Habitat use by Corn Buntings *Miliaria calandra* in winter and summer

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The winter habitat use, winter diet and nesting habitat of Corn Buntings *Miliaria calandra* were studied on the South Downs, south-east England. The most heavily used habitat relative to availability was initially cereal stubbles in early winter, but subsequently cattle feed and then spring-sown cereals. These habitats and brassica strips with game feeders provided access to cereal grain, which was present in virtually all faecal samples. Grassy field margins and spring-sown barley were used for nesting more than expected from their availability. Winter-sown wheat was used for nesting roughly as expected by chance and improved grass was avoided. Cereals were important to Corn Buntings throughout the year. Spring-sown cereals may be particularly valuable. During the winter they provided long-lasting stubbles and abundant food in the form of surface grain when first sown. In the breeding season, they were among the most used habitats for nesting and for collecting chick food. Agri-environment schemes to benefit Corn Buntings should support spring-sown cereal crops and smaller-scale measures such as the creation and maintenance of grassy field margins.

Corn Buntings *Miliaria calandra* have declined in geographical range and numbers throughout northern Europe (Hagemeijer & Blair 1997, Siriwardena *et al.* 1998). Their close association with arable farmland means that the agricultural intensification of the last three decades has been implicated in their decline. Suggested causal mechanisms are the impacts of reduced food availability on overwinter survival (Donald 1997, Shrubb 1997) and breeding success (Aebischer & Ward 1997, Brickle *et al.* in press). Full-grown Corn Buntings are largely granivorous, but the chicks are fed mainly on invertebrates (Cramp & Perrins 1994). This suggests that their habitat requirements differ seasonally, an idea that we tested for Corn Buntings on lowland farmland on the South Downs.

Wintering Corn Buntings are often associated with cereal stubbles (Donald & Evans 1994), which have become scarcer over the last three decades owing to a major switch from spring to autumn sowing of crops. Furthermore the densities of wild-plant seeds and cereal grain on stubbles have fallen, owing to increased herbicide use and more efficient harvesting respectively. These changes are strongly implicated in the decline of the Cirl Bunting *Emberiza cirlus* (Evans & Smith 1994, Evans 1997) and have probably contributed to those of Reed Buntings *E. schoeniclus* (Peach *et al.* 1999) and Corn Buntings (Shrubb 1997). Unfortunately, little is known about the diet of Corn Buntings in winter; although many accounts stress the importance of grain, the only quantitative study of diet did not (W.E. Collinge in Cramp & Perrins 1994). We therefore examined the composition of the winter diet. Walpole-Bond (1938) suggested that stubbles were used less in late winter, when food availability would be expected to be low. This suggests that the availability and quality of habitats other than stubble could influence over-winter survival. We therefore tested for changes in habitat use during the winter.

Nest Record Scheme data suggest that Corn Bunting nests have become more successful during the population decline (Crick 1997). On the South Downs (1995-97), however, only 25% of nests fledged young and few females made second nesting attempts, even after failures (Brickle *et al.* in press). Most of the invertebrates fed to chicks (Aebischer & Ward 1997, Brickle & Harper 1999) have declined in abundance on farmland over the last three decades (Campbell *et al.* 1997), owing in part to pesticide use and loss of stubbles (Aebischer 1990). On our study site, Corn Buntings were commonest where cereals had high densities of caterpillars (Lepidoptera and Symphyta), which are important chick-food items (Aebischer & Ward 1997). Elsewhere, we have examined habitat use by adults collecting food for nestlings (Brickle *et al.* in press). Here, we examine nesting habitat at two spatial scales (Beck & George 2000) - the nest site and the area within 150 m - and compare them with the composition of the whole study area.

METHODS

Study area

Between 1995 and 1997, we studied Corn Buntings on 10.5 km^2 of farmland, north of Worthing, West Sussex. The study area, between TQ 0306 and TQ 2013, was part of that described by Potts (1986) and Aebischer & Ward

Table 1. Mean habitat composition of the 10.5-km^2 study site in the winters of 1995-1996 and 1996-1997 by period. Period 1: 1 October-10 December; Period 2: 11 December-10 February; Period 3: 11 February-31 March.

Habitat	Mean %		
	Period 1	Period 2	Period 3
Stubble fields	23	12	8
Improved grass with cattle	13	15	14
Brassicas[a]	5	4	1
Spring-sown barley[b]	0	0	10
Other[c]	59	69	67

[a] Fodder rape, kale.
[b] From day of drilling.
[c] Winter-sown wheat, improved grass without cattle, non-rotational set-aside, woods, hedges, tracks, buildings, bare ground, grassy margins, ungrazed grass.

(1997). Tables 1 and 2 summarise the mean habitat composition during the study in winter and summer respectively (analyses use the values for each year separately rather than these means). Our study area was typical of much of the breeding habitat occupied by Corn Buntings in Britain, although it lacked oilseed rape, which is used elsewhere (see Discussion).

