Habitat selection by territorial male Corn Buntings *Miliaria calandra* in a Danish farmland area

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(Med et dansk resumé: Habitatvalg af Bomlærke Miliaria calandra *i et dansk landbrugsområde)*

Abstract Male Corn Buntings *Miliaria calandra* were mapped in a 28 km^2 farmland area in Djursland, Denmark. Mean territory density was 8.8 territories km^{-2} but with great local variation, up to a maximum of 23.9 territories km^{-2}. The distribution of birds and habitat characteristics (crops, hedgerows, soil types etc.) were analysed by using Principal Component Analysis (PCA) and linear multiple regression.

The highest Corn Bunting densities were found on the most fertile soil type, while the birds strongly avoided bog, forest and humus soil areas. There was a clear preference for areas with the greatest proportion of tillage, but with a strong preference for tilled land with many fields and high crop diversity. Corn Bunting density correlated significantly with several crop types, but sometimes this was merely due to a preference for tilled land per se. After controlling for extent of tilled land, only winter rape, beets and mixed spring barley/peas showed significant positive partial correlation coefficients with Corn Bunting density while rye was avoided. In the tilled land density was highest were small grassy habitats made up 1-5% of all habitats.

The decline in the Corn Bunting population in Denmark during several decades and the partial recent recovery is discussed. Changes in farming systems from traditional mixed farming to more specialized and intensive farming seems to have been an important factor in the decline.

Introduction

In the twentieth century the Corn Bunting *Miliaria calandra* suffered a dramatic decline in number and range in central and north-western Europe (see Donald 1997 for a review), following the same population trend as many other farmland species (Schifferli 2000). Several hypotheses have been proposed to explain the decline, most of which relate to changes in agricultural practice. The rapid decline has been shown to coincide with a number of radical changes in farming practices: increased use of pesticides, autumn instead of spring tillage, loss of traditional rotations, improved harvesting methods, and earlier mowing of grass crops (Donald et al. 1994, Donald & Evans 1995, Aebischer & Ward 1997, Donald 1997, Gillings & Watts 1997, Newton 2004). Climatic changes have also been proposed as a factor in the decline, since declines seem to have been greater at the northern and western limit of the species range (Donald 1997).

In Denmark, the Corn Bunting has undergone a similar decline in population, but with an estimated population of 31 000 "pairs" (Jacobsen 1997) it is still one of the largest populations in northern Europe (Hagemeijer & Blair 1997). The decline was evident from the 1940s (Grell 1998), and for 1976-1993 the Danish breeding birds monitoring scheme based on point counts has demonstrated a more than 60% decline. In recent years the population seems to have recovered to some extent (Heldbjerg 2005). The species is yellow-listed in terms of conservation concern (Stoltze & Pihl 1998). The distribution in Denmark is almost entirely confined to farmland, particularly arable land. The highest numbers of Corn Buntings are found in north and west Denmark, while the species has disappeared from many places in the south-east of the country (Grell 1998).

This paper is based on data on singing males collected in a single, large farmland area. The aim of the study was to examine the relationships between the distribution of male territories and different habitat structures, particularly soil type, crop type, and availability and type of song posts. The results are discussed in relation to the farming system and in light of the recent changes in the Danish population of Corn Buntings.

Study area

Fieldwork was carried out in spring 1995 in north-eastern Djursland in Jutland, Denmark (56º27'N, 10º52'E). This area was chosen because it was known to hold a high density of Corn Buntings. Furthermore, the farmland in the study area is comparable to most of the farmland in south-eastern Denmark with respect to climate and soil quality, allowing habitat associations to be placed in a wider regional context.

The study area covered approximately 28 km^2 of which 91% was farmland, the remaining being villages, tracks, roads and woodland. The farmland was mainly arable (81%) with 14% grassland (permanent or non-permanent) and 5% farms, hedgerows etc. A few small villages and scattered farms and smallholdings characterized the landscape. Two streams ran through the area. The most common field types were winter wheat (31%), spring barley (18%), winter barley (15%), winter rape (9%), temporally grazed (5%), rye (4%), hay/silage (3%) and set-aside (3%). Cereals made up two thirds of the farmland.

Based on soil type the study area could roughly be separated into three parts (Fig. 1): a clayey-sandy soil forming the major part, a fine-sandy soil to the south, and a coarse-sandy soil towards the southwest. A fourth soil type, humus soil, was present along the river systems. Wheat and barley fields with relatively few windbreaks dominated the main part. Towards the southwest windbreaks became more numerous. The terrain varied from 5 m to 50 m above sea level. The study area was situated close to Kattegat, with limestone cliffs characterizing the coastline. The annual precipitation in east Djursland, including the study area, is relatively low (550-600 mm, compared to the national average of 712 mm (Frich et al. 1997)).

