in many counties (Donald *et al.* 1994). A big difference between these two periods, however, is that most barley nowadays is sown in the autumn rather than in the spring, a change which could affect Corn Bunting numbers in two ways. Firstly, autumn-sown crops are generally harvested earlier than spring-sown crops, and the chance of harvesting operations disrupting Corn Bunting nesting attempts is therefore greatly increased, as the species has an unusually late breeding season (Harper 1994). Secondly, the change to autumn sowing has resulted in the virtual disappearance of winter stubble fields, which are an important source of grain for wintering Corn Buntings (Donald & Evans 1994).

Many farming practices have altered in recent years, and it is not clear to what extent changes such as that from cropping grass for hay to cutting for silage have affected the Corn Bunting. Reductions in flora and invertebrate diversity have been shown to result from the re-seeding of grass swards for silage cutting (Smith & Jones 1991) and from the increased use of fertilisers on silage crops compared to hay crops (Mountford *et al.* 1993). Earlier cutting of grass for silage, and the removal of more than one crop per season (enabled by greater fertilisation) are also likely to have reduced the number of plant and invertebrate species within grass fields, which in turn may have influenced the nesting success of the Corn Bunting.

Donald & Evans (1994) found that 60% of the Corn Buntings located in the BTO Winter Corn Bunting Survey of 1992-1993 were feeding on cereal stubbles, making this the single most important winter habitat type, with the remaining birds being almost evenly distributed across the other categories. The Survey demonstrated the importance of winter stubbles, and especially weedy stubbles, for Corn Bunting flocks. The inference is that the loss of this habitat as a result of the change from spring to autumn sowing of cereal crops may have contributed to the decline of the species.

The increased use of pesticides on farmland since 1950 may also have contributed to the Corn Bunting's decline (Donald *et al.* 1994), although the impact of pesticides on the species has not been assessed experimentally. It is known that Corn Buntings are particularly susceptible to poisoning by mercuric compounds (Otterlind & Lennerstedt 1964), and the BTO's Nest Record Scheme has suggested possible sublethal poisoning of Corn Buntings by organochlorine chemicals (Crick *et al.*, in press).

The indirect effects on Corn Buntings of widespread pesticide use remain unquantified, although such effects have been well documented for the Grey Partridge (Potts 1986). Such effects act through the food chain by depleting invertebrates that the birds may feed on. The use of herbicides since the 1950s has eliminated or at least reduced many of the crop weeds that serve as insect hosts, thereby approximately halving insect density in cereals by the late 1960s (Southwood & Cross 1969). Fungicides, introduced in the 1970s, may be responsible for declines in numbers of small beetles (Coleoptera) that feed on fungal diseases such as rusts and mildews within cereal crops; some fungicides are also known to be insecticidal (Sotherton & Moreby 1988). The use of insecticides in cereals became important in the 1980s, and their direct toxic effects on non-target invertebrates has been shown to have long-lasting repercussions on invertebrate fauna (Vickerman & Sunderland 1977, Duffield & Aebischer 1994, Greig-Smith *et al.* 1992).

This six-month study aimed to investigate the existence and nature of a link between changes in local Corn Bunting distribution and agricultural practice, paying particular attention to the dietary requirements of the birds. It was based on a count of singing male Corn Buntings made by The Game Conservancy Trust in its Sussex study area in 1970, followed up by a field survey of Corn Buntings carried out during the summer of 1994. The study relied extensively on a database held by The Game Conservancy Trust on annual insect abundance, farm management practices and cropping patterns since 1970. The report makes recommendations for future research into Corn Bunting ecology based on this year's pilot study.

3. Study Area

The study area consisted of 34 km^2 of farmland, comprising six farms, across the South Downs in West Sussex, between the Rivers Arun and Adur (see Fig. 1). It is part of a larger area which has been monitored by The Game Conservancy Trust over the last 25 years (Potts & Vickerman 1974, Potts 1980, 1986, Aebischer & Potts 1990, Aebischer 1991), in relation primarily to Grey Partridges. Details of crop type and farm management have been recorded annually for the area since 1970, forming a comprehensive historical database of agriculture on the Sussex Downs.

Records for the area include annual data on invertebrate abundance in cereal crops, obtained by D-vac sampling (Dietrick 1981) in the second half of June. At the same time, the abundance of broadleaved and grass weeds in crops was recorded, as well as crop type for each field within the study area. In addition to this information, singing male Corn Buntings were counted in the spring of 1970, enabling current knowledge of the species' numbers and distribution to be linked to the changing agriculture of the six farms between 1970 and 1994.

The years from 1970 to 1994 have been years of great agricultural change throughout the British Isles (Jenkins 1984, Barr *et al.* 1993), and the changes which have occurred in Sussex reflect the extent and nature of those nationwide. At the beginning of The Game Conservancy Trust's work in the study area, four farms used a system of traditional ley rotation through undersowing, one was a mixture of non-rotating arable and grass, and one was completely given over to arable (Aebischer 1991). However, 24 years later, only one farm continues to use a traditional system. The others have all intensified in one way or another: one specialises in winter wheat, three have a mixture of arable and permanent grass, and one is almost entirely permanent grass.