Habitat use in winter

A set route was walked at 2- to 3-week intervals between October and March during the winters of 1995-96 and 1996-97, passing within 20 m of every point in the study area. The direction of the route was alternated between visits. Surveys were done between 10:00 and 16:00 GMT, avoiding heavy rain or strong wind. All Corn Buntings were plotted on maps, recording the destination of flushed birds to minimise double-counting, but excluding birds seen only in flight. Since the route took two days to walk, the data can be used to estimate habitat use but not population size. Three periods were defined, including roughly equal numbers of surveys, and five habitat categories (Table 1). The proportion of birds in each habitat during a survey was compared with habitat availability at the time of that survey.

In the winter of 1996-97, the areas from which Corn Buntings (and no other species) had been flushed were searched for fresh faeces. Droppings were stored in alcohol and subsequently analysed following Moreby (1988). Invertebrate body parts were used to estimate the minimum number of individuals of each order present, following Brickle & Harper (1999). Seeds were identified using Hanf (1988) and a reference collection. Data were pooled for each flock from which faeces had been collected.

During the winter of 1996-97, seed availability was sampled in ten fields following Wakeham-Dawson &

Table 2. Mean habitat composition of the 10.5-km^2 study site in the summer (1995-97) and the percentage use of each habitat by breeding Corn Buntings.

Habitat type	Mean %			
	Study area[a]	Territory locations[b]	Nest locations[c]	Foraging locations[d]
Winter wheat	34	33	33	13
Improved grass[e]	32	8	0[f]	0
Spring barley	12	34	36[g]	32
Non-rotational set-aside	9	9	15[h]	18
Other[i]	5	4	0	0
Brassicas[j]	3	1	0	0
Woodland and scrub	2	< 1	0	0
Grassy margin[k]	2	3	8[h]	29
Ungrazed grass[l]	1	7	8[m]	8

[a] Differences between years for each habitat represented < 3% of study area.
[b] Area within 150 m of nest; data for 120 nests.
[c] n = 120 nests (24 in 1995, 46 in 1996 and 50 in 1997).
[d] Adults collecting food for nestlings (Brickle *et al.* in press); data for 67 nests.
[e] Grazed.
[f] Second partition of overall chi-square (see text), $\chi^2_1 = 43.5$, $P < 0.001$.
[g] Third partition of overall chi-square (see text), $\chi^2_1 = 38.8$, $P < 0.001$.
[h] Fourth partition of overall chi-square (see text), pooling these two habitats, $\chi^2_1 = 20.7$, $P < 0.001$.
[i] Tracks, buildings, bare ground, etc.
[j] Fodder rape, kale.
[k] Often tussocky and deliberately provided for gamebirds; usually under 3 m wide.
[l] Chalk downland, hay fields.
[m] First partition of overall chi-square (see text), $\chi^2_1 = 41.1$, $P < 0.001$.

Aebischer (1998). These fields included four habitats - stubble, improved grass, bare till and spring-sown barley - although the type in some fields changed, and not all habitats were surveyed in each of the periods defined in Table 1. To collect a sample, five 25x25-cm quadrats were thrown at random. All the surface material within the quadrat was collected using a 12-V hand-held vacuum cleaner (sampling was only carried out when there had been no rain for several days). This technique was considered appropriate because Corn Buntings feed almost entirely on the ground and do not dig for food (Cramp & Perrins 1994). The collected material was transferred to plastic bags and frozen. Later, it was emptied into a tray of water and seeds separated under a binocular microscope. Seeds were identified to family using Hanf (1988) and Rose (1981), distinguishing cereal grains from other grass seeds.

Nesting habitat

Nests were found by systematically watching territories for at least one hour, at intervals of no more than three days, from mid-April until mid-August. The habitat in which the nest was built and the composition of habitats within 150 m of it were compared with the availability of habitats across the study site. A distance of 150 m corresponded to the upper 95% confidence interval of all mean foraging distances (Brickle 1999) and was used to define the general vicinity of the nest.

Statistical analysis

Tests were two-tailed; means are expressed ± 1 *se*. Analyses were made using SPSS Version 7 (Norušis 1996) and specially written randomisation programs (see Acknowledgements). We compared habitat use with habitat availability, using compositional analysis (Aebischer *et al.* 1993a, 1993b), testing the null hypothesis of random habitat use by multivariate analysis of variance (Kendall 1980). If the assumptions of normality required by MANOVA were not met, significance was determined by randomisation (Manly 1997). Whenever habitat use was significantly non-random, the habitats that were used less or more than expected were identified using single-sample *t*-tests (Aebischer *et al*. 1993b). Given that the tests were carried out only when Λ indicated significant departure from random use, we stayed with standard significance levels for *t* by analogy with the protected least-significant-difference method (Carmer & Swanson 1973, Snedecor & Cochran 1980). Flocking behaviour can create analytical difficulties as it is unclear whether individual birds behave independently. To avoid the problem, habitat use in winter was analysed twice, treating individuals and then observations (one or more birds) as independent. We tested for differences in faecal composition using compositional analysis, following Brickle & Harper (1999).