The study area was divided into a grid net of squares measuring 500×500 m. This square size was chosen as a compromise aiming at reducing edge effects (e.g. accidental registration of birds from neighbour squares), reducing the risk of obtaining habitat data of no relevance to the territory densities, and obtaining an adequate number of squares and an appropriate dispersion of territory densities.

Methods

Territory mappings. The number of Corn Bunting territories was estimated by using the Territory Mapping Method (Bibby et al. 1993). Corn Bunting is a polygynous species, which implies that number of territories cannot directly be related to number of breeding females. Males were considered to be holding territories if they were singing, or if aggressive encounters between males were recorded. Only males were mapped and no attempts were made to locate nests.

Corn Buntings were registered on eight visits between 1 May and 25 May 1995 in calm sunny weather. On each visit, the position of each bird was marked on a detailed map. The behaviour of the birds was noted as well as their choice of song post. Every survey took on average 10 hours and was carried out cycling very slowly along roads, tracks and paths. On every visit the route started in a different part of the area. In this way every part

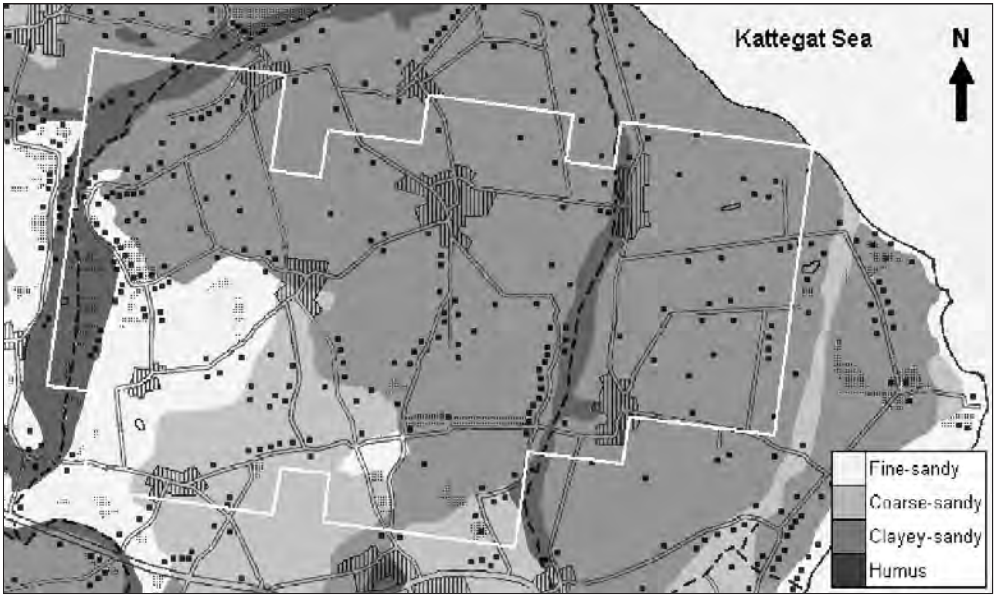

Fig. 1. The study area and the distribution of the four registered soil types. In addition, the map shows roads, villages (vertical shading), wooded areas (dotted shading), individual farms and houses (squares) and streams (broken lines).
Undersøgelsesområdet og fordelingen af dets fire jordtyper. Veje, landsbyer (skraveret), skov (prikket), fritliggende ejendomme (firkanter) og vandløb (stiplet) er vist.

was at least once visited during the expected period of maximum song activity in the early morning hours. Only a few fields, not accessible from roads or tracks, were covered on foot. To ensure optimal coverage of the Corn Buntings in all habitats, only areas within a distance up to 300 m from accessible roads or tracks were included in the study. This distance was considered to be adequate for recording the males' distinctive and persistently uttered song from an elevated position.

All observations (except a very small number excluded because they concerned flocks) were copied to a single map and the number of territories was found by clustering registrations of birds. Only clusters with at least three registrations of singing males were considered to represent territories. The proportion of registrations in each territory falling in different grid squares was calculated, after which Corn Bunting territory density in each square could be computed.

Habitat composition. Land-use and hedgerow characteristics were recorded during June and July 1995, directly recorded onto aerial photographs (1:10000, from 1993). The grid net was transferred to the aerial photos and length/area of relevant habitats was measured by use of transparent graph paper. Soil types were extracted from geophysical maps (1:50000) (Sekretariatet for Jordbundsklassificering 1978). To describe the undulating terrain, length of contour lines (five-metre lines) were measured on 1:25000 scale maps.

Landscape components occurring in 5% or less of the squares were excluded from the analysis. In all, 49 parameters were used in the analyses (Table 1). Considered land-use types or landscape structures were those expected to influence habitat choice by Corn Buntings, e.g. preferred song posts, potential nesting habitats, and expected foraging habitats, or those major elements in the landscape likely avoided by the species (forests, towns etc.). Some landscape structures were measured in more than one way, e.g. farmland was expressed as total area, average field area, number of fields, and by a crop diversity index. The parameters were not mutually exclusive, e.g. spring barley area contributed to both total barley area and area of tilled land besides other farmland categories.