In 1987, the Ministry of Agriculture, Fisheries and Food (MAFF) introduced the first tranche of their Environmentally Sensitive Areas (ESA) scheme in the South Downs in Sussex. This first stage included the eastern side of the study area, although since then the South Downs ESA has been expanded to cover the entire study area. The aim of the ESA scheme in the South Downs is to restore traditional grazing pasture to the Downs. MAFF intends to achieve this through offering subsidies to farmers to encourage the reversion of arable land to permanent pasture. These subsidies are available on two levels, according to the mix of species sown for arable reversion.

Corn bunting numbers in Sussex have followed similar trends to those in the rest of the British Isles, although these trends have been less marked in Sussex than elsewhere (Donald *et al.* 1994). A marked decline took place during the 1930s, although Walpole-Bond (1938) observed that the bird was still locally common in the county towards the end of that decade. Following this early decline, the species expanded its range in Sussex to include northern and non-downland areas, before suffering a second decline from the early 1980s (Donald *et al.* 1994). Little change in the distribution of Corn Buntings in Sussex occurred during the 1970s and 1980s when viewed on a 10x10 km grid basis, despite this second decline in numbers (Harper 1993).

In order to preserve anonymity and to maintain confidentiality, the farms have been numbered in random order starting with the traditional farm.

4. Methods

4.1. Surveys

In March 1970, during the annual spring count of partridges, The Game Conservancy Trust carried out a count of singing male Corn Buntings over most of the study area (see Fig. 4), marking each bird on maps. The survey was carried out from a vehicle and covered accessible fields.

The current investigation, a field survey of Corn Buntings carried out during the summer of 1994 in the same study area as 1970, comprised two parts. The first part consisted of a survey of all singing male Corn Buntings within the study area during the first three weeks of June (see Fig. 5). The second part was an investigation of chick diet and survival, and adult nesting behaviour, within two farms of contrasting management practices. For reference purposes, these farms will be distinguished by calling them "modern" and "traditional".

For the purposes of the survey, each farm was visited three times between 31st May and 22nd June 1994. First, second and third visits took place from 31st May-8th June, 9th-14th June and 15th-22nd June respectively. On each occasion all singing males were marked on a map of the farm; female or unsexed Corn Buntings were also noted, as were the date, details of the song post for each male, and the bird's activity. Simultaneous records were joined by a dashed line to denote separate birds, and simple notation used for other activities as follows: a circle around a record was used for a singing bird; a line beneath a record for a calling bird; and a solid line for a flight path, with an arrow representing the direction of flight. The farms were covered on foot to increase the likelihood of recording every male; the routes taken through the farms were different for each visit, but ran along all field margins and across the centre of any fields where size or topography were likely to prevent the detection of a singing bunting.

During the second, intensive, part of the study, counts of singing males were made on the modern and traditional farms every week from 23rd June to 19th August. Foraging trips made by males on both farms were recorded, with details of the crop type at the starting point of the trip, crop type where the bird was foraging, and the distance travelled in each case. At the end of July (29th July to 2nd August), a further survey of all six farms was made, counting singing males, females and young birds on each farm.

During the survey, details of crops were taken for every field on each of the six farms of the study area. Information was also collected on which fields (if any) were sprayed with insecticide in May and June 1994, and the name and nature of the insecticide applied in each case. For the modern and the traditional farm which were used for the nest study, records were also obtained on the use of fungicide and herbicide between sowing and 1994 harvesting, in order to compare the number of pesticide applications for each crop type under the different management systems.

4.2. Nest Finding

The collection of information on Corn Bunting nesting habits and chick diet followed the count of singing males, and took place from 23rd June to 19th August. Sixteen nests were located through careful observation of the adults, and for each nest details of the location, date and contents were recorded on BTO Nest Record Cards (Crick *et al.* 1994). Once located, nests were visited every 1 or 2 days where possible, until either the chicks had left the nest, or failure of the nest at the egg or chick stage had occurred. Unfortunately, no visits were made between 12th and 16th July owing to illness. Details of the progress of each nest was also recorded on Nest Record Cards. Care was taken in all instances to avoid causing disturbance to the birds or surrounding vegetation, and to avoid drawing attention to the nest in any way.

4.3. Foraging Behaviour

For all adult Corn Buntings known to be associated with a nesting attempt, observations were made, as for individual males, on the birds' foraging trips. The crop types at the starting point of the trip and at the point of foraging were noted, as well as the distance travelled. The breeding status of each nesting adult (i.e. monogamous or polygamous) was recorded, and the behaviour of nesting birds, particularly in relation to potential threats, noted.

4.4. Faecal Samples

Where chicks were present in a nest, these were carefully handled one at a time in order to encourage defaecation. Faecal samples from the chicks were collected in tubes, and were later sieved with water through a 210 µm brass mesh, which was known to be fine enough to capture all fragments likely to be of importance in analysis of the samples (Moreby 1987). Material retained by the sieve was then immersed in alcohol for storage. All samples from each nest for the same visit were placed in a single tube, and labelled with the date and the nest details. Faecal samples for adult birds were collected from song posts on the two farms, and were treated and stored in the same way.