RESULTS

Habitat use in winter

Corn Buntings were sighted 2,671 times, with a mean of 76 ± 3 birds per survey (range 1-225, n = 35). Most sightings (80%) were of birds in flocks of two to approximately 220 birds. Corn Buntings were mainly recorded in stubble fields, grass fields with cattle, brassicas *Brassica* sp. and spring-sown barley fields (Table 3). The 'other' habitats used were: a baited trapping site, Blackberry *Rubus fruticosus* bushes (early winter only), rough grassland, game feeders in scrub, trees. Habitat use relative to availability varied significantly between periods (pooling brassicas, spring-sown barley and 'other' because the first two were absent in at least one survey: observations, Wilk's Λ from MANOVA = 0.471, $F_{4,56}$ = 6.41, P < 0.001; individuals, Wilk's Λ = 0.406, $F_{4,56}$ = 7.98, P < 0.001), with no variation between years (observations, Wilk's Λ = 0.982, $F_{2,28}$ = 0.26, P = 0.772; individuals, Wilk's Λ = 0.991, $F_{2,28}$ = 0.13, P = 0.875) and no interaction (observations, Wilk's Λ = 0.842, $F_{4,56}$ = 1.26, P = 0.298; individuals, Wilk's Λ = 0.889, $F_{4,56}$ = 0.85, P = 0.499). Within each period, habitat use differed significantly from random with respect to availability (Table 3). Habitat use matrices (Table 3) revealed the following patterns:

(a) Period 1. Stubble was the habitat used most relative to availability (over half of individual birds and observations), followed by brassicas. Both habitats were used significantly more than grass fields with cattle and 'other' (although the comparison between brassicas and cattle was only significant if analysed by individual).

(b) Period 2. The most used habitat relative to availability was grass with cattle, used significantly more than stubble fields, which were used much less than previously in Period 1. Cattle fields, stubble and brassicas were all used significantly more than 'other'.

(c) Period 3. Freshly drilled spring-sown barley fields became the most used habitat relative to availability, used significantly more than all other categories.

Diet in winter

Seven faecal samples were collected (containing 52 droppings): three from stubble fields in period 1, two from grass fields with cattle in period 2 and two from spring-sown barley fields in period 3. Thus, we collected samples from the most heavily used habitat in each period (Table 3).

Grain was found in most faeces and formed 50% of identified items (Table 4). The only other common items

Table 3. Summary of differences in habitat use by Corn Buntings during three periods of winter, using observations (one or more birds) as independent units; spring-sown barley was only available in period 3. A positive sign represents greater use of the row habitat relative to the column habitat. If the sign is tripled the difference is significant at $P < 0.05$.

	Stubble	Cattle	Brassica	Spring barley	Other	Rank[a]	Mean % Observations (Individuals)
Period 1 (1 October-10 December)[b]							
Stubble		+++	+		+++	1	67 (63)
Cattle	---		-[c]		+	3	6 (4)
Brassicas	-	+[c]			+++	2	19 (29)
Other	---	-	---			4	8 (5)
Period 2 (11 December-10 February)[d]							
Stubble		---	-		+++	3	22 (12)
Cattle	+++		+		+++	1	49 (62)
Brassicas	+	-			+++	2	23 (25)
Other	---	---	---			4	5 (2)
Period 3 (11 February-31 March)[e]							
Stubble		-	---	---	+++	4	9 (9)
Cattle	+		-	---	+++	3	27 (25)
Brassicas	+++	+		---	+++	2	10 (13)
Spring barley	+++	+++	+++		+++	1	45 (52)
Other	---	---	---	---		5	8 (2)

[a] The row habitats are ranked by their use relative to availability, with rank 1 indicating the most heavily used.
[b] 834 individuals in 71 observations; 11 surveys; MANOVA testing null hypothesis of random habitat use, Wilk's $\Lambda = 0.185$, $P = 0.003$ by randomisation (treating individuals as independent, $\Lambda = 0.192$, $P = 0.007$).
[c] If analysed by individuals rather than observations, $P < 0.05$.
[d] 1204 individuals in 41 observations; 12 surveys; MANOVA testing null hypothesis of random habitat use, Wilk's $\Lambda = 0.129$, $P = 0.002$ by randomisation (treating individuals as independent, $\Lambda = 0.066$, $P = 0.001$).
[e] 633 individuals in 45 observations; 12 surveys; MANOVA testing null hypothesis of random habitat use, weighted Wilk's $\Lambda = 0.002$, $P = 0.001$ by randomisation (treating individuals as independent, $\Lambda = 0.014$, $P = 0.001$); for weighting method, see Aebischer *et al.* (1993b).

were Polygonaceae seeds. Non-cereal grass seeds and invertebrate remains were scarce. Faecal sample composition (simplified to grain, other seeds and invertebrates) did not vary significantly between habitats, and thus periods (Wilk's $\Lambda = 0.126$, $F_{4,6} = 2.73$, $P = 0.131$).