Detailed information about farming practises (e.g. fertiliser and pesticide use) was not collected, but all farms in the study area were conventionally managed.

Table 1. Landscape parameters measured in each of the 111 squares used in the analysis. For some landscape components several aspects were measured, each counting as a parameter. These aspects are given by a code: a area, d diversity index, fz average field size, l length, n number of fields/trees, p proportion to farmland area. The code is only stated in the text if multiple choices are possible.
Landskabsparametre registreret i de 111 kvadrater, der indgår i databehandlingen. Nogle landskabstyper er opmålt ved hjælp af flere metoder, hver betragtet som én parameter. De forskellige metoder er angivet med en kode: a *areal,* d *diversitetsindeks,* fz *gennemsnitligt markareal,* l *længde,* n *antal marker/træer,* p *andel af landbrugsland. Koden er kun angivet i teksten, hvor forveksling er mulig.*

Crop types *Afgrøder*	**Soil types *Jordtyper***
Farmland (a,d,fz,n) *Agerland*	Fine-sandy soil (a) *Finsandet sandjord*
Tilled land (a,d,fz,n,p) *Pløjet land*	Coarse-sandy soil (a) *Grovsandet sandjord*
Total barley (a) *Byg*	Clayey-sandy soil (a) *Lerblandet sandjord*
Winter barley (a) *Vinterbyg*	Humus soil (a) *Humusjord*
Spring barley (a) *Vårbyg*	**Wooded land *Træbevokset***
Rye (a) *Rug*	Total wooded land[4] (a) *Samlet træbevokset*
Winter wheat (a) *Vinterhvede*	Forest (a) *Skov*
Total rape (a) *Raps*	Hedgerow (l) *Læhegn*
Winter oil-seed rape (a) *Vinterraps*	Solitary tree (n) *Enligt træ*
Spring oil-seed rape (a) *Vårraps*	**Other *Andet***
Mixed spring barley/pea (a) *Blandet vårbyg/ært*	Bog (a) *Mose*
Beets (a) *Roe*	Stream (l) *Vandløb*
Maize (a) *Majs*	Treeless boundary[5] (l) *Træløst skel*
Pea (a) *Ært*	Road verge (l) *Vejkant*
Potato (a) *Kartoffel*	Field boundary (l) *Markskel*
Grassland (a) *Græsklædt land*	Town (a) *By*
Total grazed land (a) *Afgræsning*	Farm/house (a) *Ejendom*
Temporally grazed[1] (a) *Midlertidig afgræsn.*	Road (l) *Landevej*
Permanent pasture[2] (a) *Permanent afgræsn.*	Track (l) *Markvej*
Set-aside[3] (a) *Brak*	Overhead wire (l) *Højspændingsledning*
Hay/silage (a) *Hø/ensilage*	Fencing wire (l) *Hegnstråd*
Seed grass (a) *Frøgræs*	Contour line[6] (l) *Højdekurve*

[1] Short-term rotational land typically in otherwise tilled land *Midlertidigt græsningsareal i det dyrkede land*
[2] Grazed at the moment of registration, but probably at other times hay/silage fields and long-term rotational, typically on wet land *Enge afgræsset på observationstidspunktet, men kan til andre tider være høenge, er i lang rotation*
[3] The European Union set-aside scheme *EUs braklægningsordning*
[4] Including nurseries and orchards *Inkluderer planteskoler og frugthaver*
[5] Boundaries along roads and tracks or between fields *Skel langs landeveje, markveje og mellem marker*
[6] Measured as 'length of five-meter lines x number of levels of five-meter lines' *Opmålt som 'længden af 5 meter-kurver x antal niveauer af 5 meter-kurver'.*

Statistical analyses. Some of the more inaccessible fields were not sufficiently surveyed during the mapping of Corn Buntings, and consequently it was decided that grid squares with less than 60% surveyed area were excluded from the analyses. Squares with more than 40% woodland were also excluded. In all, 111 grid squares were included in the analyses. Of these, 78 were completely surveyed, and 19 other grid squares were at least 75% surveyed. Before the analyses were performed, data from partly surveyed squares were adjusted by multiplying with a factor which expressed the difference between the fully surveyed and actually surveyed area.

Before statistical analyses, all parameters were transformed to fit the assumptions of parametric tests and to allow analysis assuming a normal error structure for all parameters (Sokal & Rohlf 1997). All areas were proportional measures because they were inherently constrained to a part area as a proportion of the grid square size (0.25 km^2); thus area measures were arcsine square root transformed (arcsin $\sqrt{p}$), where p is the proportion. Length measures were log transformed ($\log_{10}(X+1)$) while counts, such as number of Corn Bunting territories or isolated trees, were square root transformed ($\sqrt{X+0.5}$).