Following the completion of field work, the faecal samples were examined in the laboratory using a binocular microscope, identifying fragments of invertebrates to their different taxa (Moreby 1987). The numbers of individuals in each taxon was determined by counting numbers of characteristic parts, dividing by the number of parts per individual, and rounding up. Vegetable matter was also recorded, as an approximate percentage of the total volume of the faecal sample as estimated from coverage of a 1-cm grid. The results of the faecal analysis were then used to determine those invertebrate groups that played a major rôle in the birds' diet.

4.5. Spatial Representation of Data

The results of the field survey were transferred to the computerised mappable database MAPINFO 3.0 (Ritter 1994), for which a detailed computerised map of the study area had been prepared. A database that has the ability to represent objects spatially is known as a Geographical Information System (G.I.S.). The survey results included a point location on the computerised map for each singing male Corn Bunting recorded in 1970, and during each visit in 1994. The results of the 1994 survey were also combined into a single data set to represent all individual singing males recorded during the 1994 count period. To do this, occurrences which represented the same bird on different occasions were added as a single bird, and only those birds singing simultaneously or identified by other forms of territorial behaviour as separate individuals were marked as multiple birds on this combined map. This ensured that, as far as possible, the end result was a true count of singing male Corn Buntings in the area for the first three weeks of June 1994. There were therefore five different sets of mapped records: one for March 1970, one for each of the three visits in 1994, and one summary of all 1994 surveys.

Crop data from The Game Conservancy Trust's database for 1970, and from field work for 1994, were also computerised in this way, allowing the computerised maps of Corn Bunting locations to be superimposed on the crop maps, and then analysed or manipulated as required. Invertebrate data from 1970 and 1994 were extracted according to the taxa highlighted by the Corn Bunting faecal analysis, and were then added to the mapped database as numbers per sample corresponding to an approximate area of 0.5 m^2 of cereal crop. These details were then used, both within and outside the mappable database, to link the Corn Bunting distribution in 1970 and 1994 to features of the agricultural landscape of the study area in those years.

Although the survey was carried out on a farm-by-farm basis, analysis of Corn Bunting distribution was not done by farm, as many Corn Buntings were located along farm boundaries, and were thus impossible to allocate to one or other farm. For comparison of distribution between 1970 and 1994, therefore, areas of different densities of Corn Buntings were highlighted by calculating density contours for each year.

To create contours of Corn Bunting density, the map co-ordinates giving the point location of each singing bird were extracted from the mapped database. Using SYSTAT 5.0 (Wilkinson 1990), contours corresponding to increasing densities of points were calculated using kernel smoothing (Silverman 1986), for the eastern and western sides of the study area separately. The technique assumed that no buntings were present in the surrounding unsurveyed land. This assumption was reasonable given that the study area was bordered by unsuitable habitat: to the south the conurbations of Arundel, Worthing and Lancing, and to the north the wooded scarp slope of the Downs. The contour regions were transferred back to the mapped system, and superimposed onto the crop and invertebrate maps to give crop areas and invertebrate counts within each contour region. Corn Bunting density was calculated for each contour region by dividing the number of birds within the contour region by the total area of land surveyed within it.

Although contours were excellent at highlighting areas holding concentrations of Corn Buntings in 1970 and 1994, a different method was required to compare Corn Bunting density between the two years for a specific area. By superimposing grids of 1 km^2 (1x1 km) and 0.25 km^2 (0.5x0.5 km) over the survey maps, Corn Bunting density within a given grid square in 1970 could be compared to that within the same grid square in 1994. The grids were also superimposed onto the crop and invertebrate maps to give crop areas and invertebrate counts within each grid square.

4.6. Statistical Analysis

Means are presented $\pm$ 1 standard error, and are arithmetic means unless otherwise stated. For analyses of invertebrate abundance in relation to crop type, the dependent variables were logarithmically transformed before analysis, using log(x+1) to normalise the distribution and equalise the variances.

The comparison of Corn Bunting densities with invertebrate densities was done by simple regression (each year separately) or analysis of covariance (both years together, including year as a covariate as an initial step to account for year differences in Corn Bunting density associated with the different survey methods). The relationships between bunting densities and cropping pattern were examined by multiple stepwise regression. For a given contour region or grid square, the crop types were inherently constrained because their areas added up to the total area of the contour region or square; the constraint was taken into account in the analysis by excluding the constant in the regressions (in this way, the coefficient of each crop variable could be viewed as the density per unit area of Corn Buntings associated with that crop; this interpretation presupposes, however, that all coefficients are positive - not always the case). As for the invertebrate analyses, a joint 1970-1994 analysis was carried out by analysis of covariance.