Seed distribution in winter

The density of grain varied significantly between habitats (Table 5; $F_{2,13} = 14.88$, $P < 0.001$), but neither between periods ($F_{2,13} = 0.07$, $P = 0.935$) nor between fields after the effect of habitat had been accounted for ($F_{8,13} = 1.57$, $P = 0.226$). Stubble fields had significantly less grain than spring-sown barley fields (Tukey test, $P = 0.008$), but more than grass fields or bare till. When the ANOVA was repeated using all seeds potentially eaten by Corn Buntings (Table 5), seed density did not vary significantly between habitats ($F_{2,13} = 1.33$, $P = 0.297$) or between periods ($F_{2,13} = 1.38$, $P = 0.285$), but did between fields ($F_{8,13} = 3.76$, $P = 0.017$).

Nesting habitat

Nests were not sited in habitats at random (Table 2; using habitat availability in each year rather than mean, $\chi^2_8 = 182$, $P < 0.001$). The largest deviation occurred because ten nests were in ungrazed grass that covered only 1% of the study area. We partitioned the chi-square by comparing ungrazed grass with all other habitats and then following the method of Siegel & Castellan (1989). The other results contributing significantly to the overall chi-square (see Table 2) were the absence of nests from improved grass (covering about a third of the study area) and unexpectedly high numbers of nests in spring-sown barley (together with margins and set-aside if these habitats were pooled).

The habitat within 150 m of nests differed significantly from random with respect to availability (Wilk's $\Lambda = 0.230$, $P < 0.001$ tested against 999 randomisations). There were no significant differences between years (Wilk's $\Lambda = 0.828$, $P = 0.071$ tested against 999 randomisations). Grassy margins were significantly commoner near nests relative to their availability than any other habitat (Table 6). The next most highly ranked habitats were ungrazed grass, spring-sown barley and winter-sown wheat.

Table 4. Contents of Corn Bunting faeces collected in the winter of 1996-97, with food groups listed in descending order of overall proportion of identified items.

Food group	Overall proportion	Mean proportion	Percentage presence	
	n = 308 items	*n* = 7 samples	*n* = 7 samples	*n* = 52 faeces
Cereal grain	0.500	0.739	100	94
Polygonaceae[a]	0.386	0.169	57	31
Gramineae[b]	0.081	0.053	43	21
Coleoptera	0.016	0.024	57	9
Araneae	0.010	0.010	29	6
Diptera	0.006	0.006	29	4

[a] Most were Black Bindweed *Fallopia convolvulus*; with a mean dry weight of 1.28 mg (Grime *et al.* 1990) and an energy content of 19 kJ g^{-1} (Potts 1986), a Black Bindweed seed yields less than 5% of the energy value of a wheat grain.
[b] Excluding cereal grain. Even Sterile Brome *Bromus sterilis* with an unusually high mean dry weight of 8.4 mg (Grime *et al.* 1990) is only about a fifth as heavy as a wheat grain.

DISCUSSION

Winter diet and habitat use

Although Corn Bunting faeces contained substantial numbers of seeds from the Polygonaceae and wild grasses, the most frequent items were cereal grains. The seed weights in Grime *et al.* (1988) suggest that grain may have accounted for over 94% of the seed material by dry weight. Habitat-use data also suggested that grain was important. Stubbles were used heavily only until grain became more easily available elsewhere, from late December at cattle troughs and between mid-February and late March on

Table 5. The mean density of seeds (number m^{-2}, ± *se*) in each of four habitats in winter. Seeds were identified to family, and grouped according to whether or not they occurred in the diet of Corn Buntings. Grasses (Gramineae) were divided into cereals and non-cereals.