Two different crop diversity indices were calculated by use of the Shannon-Weaver formula ($H = -\sum p_i \ln p_i$), were p_i is the proportion of the different habitat parameters (Fowler & Cohen 1995). First, a diversity index based upon all crop types included

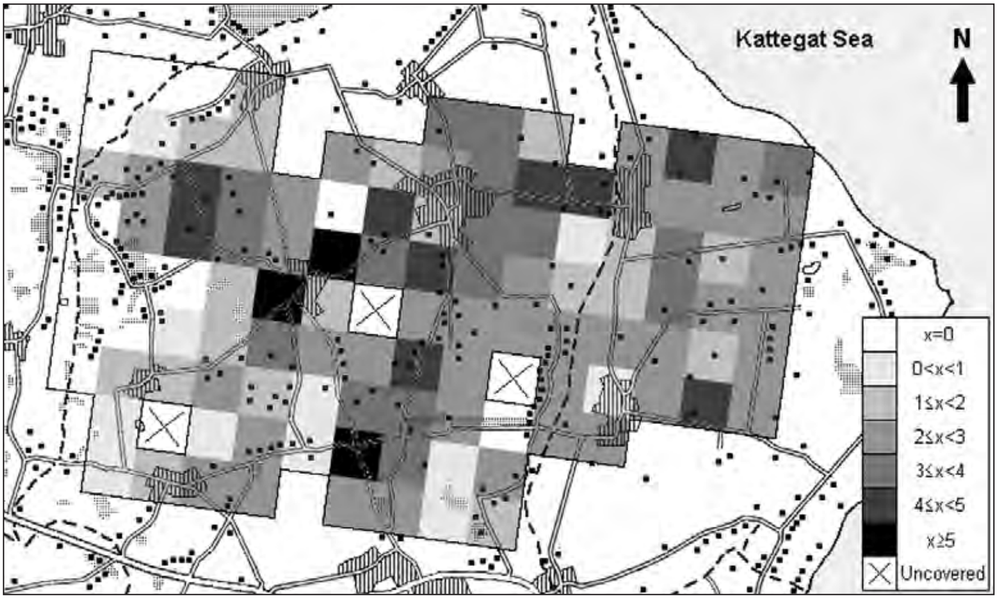

Fig. 2. The 111 grid squares (each 500×500 m) covered in the present study area. Corn Bunting densities (numbers of territories per square) are shown as shading of increasing intensity.
De 111 kortlagte kvadrater i undersøgelsesområdet. Bomlærketætheden (antal territorier pr kvadrat) er vist med gråtoner.

in *Farmland* was calculated (Table 1). Second, an index was calculated only for the most intensively managed farmland (*Tilled Land*). The diversity indices were calculated on transformed data.

Correlations between selected parameters were examined by Pearson's partial correlations. To test for non-linear relationships between Corn Bunting density and the different habitat parameters, all transformed parameters were squared and their quadratic terms included in the multiple regression analysis.

Principal component analysis (PCA) was used in order to describe the main trends in land use and habitat composition. On the basis of the correlation matrix of the transformed parameters, PCA reduced the original set of parameters to a smaller number of mutually independent linear combinations of parameters (principal components). The components were interpreted by inspection of their eigenvector coefficients. The result of the ordination was also used in single-factor regressions to examine the correlation between the components and Corn Bunting densities. Only the three first components were considered since these explained 40% of the total variance.

To construct a model that describes the relationships between Corn Bunting densities and habitat composition with as few parameters as possible, stepwise multiple linear regression analysis was used, whereby parameters were added one at a time to maximize the variance explained at each step. The final model was adopted when no additional parameter was significant at $P < 0.05$. The three principal components were included in this analysis.

All statistical calculations were performed using the SAS statistical package (SAS Institute Inc. 1996).To secure a reliable regression model, the assumptions of homoscedasticity and of low multicollinearity were tested by use of appropriate options in the SAS REG Procedure. The possibility of autocorrelation was tested by use of the Durbin-Watson statistic. The parameters in the final model were also examined for intercorrelation with rejected parameters to investigate possible associations between Corn Bunting and habitat not described by the model.

Results

General analyses

The number of singing males on the eight visits in May varied between 105 and 165. There was a significant increase in counts of singing males during the month ($r^2 = 0.70$, $F_{1,6} = 14.1$, $P < 0.01$), indicating that some birds had not occupied territories at the beginning of the period.

Of the 111 grid squares covered in the study, 98 (88%) held Corn Buntings. A total of 231 territories were registered, from which it was estimated there were 245 territories in the whole study area (correcting for parts of squares not surveyed). Overall Corn Buntings density was 8.8 territories km^{-2} (SE = 0.54). In occupied squares densities ranged from 1.1 to 23.9 territories km^{-2} (mean = 10.0, SE = 0.51). The Corn Buntings were least common in the westernmost part of the survey area (Fig. 2).