5. Results

5.1. Agriculture

For all crops grown in 1970 and 1994, twelve categories were defined: rotational grass, non-rotational grass, scrubby downland, downland turf, woodland/scrub, spring barley, winter barley, winter wheat, winter oats, oilseed rape, miscellaneous, and set-aside.

Scrubby downland was defined as land (much of it on the scarp slope to the north of the study area) which was grazed in places but which also had areas of chalk scrub scattered across it. A small area of traditionally managed species-rich sward was given a separate category of downland turf. Barley was categorised according to the time of sowing (winter barley or spring barley). Both rotational (r) and non-rotational (nr) set-aside were included under the heading 'set-aside'. Miscellaneous crops differed in each of the two years: those grown in 1970 were beans, broccoli, lucerne, peas and potatoes; in 1994 miscellaneous crops were beans, kale, lucerne, linseed and maize. The crop maps for 1970 and 1994, using these categories, are given in Figs 2 and 3.

Table 1 describes the land use on each farm in 1970 and 1994. The total area of spring barley decreased from 1033 ha in 1970, to 131 ha in 1994, while the area of winter wheat grown rose from 381 ha to 879 ha in the same time. Non-rotational grass increased from 175 ha in 1970 to 938 ha in 1994, whereas rotational grass crops declined from 535 ha to 66 ha. Set-aside did not exist in 1970, but in 1994 occupied 260 ha of the study area. Crop management also changed, and the use of cereals as a nurse crop for grass and legume mixes decreased from 14% of sampled cereal fields being undersown in 1970 (Aebischer 1991) to 6% in 1994.

Some of the changes in crop area can be explained by recent agricultural policies. For example, the set-aside scheme had not been introduced in 1970, but by 1994, 260 ha of the 3400 ha of the study area were set aside under the scheme. Similarly, the increase in non-rotational grass coincides with the introduction, in 1987, of the South Downs Environmentally Sensitive Area (ESA) scheme. This system of MAFF subsidies aims to encourage reversion of arable to grass throughout the South Downs, and has resulted in widespread land-use change in the study area. Farm 6 now has over 300 ha covered by the ESA scheme, and all five farms have shown a reduction or complete loss of rotational grass cropping, with the exception of Farm 1. The loss of rotational grass leys has in turn obviated the need for undersowing of cereal crops to produce the ley for the following year, and resulted in the decline in undersowing described above.

The shift from spring sowing to autumn sowing and, in particular, from spring barley to winter wheat, that has taken place on Farms 2 to 6 follows the national trend (Brown 1992). Farm 1 does not show any marked change in proportions of wheat and barley between 1970 and 1994. It has successfully incorporated both set-aside and the ESA scheme into its cropping system, without necessitating any real change in management.

Three of the six farms of the study area sprayed insecticide during May and June 1994, these being Farms 2, 5 and 6 (Table 2). Farm 2 sprayed oilseed rape and linseed, as well as spraying winter wheat against orange wheat blossom midge (*Contarinia tritici*). Farm 6 did not spray against the midge, but only sprayed oilseed rape, whereas Farm 5 sprayed winter wheat against the midge. A total area of 564 ha was sprayed, 34% of the total cropped area of 1678 ha which could have received insecticide. In each case where insecticidal sprays were used, the chemical was broad-spectrum rather than specific to a narrow group of invertebrates (Table 3).

Comparing pesticide use on the modern and traditional farms, the average number of applications of fungicide, herbicide and insecticide were consistently higher on the modern farm than on the traditional one when comparing the same crops (Table 4). On the modern farm, insecticide was sprayed in early June, 10 days before the date on which insect sampling was carried out.

5.2. Surveys and Contouring

The 1970 survey located 58 singing males, 29 each on the western and eastern sides of the study area (see Fig. 4). The distribution across the area was not even, but appeared as groups or clusters of birds, surrounded by areas with few or no Corn Buntings. In 1994, a total of 127 singing males was recorded, 53 on the western side of the area, 74 on the eastern side (see Figs 5 to 8). There was no significant change in the east/west distribution of birds between the two years ($\chi^2_1 = 0.79$, n.s.).

The apparent overall increase in numbers of birds detected between 1970 and 1994 reflects the differences in timing and methodology of the surveys in the two years, rather than constituting a genuine rise in abundance. The 1994 survey was much more intensive and coincided with the main period of reproduction, whereas the 1970 one was done during partridge counting in March, from a Landrover. Although the absolute abundance of Corn Buntings was not therefore comparable, the distributions of the birds in the two years were.

The 1994 surveys showed a strong numerical pattern over the three weeks of the count period. No great change occurred in the number of birds located between the first and second counts, the first count in Week 1 of June having 43 birds, compared to 53 in the following week (second count). The third set of counts, however, showed a large and sudden increase in the number of Corn Buntings singing across the entire study area, the number of records rising to 95 birds. The survey carried out between 29th July and 2nd August did not locate any singing males on any of the six farms, and neither were any female or young birds located at this time.

The contours of Corn Bunting density for 1970 showed five areas of high density, spread across the study area (see Fig. 9). On the western side, concentrations of birds occurred in the south-west and centre, with an area of even higher density at the eastern edge. On the eastern side of the study area, concentrations occurred on the north-west and near the centre. A lesser concentration of birds appeared in the north-west of the western side of the study area.