Seed group	Stubble *n* = 10[a]	Improved grass *n* = 11[b]	Bare till *n* = 3[c]	Spring-sown barley *n* = 3[d]
In Corn Bunting diet[e]				
Gramineae: non-cereals	36 ± 12	37 ± 10	1 ± 1	24 ± 9
Gramineae: cereals	31 ± 4	-	1 ± 1	56 ± 14
Polygonaceae	18 ± 8	1 ± 1	36 ± 8	13 ± 2
Cruciferae	19 ± 19	< 1	3 ± 2	2 ± 1
Caryophyllaceae	6 ± 2	< 1	14 ± 10	3 ± 3
Sub-total	110 ± 24	39 ± 10	55 ± 9	97 ± 20
Not in diet[e]				
Leguminosae	-	12 ± 5	-	-
Papaveraceae	3 ± 1	< 1	14 ± 12	18 ± 10
Chenopodiaceae	3 ± 1	-	3 ± 2	10 ± 3
Compositae	< 1	3 ± 1	-	1 ± 1
Other families[f]	2 ± 1	7 ± 5	3 ± 2	2 ± 1
Sub-total	7 ± 2	23 ± 9	20 ± 12	31 ± 9
Total all seeds	117 ± 25	61 ± 18	76 ± 20	128 ± 18

[a] *n* = 5, 3 and 2 in periods 1-3 respectively (dates in Table 1).
[b] *n* = 4, 3 and 4 in periods 1-3 respectively.
[c] Period 2 only.
[d] Period 3 only.
[e] Cramp & Perrins (1994); N.W. Brickle & D.G.C. Harper pers. obs.
[f] Families with overall mean < 1seed m^{-2}, in descending order of abundance:
Ranunculaceae, Violaceae, Scrophulariaceae, Umbelliferae, Fumariaceae, Euphorbiaceae.

Table 6. Habitat composition within 150 m of Corn Bunting nests compared with that of the whole study area. A positive sign represents greater use of the row habitat relative to the column habitat. If the sign is tripled the difference is significant at $P < 0.05$.

Habitat	W	Ba	I	U	Br	M	S	Wo	O	Rank
Winter wheat (W)		-	+++	+	+++	—-	+++	+++	+++	3
Spring barley (Ba)	+		+++	+++	+++	—-	+++	+++	+++	2
Improved grass (I)	—-	—-		—-	+	—-	-	+	-	7
Ungrazed grass (U)	-	—-	+++		+++	—-	+++	+++	+	4
Brassicas (Br)	—-	—-	-	—-		—-	—-	-	—-	9
Grassy margin (M)	+++	+++	+++	+++	+++		+++	+++	+++	1
Set-aside (S)	—-	—-	+	—-	+++	—-		+	-	6
Woodland (Wo)	—-	—-	-	—-	+	—-	-		—-	8
Other (O)	—-	—-	+	-	+++	—-	+	+++		5

freshly drilled fields. Although direct-drilling machinery is designed to plant grain at some depth, densities on the surface can be as high as on stubbles (Table 5). Corn Buntings were often seen in brassicas (Table 3), where they ate grain at game feeders in Kale *Brassica napus* (Brickle 1997).

The main sources of grain in our study (stubbles, accessible cattle feed, spring-sown cereals) have all become scarcer over the last 50 years in Britain (Shrubb 1997). Furthermore, inadequately protected grain stores and rickyards, which were used heavily in the past (Harper 1995), have virtually vanished. Thus, reduced access to grain may well have contributed to the Corn Bunting's decline. Grain is, however, not essential for Corn Buntings since large flocks occur on oilseed rape stubble (Watson & Rae 1997a, D.G.C. Harper pers. obs.). The only previous quantitative study of their winter diet (by W.E. Collinge in the 1920s, Cramp & Perrins 1994) found that little grain was eaten between November and July.

Although our sample sizes were small, the densities of 'weed' seeds seem unlikely to predict habitat use. The common ones in the diet (Table 4) were at highest density on improved grass and bare till (Table 5), which rarely attracted Corn Buntings (Table 3). Similarly, a nationwide survey found that Corn Buntings did not use 'weedy' stubbles significantly more than 'clean' ones (Donald & Evans 1994), consistent with the idea that grain is the more important food. The same survey found more Corn Buntings in tetrads with 'weedy' stubbles than in those without, an association that might arise in the breeding season rather than the winter (Watson & Rae 1997a).

Habitat use in summer

Corn Buntings were not distributed across the study area at random (Tables 2 and 6). In particular, grassy field margins were commoner near Corn Bunting nests than expected (Table 6), as in Denmark (Møller 1983). The next two most highly ranked habitats (Table 6) were spring-sown barley and winter-sown wheat. Numerous studies have noted an association between breeding Corn Buntings and cereals (see Donald & Forrest 1995, Aebischer & Ward 1997). Most report greater use by breeding Corn Buntings of spring-sown cereals than winter-sown ones (Donald 1997, Gillings & Watts 1997). Like Donald & Forrest (1995), however, we did not find that territories were significantly more associated with spring-sown barley than winter-sown wheat. Although brassicas were little used in our study (Table 6), oilseed rape is used elsewhere for nesting (Harper 1995, Watson & Rae 1997a) and a nationwide survey found that breeding density was more strongly correlated with the area of all tillage crops than that of cereals alone (Donald & Evans 1995). Some breeding Corn Buntings show little, if any, association with tillage of any kind, nesting in wet grassland and marshes (Hegelbach & Ziswiler 1979).