Analysis of soil type preferences revealed that there was no significant difference in Corn Bunting density between the two sandy soil types *Fine-sandy soil* and *Coarse-sandy soil* (t = 1.40, ns), while density varied significantly (t = 2.57, P < 0.05) between grid squares dominated (at least 75%) by the two sandy soil types grouped (mean = 1.67, n = 23) and squares dominated by *Clayey-sandy soil* (mean = 2.48, n = 67). In five cases *Humus soil* made up more than 60% of a square, all of which lacked Corn Buntings.

Initially the correlation matrix between Corn Bunting density and landscape parameters was examined to identify the main trends in the data. In general, the most negatively correlated parameters were those describing humid, wooded or coarse-sandy areas. The three strongest negative correlations were with *Bog* (r = -0.47), *Forest* (r = -0.45) and *Humus soil* (r = -0.45). The most positively correlated parameters were those describing intensively managed farmland. The three parameters most strongly correlated with Corn Bunting density was *Tilled land-a* (r = 0.45), *Tilled land-p* (r = 0.44) and *Clayey-sandy soil* (r = 0.44) (in all six cases df = 110 and P < 0.0001).

The single crop most strongly correlated with corn bunting densities was *Winter rape*, but other crop-types were also significantly correlated (Table 2). However, correlation between specific crops and Corn Bunting density may have occurred simply because the crops were most common in areas with a high proportion of tilled land. Partial correlation coefficients were therefore calculated in order to examine the correlation between density and different crops whilst controlling for the correlation between density and *Tilled land-a* (Table 2).

Table 2. Correlation coefficients (r) and partial correlation coefficients ($r_{partial}$) between Corn Bunting density and areas of the most common crops and other land measures. * P < 0.05, ** P < 0.01, *** P < 0.001, **** P < 0.0001, ns: not significant, df = 109.
Korrelationskoefficienter (r) og partielle korrelationskoefficienter ($r_{partial}$) mellem bomlærketætheden og udvalgte landskabsparametre. Se Tabel 1 for danske navne på landskabsparametre.

Parameter	r		$r_{partial}$	
Winter rape	0.39	****	0.26	**
Winter barley	0.28	**	0.15	ns
Winter wheat	0.22	*	-0.06	ns
Beets	0.20	*	0.20	*
Mixed spring barley/pea	0.18	ns	0.29	**
Spring barley	0.08	ns	0.03	ns
Rye	-0.29	**	-0.27	**
Total grazed land	-0.32	ns	0.01	ns
Temporally grazed	0.00	ns	0.17	ns
Permanent pasture	-0.45	****	-0.22	*
Set-aside	-0.16	ns	0.02	ns
Hay/silage	-0.16	ns	0.11	ns
Farmland-n	0.01	ns	0.18	ns
Tilled land-n	0.35	***	0.22	*
Farmland-fz	0.15	ns	-0.16	ns
Tilled land-fz	0.23	*	-0.12	ns
Farmland-d	0.01	ns	0.34	***
Tilled land-d	0.38	****	0.37	****

For some of the crop types the results showed that the apparent correlations with density were explained by the correlations between these and *Tilled land-a* (e.g. *Winter wheat* and *Winter barley*). For other crops (e.g. *Winter rape*, *Beet* and *Mixed spring barley/pea*) the correlation coefficients were almost unchanged or improved, indicating some degree of association between the specific crop and Corn Bunting density.

The positive correlation between Corn Bunting density and measures of field sizes could be an expression of the preference for the arable farmland, as fields of grassland in general were much smaller than the intensively managed fields (on average 50%). The partial correlation coefficients also showed that, within the intensively managed farmland, high crop diversity (*Farmland-d* and *Tilled land-d*) and a high number of fields (*Tilled land-n*) were good indicators of Corn Bunting density (Table 2).

To test whether the positive value of *Farmland-d* partial correlation coefficient reflected an importance of the presence of small-scale grassland in the arable farmland, the combined area of four ungrazed grassy habitat types was analysed: *Set-Aside*, *Hay/silage*, *Road verge* and *Field boundary*. The 111 squares were separated into four classes with different proportions of grassland to farmland. Mean territory density was then calculated within each class. The results (Fig. 3) suggested that some grassland (but not too much) was optimal for Corn Buntings.

Principal component analysis

The first component (Table 3) clearly represented a gradient from intensive farming with large cereal fields to a low-intensive farming with pasture, meadows and woods. This component also reflected a gradient of humidity. The second principal component reflected a transition from a homogeneous and monotonous landscape (farming or non-farming) towards a more diverse agricultural landscape with many farms and smaller fields, but still with intensive farming. The third principal component apparently reflected a transition from an open landscape with few hedgerows to a more enclosed landscape. This component, however, could also be a measure of the transition from the clayey and fertile eastern part of the study area to the sandier, undulating south-western part.