A very high density of birds in the south-east of the eastern side was the most noticeable feature of the 1994 survey (Fig. 10). A lesser concentration of birds occurred towards its western boundary. Other areas of high density appeared in the north-west, and to a lesser degree in the centre, of the western side.

The 1994 contour map highlighted a number of changes in distribution since 1970. On the eastern side of the study area, the absence of any contours in the north-west, which had previously displayed a strong peak in Corn Bunting density, emphasised the disappearance of birds from this area. A clear peak in density, previously situated near the centre, had been replaced by a less obvious peak in 1994. The south-east, which displayed a high density of Corn Buntings in 1994, was not surveyed in 1970. On the western side, the contours also showed the loss of birds from the south-west, and the weakening of a strong peak in the centre. In contrast, numbers of birds in the extreme north-west seemed to have increased.

To summarise, the number of clear peaks in the contours decreased from six in 1970 to three in 1994, over the area which was counted in both 1970 and 1994.

From the average density of Corn Buntings per contour region, and the area of each contour region within each farm, it was possible to estimate Corn Bunting density per km^2 for each farm in 1970 and 1994 (Table 5). Despite the differences in timing of the two surveys, Corn Bunting density decreased dramatically between 1970 and 1994 on Farm 6, and declined to a lesser extent on Farm 2.

Representation of Corn Bunting density in both years using an overlaid grid confirmed the observations made from the contour maps (see Figs 11 to 14), although the random placing of the grid squares with respect to Corn Bunting locations influenced the pattern of distribution (density could fluctuate artificially in adjacent squares through one or more records happening to fall on one particular side of a grid line).

Corn bunting densities for grid squares of both sizes were classed as either high or low density, high density being defined as the upper half of the density range represented by the squares, and low density being equivalent to the lower half of the range. Change in density from low to high, or high to low, between 1970 and 1994 was then assessed for each grid square and described as either an increase in density, or a decrease respectively (Figs 15 and 16).

Using the 1x1-km grid squares, 7 out of a total of 36 which were surveyed in both years showed a decline from high density to low density between 1970 and 1994, and two squares revealed an increase in density over this time. Of the 0.5x0.5-km squares, 129 were surveyed in both 1970 and 1994; in 14 of these, Corn Bunting density had declined, and increased in 10 from 1970 to 1994.

5.3. Nesting Ecology

5.3.1. Behaviour of Singing Males

The single most noticeable feature of the behaviour of singing male Corn Buntings during the field study was the dramatic increase in numbers which occurred between the second and third count visits, that is, between the second and third weeks of June. Although not detected by the counts, equally marked was the subsequent reduction in singing which occurred during July, leading to a complete absence of singing males by the second week of August. The survey of the entire study area between 29th July and 2nd August did not locate any singing males, suggesting that the pattern of singing over time was likely to have been uniform across the six farms. A plot of numbers of males singing during the course of summer 1994 is shown in Figure 17, for the two farms where the nesting work was carried out.

The time spent singing by different males also showed considerable variation, but this variation was between farms rather than between surveys. It was most noticeable on the two farms where the work on nesting behaviour and success was done. Although similar numbers of birds were recorded for each of the two farms, the males on the traditional farm were reliably found to be singing on almost every visit, whereas those on the modern one were unpredictable, and likely to be located on only one visit in five, on average.

In order to investigate possible reasons for this variation in time spent singing, foraging trips made by unpaired males on the two farms were noted, so that the distances travelled on each farm could be compared, and linked to differences in farming practice. The distances for each foraging trip are shown in Table 6, the mean distances per farm being 293 $\pm$ 67 m (modern farm) and 145 $\pm$ 32 m (traditional farm). Although birds on the modern farm were travelling twice as far, on average, as those on the traditional one, there was no significant difference between the distances travelled for each farm (Mann-Whitney $U = 31.0$, n.s.).

Of males foraging on the modern farm, 63% were feeding in set-aside, and 37% were feeding in winter wheat, although winter wheat constituted 62% of the cropped area, and set-aside made up 17%. On the modern farm, birds seemed more inclined to leave their starting habitat to forage in a different one (set-aside) than on the traditional farm, although sample size was too low for statistical testing.

It has been suggested that the availability of suitable song posts may limit the distribution of Corn Buntings in certain areas, even if other habitat variables are correct (Cramp *et al.* 1994). For each singing male located during the 1994 field survey, details of song post were noted and are given for the two farms in Table 7, as they may relate to the inconsistency of singing between the two farms. The traditional farm has well-maintained post-and-wire fences throughout, with no bushes in the field margins except for isolated bramble (*Rubus fruticosus*) and hawthorn (*Crataegus monogyna*) bushes on an area of steep chalk grassland which borders fields on the south and west of the farm. There is one belt of mature trees near the eastern end of the farm, and a single mature elder (*Sambucus nigra*) in the centre of the farm.