Corn Bunting nests were all in tall 'grassy' habitats: cereals, margins, set-aside and ungrazed grass (Table 2). None were in improved grassland (see also Harper 1995, but see Aebischer & Ward 1997), which was also scarcer than expected close to nests (Table 2; see also Donald & Evans 1995, Donald & Forrest 1995). The non-rotational set-aside was all over 5 years old (mostly over 7 years) and was not found in the vicinity of nests more than expected by its availability (Table 6). It was, however, frequently used for nesting and foraging (Table 2). This was surprising because set-aside in northeast Scotland is rarely, if ever, used after its first summer (Watson & Rae 1997b).

Adults collecting food for nestlings visited spring-sown barley, grassy margins, ungrazed grassland and set-aside more relative to their availability close to the nest than any other habitats (Table 2; Brickle *et al.* in press). These were the four habitats with the highest availability of four common chick-food items (Lepidoptera larvae, Symphyta larvae, Opiliones, Orthoptera; Brickle & Harper 1999), as measured by sweep-netting. Breeding success was positively correlated with the abundance of these invertebrates near nests (Brickle *et al.* in press). Table 2 shows that grassy margins were used more for foraging than for nesting, while the reverse was true for winter wheat. Thus, habitat use for one activity did not tightly constrain habitat use for the other.

Woodland, hedgerow and scrub were scarce near nests (Table 2). This is not surprising in Britain, where Corn Buntings are birds of open country (Donald & Evans 1995), although in southern Europe they often live in open woodland (Finlayson 1992). The apparent avoidance of woody plants in our study might reflect competition (e.g. with Yellowhammer *Emberiza citrinella*) or risk of predation (e.g. by Sparrowhawk *Accipiter nisus*).

Habitat use throughout the year

Our results highlight, as expected (Donald 1997, Shrubb 1997), the importance of cereals to Corn Buntings throughout the year. Spring-sown cereals may be particularly valuable. In the winter they typically provide long-lasting stubbles and abundant food during spring sowing. Breeding Corn Buntings nested in, and collected food from, spring-sown barley significantly more (relative to availability) than winter-sown wheat (Table 2, Brickle *et al.* in press).

Some habitats were used for only part of the year. Brassicas and cattle fields were heavily used in winter, but not in summer (compare Tables 2, 3 & 6), probably because they contained grain only in winter. Field margins and ungrazed grass were rarely used in winter but were heavily used relative to their availability in the summer (Tables 2 & 6). This probably reflects the absence of grain in winter and high densities of invertebrates in summer (Brickle *et al.* in press).

Corn Buntings are associated with mixed farming (Shrubb 1997). Our study suggests that the potential benefits of livestock include the provision of grain in winter and the presence of ungrazed grass in summer (providing both nest-sites and food). Before the elimination of rickyards and other sources of grain around farmyards (Shrubb 1997), the benefits of mixed farming to Corn Buntings were probably greatest during the breeding season.

CONCLUSIONS

Two gaps in our knowledge about Corn Buntings stand out. The first is their habitat use and diet during the late winter and early spring if spring-sown cereals and livestock feed are unavailable. This will be the case in wetlands (Hegelbach & Ziswiler 1997) and on many intensive arable farms, and could occur on most farms after the germination of spring-sown crops and cessation of livestock feeding. The second gap is that without an estimate of annual mortality (estimated at 42% in Germany before the recent population decline, Møller 1983), explaining population changes will be hard.

Turning to land management issues, any reductions in set-aside area (MAFF 1999) or spread of herbicide-resistant crops (Marshall 1998) could reduce food supplies. Although the spread of organic farming might slowly counter these trends (Wilson *et al.* 1997), many organic farms grow few, if any, cereals (Chamberlain *et al.* 1999) and may thus be unsuitable for Corn Buntings. In addition, organic farming seems unlikely to account for extensive areas of farmland in the near future. Support by agri-environment schemes for the spring sowing of cereals would probably benefit Corn Buntings, especially if some of these fields were undersown with a grass/legume mix. As well as providing long-lasting stubble, undersown fields increase the numbers of some invertebrates over a much wider area (Potts 1997). In this context, it is encouraging that the new Arable Stewardship Scheme currently being piloted by the Ministry of Agriculture, Fisheries and Food includes an option for the undersowing of cereals. Our results suggest that some smaller-scale measures may also benefit Corn Buntings and perhaps other farmland bird species. Tussocky grass margins, beetle banks and selectively sprayed headlands around cereal fields can greatly increase the densities of 'weeds' and invertebrates (Sotherton 1991, Thomas *et al.* 1992). Despite their small area in our study, grassy margins were heavily used by breeding Corn Buntings (Table 2).