The three components combined accounted for 40.5% of the variability in the habitat data set (Table 3). The most frequently used criterion for significance is an eigenvector coefficient with a value of 0.32 or more (Tabachnick & Fidell 1996).

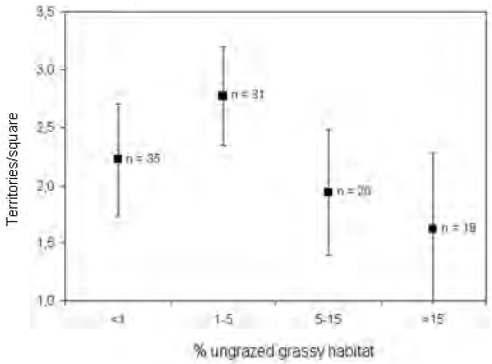

Fig. 3. Mean territory density in relation to the proportion of ungrazed grassy habitat to farmland, with 1.96·SE error bars. The grassy habitats included are set-aside, hay/silage, road verge and field boundary.
Gennemsnitlig territorietæthed (territorier pr kvadrat) i kvadrater med forskellig andel (%) af ugræsset græsareal i agerlandet (brak, hø/ensilage, vejkanter og markskel), med 5%-konfidensgrænser angivet.

Table 3. Eigenvector coefficients (ec) from the principal component analysis on habitat data. Only coefficients with the highest absolute values (5 negative and 5 positive values) for the first three principal components are shown. Eigenvalues and proportion of explained variance for each axis are given. See Table 1 for a list of parameters included in the PCA, and for explanation of measurement codes (a, d, fz, n, p).
Eigenvektor-koefficienter (ec) fra principialkomponent-analyse af landskabsdata. Kun de 10 numerisk største koefficienter (5 positive, 5 negative) fra hver af de tre første principale komponenter er vist. For hver komponent er vist eigenværdien og den forklarede andel af variansen. Se Tabel 1 for danske navne på parametre.

PC1	ec	PC2	ec	PC3	ec	Sum
Humus soil	0.24	Tilled land-d	0.35	Coarse-sandy soil	0.34	
Total grazed land	0.23	Tilled land-n	0.35	Rye	0.32	
Permanent pasture	0.23	Farmland-n	0.31	Contour line	0.28	
Bog	0.23	Farmland-d	0.27	Total wooded land	0.25	
Solitary tree	0.22	Spring barley	0.21	Forest	0.22	
Farmland-fz	-0.20	Permanent pasture	-0.15	Stream	-0.17	
Farmland-a	-0.22	Humus soil	-0.16	Farmland-n	-0.18	
Tilled land-fz	-0.23	Bog	-0.17	Wheat	-0.21	
Tilled land-p	-0.29	Tilled land-fz	-0.20	Field boundary	-0.28	
Tilled land-a	-0.30	Farmland-fz	-0.25	Clayey-sandy soil	-0.30	
Eigenvalue	10.25	Eigenvalue	5.28	Eigenvalue	3.50	
Explained variance	21.80	Explained variance	11.22	Explained variance	7.46	40.48

Only four of the coefficients meet this criterion so the three components are poorly defined.

The regression of Corn Bunting density against each of the three principal components revealed significant relationships for all three components, but explained little in the variance amongst these relationships (Fig. 4).

Multiple regression

The results of the step-forward multiple regression procedure describing the relationships between Corn Bunting densities and habitat composition are given in Table 4. In the first session of the regression procedure *Tilled land-fz* and *Tilled land-d* were both included in the model, but high intercorrelation caused the latter to be excluded again by the procedure. The two parameters are highly negatively correlated (r = -0.29) since increasing field size inevitably results in fewer fields, which in small areas like the present grid squares are likely to cause a lower crop diversity index. Analysis of partial correlations revealed that the correlation between *Tilled land-fz* and Corn Bunting density was not a preference for large fields *per se*, but just a measure of the species' general preference for tilled land (Table 2). Therefore the parameter was forced out from the regression procedure. In the new model the procedure instead included *Tilled land-a*.

The final model included ten parameters (Table 4). *Tilled land-a* was the most important predictor of Corn Bunting density, explaining 21% of the total variation in density. The crop diversity index *Tilled land-d* and the predominant soil-type *Clayey-sandy soil* were also important predictors. Among crop types, *Mixed spring barley/pea* was the best predictor of density. The rest of the parameters included in the model each only contributed a little to the total explained variation.