In contrast, the modern farm has few remaining fences, and the majority of these are overgrown with bramble, nettles (*Urtica dioica*) and tall Umbellifers. On the northern boundary of the farm, occasional hawthorn bushes give way to a tall mixed hedge of hawthorn and elder.

The use of different song post types by male Corn Buntings on the two farms was significantly different ($\chi^2_3 = 12.6$, $P < 0.01$). Although the traditional farm had fewer bushes but extensive lengths of clear fenceline, proportionally more males were recorded singing from bushes than on the modern farm. More use was made of the available fences on the traditional farm, but where they were not available on the modern one, crops were used as song perches to a far greater extent than were bushes.

5.3.2. Behaviour of Nesting Adults

Despite considerable search effort, for over 50 singing males located within the two farms used for the nesting study, only 16 nest sites were identified, and only two polygynous males located, with a total of five nesting attempts and four or five females between them. This interprets as only 13 males, or 26%, being seen to have made nesting attempts, with 74% apparently remaining unpaired, and a total of no more than 16 reproductive females. Of the 13 males known to have held breeding territories, 15% were polygynous.

Corn bunting males are generally considered to make little or no contribution to parental care (Hartley & Shepherd 1994), and have been described as having a somewhat deficient approach to protection of the female and her nest (D. Harper, pers. comm.). In this study, however, males were in all cases very responsive to possible danger within the vicinity of the nest, and unless they were off-territory at the time of any threat occurring, always appeared with the female and displayed a similar degree of alarm, calling until the perceived threat had receded to a safe distance. The male would then remain at his nearby perch while the female checked the nest, or would fly in towards the nest with the female.

5.3.3. Outcome of Nesting Attempts

During the course of the field study, a total of 16 nest sites were identified, with the outcome of the nesting attempt known for 9 of these sites. Details of the nests are summarised in Table 8. 'Date completed' represents the date on which the outcome of the nest was known.

On the traditional farm, 62% of the nests were in unimproved pasture, the so-called Downland Turf which made up 6% of the total area of the farm. 31% of nests on this farm were in improved pasture, and 7% were in undersown spring barley. Improved pasture formed 44% of the farm area, and undersown spring barley made up 11% of the farm. Improved and unimproved pasture together held 93% of the nests on the traditional farm, and together formed 50% of the farm's area.

67% of the nests on the modern farm were in improved pasture, although this crop formed 18% of the area. Set-aside, which made up 17% of the farm, contained 33% of the nests found there. Overall, 88% of the nests were in improved or unimproved pasture. The overall success rate, of the nests for which the outcome was known, was 33%, although for those nests in unimproved pasture, this rose to 50%. None of the nests in improved pasture were known to be successful, and no nests on the modern farm reached fledging.

Despite the same numbers of singing males being located on the two farms, only three nests were on the modern one, with the remaining 12 being on the traditional farm (χ^2_1 = 5.40, $P < 0.05$). On the traditional farm, 75% of the nests for which the outcome was known were situated in unimproved pasture and the nesting success rate was 38% where known.

During monitoring of nesting activity, foraging visits made by adult birds associated with each nest site were recorded, including the crop type involved and the distance travelled in each case (Table 9). The mean distance travelled by nesting adults on foraging trips was 222 ± 42 m on the modern farm, and 251 ± 73 m on the traditional one. There was no significant difference between the farms (Mann-Whitney U = 17.5, n.s.).

5.4. Faecal Analysis

Four faecal samples were collected from two nests, each nest containing four chicks. The content of these samples is summarised in Table 10a. The chicks in Nest 1 of the table were well-grown when the nest was located, and only one further visit was made the following day before the chicks exploded from the nest. Nest 2 was located while still at the egg stage, and was visited daily until the chicks had hatched and were old enough to produce faeces when handled, giving the first sample taken from this nest. When the next faecal sample was obtained from the chicks in Nest 2 nine days later, the birds were well-grown, and exploded from the nest during the visit.

In all four chick faecal samples, vegetable matter formed less than 10% of the total sample, and was identified as ripening grain. Invertebrate components of the samples consisted mainly of prey items from the taxa spiders and harvestmen (Araneae and Opiliones), large beetles (Carabidae and Elateridae), small beetles (other Coleoptera) and caterpillars (Lepidoptera and Symphyta); other invertebrates were present in smaller numbers and included flies (Diptera), ants (Formicoidea), aphids (Aphididae), wasps (Ichneumonidae) and snails (Gastropoda).

Chicks in Nest 1 were primarily being fed large Carabids, which formed 79% of the prey items over the two faecal samples. The Carabids were identified as *Pterostichus* sp., probably *Pterostichus madidus*. The samples from Nest 2 showed no strong dietary pattern, and contained fewer prey items than did the samples from Nest 1 (a total of 14 invertebrates in the two samples, compared to 47 prey items in the samples from Nest 1). The two samples obtained from Nest 1 contained a higher percentage of vegetable matter than those from Nest 2, approximately 10% on average, compared to less than 1% for Nest 2. The mean vegetable matter content for the chick faecal samples was around 5%.