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REFERENCES

Aebischer, N.J. 1990. Assessing pesticide effects on non-target invertebrates using long-term monitoring and time-series modelling. *Funct. Ecol.* **4:** 369-373.

Aebischer, N.J., Marcström, V., Kenward, R.E. & Karlbom, M. 1993a. Survival and habitat utilisation: a case for compositional analysis. In Lebreton, J.-D. & North, P.M. (eds) *Marked Individuals in the Study of Bird Populations*: 343-353. Basel: Birkhäuser Verlag.

Aebischer, N.J., Robertson, P.A. & Kenward, R.E. 1993b. Compositional analysis of habitat use from animal radiotracking data. *Ecology* **74:** 1313-1325.

Aebischer, N.J. & Ward, R.S. 1997. The distribution of Corn Buntings *Miliaria calandra* in Sussex in relation to crop type and invertebrate abundance. In Donald, P.F. & Aebischer, N.J. (eds) *The Ecology and Conservation of Corn Buntings* Miliaria calandra: 124-138. Peterborough: Joint Nature Conservation Committee.

Beck, M.J. & George, T.L. 2000. Song post and foraging site characteristics of breeding Varied Thrushes in northwestern California. *Condor* **102:** 93-103.

Brickle, N.W. 1997. The use of game cover and game feeders by songbirds in winter. *Proceedings 1997 Brighton Crop Protection Conference - Weeds*: 1183-1190. Farnham: British Crop Protection Council.

Brickle, N.W. 1999. *The Effect of Agricultural Intensification on the Decline of the Corn Bunting*, Miliaria calandra. Unpubl. DPhil thesis, University of Sussex.

Brickle, N.W. & Harper, D.G.C. 1999. Diet of nestling Corn Buntings *Miliaria calandra* in southern England examined by compositional analysis of faeces. *Bird Study* **46:** 319-329.

Brickle, N.W., Harper, D.G.C., Aebischer, N.J. & Cockayne, S.J. in press. Effects of agricultural intensification on the breeding success of Corn Buntings *Miliaria calandra. J. Appl. Ecol*.

Campbell, L.H., Avery, M.I., Donald, P.F., Evans, A.D., Green, R.E. & Wilson, J.D. 1997. *A Review of the Indirect Effects of Pesticides on Birds*. JNCC Rep. No. 227. Peterborough: Joint Nature Conservation Committee.

Carmer, S.G. & Swanson, M.R. 1973. An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. *J. Am. Statist. Assoc.* **68:** 66-74.

Chamberlain, D.E., Wilson, J.D. & Fuller, R.J. 1999. A comparison of bird populations on organic and conventional farm systems in southern Britain. *Biol. Conserv.* **88:** 307-320.

Cramp, S. & Perrins, C.M. (eds) 1994. *Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. IX. Buntings and New World Warblers*. Oxford: Oxford University Press.

Crick, H.Q.P. 1997. Long-term trends in Corn Bunting *Miliaria calandra* productivity in Britain. In Donald, P.F. & Aebischer, N.J. (eds) *The Ecology and Conservation of Corn Buntings* Miliaria calandra: 52-64. Peterborough: Joint Nature Conservation Committee.

Donald, P.F. 1997. The Corn Bunting *Miliaria calandra* in Britain: a review of current status, patterns of decline and possible cause. In Donald, P.F. & Aebischer, N.J. (eds) *The Ecology and Conservation of Corn Buntings* Miliaria calandra: 11-26. Peterborough: Joint Nature Conservation Committee.

Donald, P.F. & Evans, A.D. 1994. Habitat selection by Corn Buntings *Miliaria calandra* in winter. *Bird Study* **41:** 199-210.

Donald, P.F. & Evans, A.D. 1995. Habitat selection and population size of Corn Buntings *Miliaria calandra* breeding in Britain in 1993. *Bird Study* **42:** 190-204.

Donald, P.F. & Forrest, C. 1995. The effects of agricultural change on population size of Corn Buntings *Miliaria calandra* on individual farms. *Bird Study* **42:** 205-215.

Evans, A.D. 1997. The importance of mixed farming for seed-eating birds in the UK. In Pain, D.J. & Pienkowski, M.W. (eds) *Farming and Birds in Europe*: 331-355. London: Academic Press.

Evans, A.D. & Smith, K.W. 1994. Habitat selection of Cirl Buntings *Emberiza cirlus* wintering in Britain. *Bird Study* **41:** 81-87.

Finlayson, C. 1992. *Birds of the Straits of Gibraltar*. London: T. & A.D. Poyser.

Gillings, S. & Watts, P.N. 1997. Habitat selection and breeding ecology of Corn Buntings *Miliaria calandra* in the Lincolnshire Fens. In Donald, P.F. & Aebischer, N.J. (eds) *The Ecology and Conservation of Corn Buntings* Miliaria calandra: 139-150. Peterborough: Joint Nature Conservation Committee.