The model was in line with the results of the principal component analysis by pointing at *Tilled land-a* and *Tilled land-d* as important descriptors of Corn Bunting preference. PC 1 and PC 2 also stressed the preference for the intensively managed farmland of high crop diversity (Fig. 4). The correlation between bird density and *Contour line* (r = -0.19, P < 0.05) was most likely a function of the correlations between *Contour line* and both *Coarse-sandy soil* and *Grassland*. Hence, the presence of *Clayey-sandy soil* and *Contour line* in the model was a parallel to PC 3, and expressed the species' preference for farmland upon soils of higher quality within the study area.

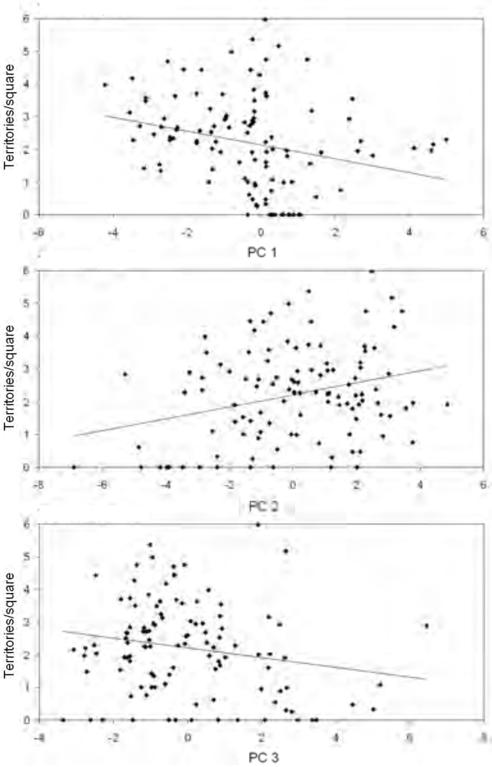

Fig. 4. Relationship between the principal component scores of grid squares, and the number of Corn Bunting territories within them. Only the first three principal components of the PCA analysis are shown, and for all three there was a significant correlation (PC 1: $r^2 = 0.07$, $F_{1,108} = 7.96$, $P < 0.01$; PC 2: $r^2 = 0.08$, $F_{1,108} = 10.11$, $P < 0.01$; PC 3: $r^2 = 0.04$, $F_{1,108} = 4.31$, $P < 0.05$). The composition of the principal components is given in Table 3.
Korrelation mellem de første tre principalkomponenter i PCA analysen og bomlærketætheden i kvadraterne (hvert punkt svarer til et kvadrat). For alle tre principalkomponenter (defineret i Tabel 3) er der en signifikant korrelation.

Discussion

The analyses revealed a positive relationship between Corn Bunting abundance and intensive tillage agriculture, while the birds clearly avoided meadows and wooded areas, and Corn Buntings occurred in lower densities on farmland on sandy soils. The preference for tilled land is well known and has been documented by numerous studies (Cramp & Perrins 1994, Donald & Evans 1995, Harper 1995), though some populations prefer large set-aside areas (Fischer & Schneider 1996) or habitats like marshes and wet grasslands (Hegelbach & Ziswiler 1979, Hustings et al. 1990).

The overall mean population density in north-eastern Djursland was 8.8 territories km^{-2} but with local densities of up to 23.9 territories km^{-2}, which is probably about the highest found anywhere in Denmark. In a study in east England up to 15 territories km^{-2} were found, but the overall density was 1.2 territories km^{-2} (Mason & Macdonald 2000). Eislöffel (1997) estimated in south-west Germany an overall density of 0.5-1.2 territories km^{-2} in different areas, with up to 6.4 territories km^{-2} in population concentrations. In Poland an area held 3.2 "pairs" km^{-2} (Tryjanowski 2000). Thus, the population in north-eastern Djursland may be one of the densest in north-western Europe. However, much higher densities are found in the central and southern Europe (Cramp & Perrins 1994).

Habitat preferences

The results highlighted several types of land-use as favourable to Corn Buntings, while others seemed unimportant to the birds and yet others were avoided. However, habitat correlations might not always be linear; indeed preference for land-use types might have limits above which they are no longer favoured. Large areas of a single crop will inevitably limit crop diversity, and this parameter was of greater importance to the birds than any specific crop type (Table 4). It is possibly that some land-use types in the study area only occurred in areas above such a limit, and therefore was rejected in the regression model, even though they may be attractive to Corn Buntings at lower values.

The regression procedure suggested that a group of parameters were good predictors Corn Bunting density, including four crop types: *Beets*, *Mixed spring barley/pea*, *Winter barley* and *Winter rape*. The presence of *Beets* and *Mixed spring barley/pea* in the model were striking, considering that both made only a small contribution to the farmland area (2.8% and 0.8%, respectively). The importance of these two crop types was supported by the partial correlations (Table 2), since both were significantly correlated with Corn Bunting density whilst controlling for area of tilled land. Both crop types had in common that they grew on relatively small fields and primarily were used as fodder for pigs or cattle.