Tables 10b and 10c give components of faecal samples obtained from song-posts on the two farms. The adult faecal samples from both farms contained a higher proportion of vegetable matter than did the faecal samples from the chicks: a mean of 95% on the modern one, and 65% on the traditional one, and a combined mean vegetable matter content of 74%. Analysis of these differences in vegetable matter content showed that there was no significant difference between the proportion of vegetable matter in the faeces of adults from the traditionally managed farm compared to those from adults on the modern farm (Mann-Whitney $U = 15.0$, n.s.). There was, however, significantly less vegetable matter in the chick faeces than in the faeces of adults from both farms together (Mann-Whitney $U = 8.5$, $P<0.05$).

5.5. Invertebrates

Invertebrate abundance for the four main taxa identified in the Corn Bunting faecal analysis declined between 1970 and 1994 across the study area. The mean numbers per sample for the four groups are given for each farm in Table 11. Araneae and Opiliones showed a significant decline on all farms except Farm 1; Carabidae and Elateridae declined significantly on Farms 4 and 5 only; but other Coleoptera showed a significant decline in numbers across all farms. Lepidoptera and Symphyta declined significantly on Farm 2 and on Farms 4 to 6, but no significant decline occurred for this group on Farm 1.

Apart from the large beetles (Carabidae and Elateridae), which are poorly sampled by D-vac, the pattern that emerges is one of a decline across all taxa on Farm 2 and Farms 4 to 6. On Farm 1, there has been no change other than in the group of small Coleoptera.

The invertebrate samples were taken only from cereal crops, so the spatial coverage of the study area in any single year had gaps where non-cereal crops were grown. In order to give a more complete visual representation, Figs 18 to 21 show the spatial pattern of abundance averaged over the two five-year periods 1970-1974 and 1990-1994. The figures underline the broad spatial nature of the decline described above. Subsequent analyses (see next section) of invertebrate abundance versus Corn Bunting distribution in 1970 and 1994 pointed out two groups of interest, spiders and harvestmen (Araneae and Opiliones) and caterpillars (Lepidoptera and Symphyta): for these two groups, the distribution in 1970 and 1994 alone are also given (Figs 22 and 23) as these were the data used in the analyses.

With respect to the pesticide use on the modern and the traditional farms, all four invertebrate groups were at least twice as abundant on the traditional farm than on the modern one, with the difference significant for all groups except large beetles (Carabidae and Elateridae). As all cereal fields on the modern farm received insecticide, and none of those on the traditional farm, it was not possible to carry out a within-farm comparison of the immediate effect of spraying. It was thus not possible to separate the effects of insecticide use from the effects of the different farming regimes.

5.6. Corn Bunting distribution, land use and invertebrates

5.6.1. Analysis based on contour regions: land use

For each contour region in 1970 and 1994, the density of Corn Buntings and the crop composition is given in Table 12a, b.

The 1970 density of Corn Buntings was most strongly related to the presence of rotational grass (r_{11}=0.728, P<0.01), and also to spring barley (r_{11}=0.602, P<0.05). The effect of spring barley vanished after taking into account the effect of rotational grass because these two variables were themselves correlated (r_{11}=0.608, P<0.05). No further variation in density was explained by other crop variables.

In 1994, the single most important crop variable in terms of explaining Corn Bunting density was set-aside (r_9=0.737, P<0.01); others that exhibited correlations with density were spring barley (r_9=0.662, P<0.05), winter wheat (r_9=0.728, P<0.05) and winter oats (r_9=0.622, P<0.05), but again these secondary relationships vanished after removing the effect of set-aside.

Corn Bunting density was significantly related to the proportion of cropped land that was undersown in 1994 (r_9=0.644, P<0.05) but not in 1970. There was no relationship between Corn Bunting density and the proportion of cropped area treated with insecticide in May and June 1994 (r_9=0.220, n.s.).

Considering the data from both years together, after removal of between-year differences in density by using year as a covariate in the analysis, the only variable significantly correlated with Corn Bunting density was woodland scrub (r_{21}=-0.481, P<0.05). This relationship was negative, unlike previous ones, indicating the avoidance of wooded or scrubby areas by Corn Buntings.

In order to capture the essential differences between methods of farming, crops were grouped into three categories: (1) those associated with mixed rotational farming (spring cereals, rotational grass) to which set-aside was also added, as in many ways it can be viewed as a latter-day surrogate of a grass ley or spring-sown crop; (2) those associated with modern intensive arable farming (winter cereals); (3) other crops including woodland, scrub, permanent pasture and downland. Estimates of the densities of Corn Buntings associated with these categories were obtained by regression (see Methods), and are presented in Table 13. Given the different survey techniques employed in 1970 and 1994, it is not possible to compare the magnitudes of coefficients for different years, but only within years. In both 1970 and 1994, the density of Corn Buntings associated with mixed rotational farming was significantly greater than zero; in 1994, when the coefficients for all three categories differed significantly from zero, it was nearly five times higher than for the intensive arable category, and the other category provided a negative density coefficient.