Grime, J.P., Hodgson, J.G. & Hunt, R. 1988. *Comparative Plant Ecology*. London: Unwin Hyman.

Hagemeijer, W.J.M. & Blair, M.J. 1997. *The EBCC Atlas of European Birds: Their Distribution and Abundance*. London: T. & A.D. Poyser.

Hanf, M. 1988. *The Arable Weeds of Europe with their Seedlings and Seeds*. London: Badische Analin Soda Fabrik.

Harper, D.G.C. 1995. Studies of West Palaearctic Birds 194: Corn Bunting. *Brit. Birds* **88:** 401-422.

Hegelbach, J. & Ziswiler, V. 1979. Zur Territorialität einer Grauammer-population *Emberiza calandra*. *Orn. Beob.* **76:** 119-132.

Kendall, M. 1980. *Multivariate Analysis*. 2nd edn. London: Griffin.

MAFF 1999. *Arable Area Payment Scheme: Explanatory Guide - 1999 Update*. London: Ministry of Agriculture, Fisheries & Food.

Manly, B.F.J. 1997. *Randomization, Bootstrap and Monte Carlo Methods in Biology*. London: Chapman & Hall.

Marshall, G. 1998. Herbicide-tolerant crops: real farmer opportunity or potential environmental problem? *Pesticide Science* **52:** 394-402.

Møller, A.P. 1983. Song activity and territory quality in the Corn Bunting *Miliaria calandra*, with comments on mate selection. *Ornis Scand.* **14:** 81-89.

Moreby, S.J. 1988. An aid to the identification of arthropod fragments in the faeces of gamebird chicks (Galliformes). *Ibis* **130:** 519-526.

Norušis, M.J. 1996. *SPSS 7.0 for Windows*. Chicago: Statistical Package for the Social Sciences Inc.

Peach, W.J., Siriwardena, G.M. & Gregory, R.D. 1999. Long-term changes in over-winter survival rates explain the decline of Reed Buntings *Emberiza schoeniclus* in Britain. *J. Appl. Ecol.* **36:** 798-811.

Potts, G.R. 1986. *The Partridge: Pesticides, Predation and Conservation*. London: Collins.

Potts, G.R. 1997. Cereal farming, pesticides and Grey Partridges. In Pain, D.J. & Pienkowski, M.W. (eds) *Farming and Birds in Europe*: 151-177. London: Academic Press.

Rose, F. 1981. *The Wildflower Key - British Isles & N.W. Europe*. London: Warne.

Shrubb, M. 1997. Historical trends in British and Irish Corn Buntings *Miliaria calandra* populations - evidence for the effects of agricultural change. In Donald, P.F. & Aebischer, N.J. (eds) *The Ecology and Conservation of Corn Buntings* Miliaria calandra: 27-41. Peterborough: Joint Nature Conservation Committee.

Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H. & Wilson, J.D. 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed CBC indices. *J. Appl. Ecol.* **35:** 24-45.

Snedecor, G.W. & Cochran, W.G. 1980. *Statistical Methods*. 7th edn. Ames: Iowa State University Press.

Sotherton, N.W. 1991. Conservation headlands: a practical combination of intensive cereal farming and conservation. In Firbank, L.G., Carter, N., Darbyshire, J.F. & Potts, G.R. (eds) *The Ecology of Temperate Cereal Fields*: 305-331. Oxford: Blackwell Scientific Publications.

Thomas, M.B., Wratten, S.D. & Sotherton, N.W. 1992. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *J. Appl. Ecol.* **29:** 524-531.

Wakeham-Dawson A. & Aebischer, N.J. 1998. Factors determining winter densities of birds on Environmentally Sensitive Area arable reversion grassland in southern England, with special reference to Skylarks (*Alauda arvensis*). *Agr. Ecosyst. Environ.* **70:** 189-201.

Walpole-Bond, J. 1938. *A History of Sussex Birds*. London: Witherby.

Watson, A. & Rae, S. 1997a. Preliminary results from a study of habitat selection and population size of Corn Buntings *Miliaria calandra* in north-east Scotland. In Donald, P.F. & Aebischer, N.J. (eds) *The Ecology and Conservation of Corn Buntings* Miliaria Calandra: 115-123. Peterborough: Joint Nature Conservation Committee.

Watson, A. & Rae, S. 1997b. Some effects of set-aside on breeding birds in northeast Scotland. *Bird Study* **44:** 245-251.

Wilson, J.D., Evans, J., Browne, S.J. & King, J.R. 1997. Territory distribution and breeding success of Skylarks *Alauda arvensis* on organic and intensive farmland in southern England. *J. Appl. Ecol.* **34:** 1462-1478.