5.6.2. Analysis based on contour regions: invertebrates

In 1970, Corn Bunting density declined significantly as the density of spiders and harvestmen (Araneae and Opiliones) increased (r_{11}=-0.908, $P<0.001$). A similar non-significant negative trend was observed in 1994; when the data from the two years were combined, there remained a significant overall negative relationship with Arachnida density after removal of between-year differences in Corn Bunting density (r_{21}=-0.662, $P<0.05$). The relationship is depicted in Fig. 24a.

Corn Bunting density in 1994 was significantly positively related to the density of Lepidoptera and Symphyta (caterpillars) (r_9=0.680, $P<0.05$). A similar non-significant trend was observed in 1970. When the data from the two years were combined, the overall relationship with caterpillar density was significantly positive (r_{21}=0.568, $P<0.05$). The relationship is depicted in Fig. 24b where, despite appearances, the slopes of the 1970 and 1994 regression lines do not differ significantly.

5.6.3. Analysis based on grid squares: land use

The 1970 density of Corn Buntings within 1x1-km grid squares was most strongly related to the presence of rotational grass (r_9=0.555, $P<0.001$). The other variables that significantly explained some of the remaining variation in Corn Bunting density were miscellaneous crops (r_8=0.383, $P<0.05$) and spring barley (r_{37}=0.329, $P<0.05$). Based on the 0.5x0.5-km squares, all three crop types made a significant contribution to jointly explaining the variation in 1970 bunting density (in order of selection: spring barley r_{142}=0.438, $P<0.001$; rotational grass r_{141}=0.298, $P<0.001$; miscellaneous r_{140}=0.264, $P<0.001$).

In 1994, the pattern was considerably more complicated. Using 1x1-km grid squares, five variables contributed significantly to explaining the variation in Corn Bunting density; in order of selection these were winter wheat (r_{47}=0.610, $P<0.001$), rotational grass (r_{46}=0.509, $P<0.001$), winter barley (r_{45}=0.493, $P<0.01$), spring barley (r_{44}=0.396, $P<0.01$) and winter oats (r_{43}=0.355, $P<0.05$). Using 0.5x0.5-km grid squares, the number of variables increased to nine: spring barley (r_{166}=0.409, $P<0.001$), winter wheat (r_{165}=0.413, $P<0.001$), downland turf (r_{164}=0.275, $P<0.001$), set-aside (r_{163}=0.260, $P<0.001$), oilseed rape (r_{162}=0.262, $P<0.001$), winter barley (r_{161}=0.200, $P<0.05$), non-rotational grass (r_{160}=0.182, $P<0.05$), woodland scrub (r_{159}=-0.190, $P<0.05$) and winter oats (r_{158}=0.182, $P<0.05$). In all cases except woodland scrub, the relationships were positive.

There was no relationship between Corn Bunting density and the proportion of cropped area that was undersown in 1970 or 1994, for either size of grid.

Considering the data from both years together, after removal of between-year differences in Corn Bunting density, the analysis based on 1x1-km grid squares selected three crop variables that explained the variation in density: rotational grass (r_{87}=0.315, P<0.01), winter wheat (r_{86}=0.223, P<0.05) and downland turf (r_{85}=0.253, P<0.05). Using 0.5x0.5-km grid squares, five variables were selected: downland turf (r_{309}=0.231, P<0.001), woodland scrub (r_{308}=-0.190, P<0.01), spring barley (r_{307}=0.163, P<0.01), set-aside (r_{306}=0.123, P<0.05) and rotational grass (r_{305}=0.116, P<0.05). The relationships were all positive except for that involving woodland scrub, which was negative.

The picture was much clearer when viewed in the light of the three crop categories defined on the basis of farming practice (see 5.6.1). In both 1970 and 1994, and for both grid sizes, the density of Corn Buntings associated with mixed rotational farming was two to three times as high as that associated with intensive arable farming, and over six times as high as the category that included woodland and permanent grass in the single case where the latter differed significantly from zero (Table 13).

5.6.4. Analysis based on grid squares: invertebrates

Using the 1x1-km grid squares, there was no detectable relationship between Corn Bunting density and any of the four main invertebrate groups, either in 1970, 1994 or pooling information from both years.

Using the 0.5x0.5-km grid squares, Corn Bunting density was significantly and positively related to caterpillar (Lepidoptera and Symphyta) density in 1994 (r_{165}=0.199, P<0.05). A similar non-significant trend was observed in 1970. When the data from the two years were combined, the overall relationship with caterpillar density was significantly positive (r_{307}=0.201, P<0.01). There was no significant relationship with any other of the four main invertebrate groups.

5.6.5. Relationship between crop types and invertebrates

The abundance of invertebrates in 1970 and 1994 according to crop type is given in Table 14. In 1970, the numbers of spiders and harvestmen (Araneae and Opiliones) differed significantly between crops; the differences were entirely attributable to whether the crops were sown in the spring or the autumn. The same was true of caterpillars (Lepidoptera and Symphyta) in 1994.