Several studies have reported greater use of spring-sown than winter-sown cereals by breeding Corn Buntings (Donald 1997, Gillings & Watt 1997), though others did not find such an association (Donald & Evans 1995, Donald & Forrest 1995, Brickle & Harper 2000). In the present study it was not possible to correlate Corn Bunting density with spring-sown cereals. *Spring barley*, covering 86% of the spring cropping area and 18% of the total farmland, did not correlate with Corn Bunting density (Table 2) and was rejected in the regression model. Thus it was not as a spring-sown crop that *Mixed spring barley/pea* correlated with density, nor was it because of the peas that, as separate fields, did not correlate with density ($r = 0.09$, ns). Undersown fields are rich in some in-

Table 4. Results of the multiple linear regression model (stepwise forward) on transformed parameters that best explain the variation in Corn Bunting density ($r^2_{adj} = 0.552$, df = 110, $F = 14.54$, $P < 0.0001$). Total r^2 is not the sum of partial r^2 values, due to the intercorrelations between the predictor variables. Parameters are listed in the order they entered the model. See Table 1 for a list of all parameters included in the test.
Resultatet af den multiple regressionsmodel (transformerede data), der bedst forklarer variationen i bomlærketætheden. Parametrene er opstillet i den rækkefølge, de indgik i modellen. Se Tabel 1 for danske navne på parametre.

Parameter *Parameter*	Coefficient *Koefficient*	SE	Partial r^2	F	P
Tilled land-a	0.247	0.145	0.207	28.39	<0.0001
Tilled land-d	0.425	0.126	0.107	16.87	<0.0001
Clayey-sandy soil[1]	0.135	0.034	0.094	17.06	<0.0001
Mixed spring barley/pea[1]	3.352	0.900	0.053	10.41	<0.01
Contour line[1]	-0.034	0.014	0.026	5.41	<0.05
Beets[1]	2.142	0.627	0.026	5.53	<0.05
Road verge[1]	0.060	0.028	0.025	5.57	<0.05
Winter barley	0.348	0.160	0.018	4.06	<0.05
Winter oil-seed rape	0.348	0.157	0.019	4.41	<0.05
Overhead wire[1]	0.043	0.020	0.018	4.37	<0.05

[1] The quadratic term *Kvadratet på variablen*

Photo: Søren Kristoffersen.

I yngletiden foretrækker Bomlærken åbenbart næringsrige jorder med en varieret udnyttelse – mange marker og høj afgrødediversitet. De største tætheder fandter i områder, hvor der derudover var et islæt af "fristeder" som markskel, vejkanter, brakmarker o.a.

vertebrate species (Ward & Aebischer 1994, Potts 1997), and are attractive not only to Corn Buntings (Ward & Aebischer l.c.) but also to, e.g., Skylarks *Alauda arvensis* (O'Connor & Shrubb 1986) and Grey Partridges *Perdix perdix* (Potts 1997). Possibly, a similar benefit exists with cereals mixed with legumes. In addition, a mixed crop may also provide better nest covering possibilities. Suter et al. (2002) found nesting success to be significantly higher in weedy fields than in more intensively managed fields. However, Skylarks did not nest in pea fields due to the density of the vegetation (Wilson et al. 1997).

Modern methods of beet growing, relying heavily on herbicides, reduce the availability of food items and suitable nest sites (Donald 1997). However, fodder beets are characteristic for mixed farming, hence *Beets* may also be a good indicator of the presence of more diverse agricultural practice.

The other two crop types in the model, *Winter rape* and *Winter barley*, were both common crops in the farmland. The significance of *Winter rape* for Corn Buntings is surprising, since this fast-growing crop forms very tall and dense vegetation and thus probably is less suitable for foraging or nesting. In England Skylarks clearly avoid this crop for nesting (Wilson et al. 1997), while it was favoured for foraging by Yellowhammers *Emberiza citrinella* (Stoate et al. 1998). Early in the season, when rape seed fields are still open, they are reportedly used by Corn Buntings for foraging as well as for nesting purposes (Harper 1995, Watson & Rae 1997). Among the crop types *Winter rape* was also the most commonly used for song posts, although it was used in only 5% of 1049 registered song posts (Lilleør in press). *Winter rape* and *Winter barley* were, together with *Winter wheat*, the crop types best correlated with breeding density (Table 2). But in line with the findings of Donald & Evans (1995) the correlations between density and *Winter barley* and *Winter wheat* were merely an expression of the preference for tilled land in general (Table 2). Gillings & Watt (1997) also found winter barley to be correlated with Corn Bunting density. They suggested this to be linked to the ripening of the grains near the egg hatching date, giving the birds an alternative food supply when invertebrates were limited.

The regression model included *Road verge* in the model. This was not an artefact caused by the method of bird registration, since Corn Bunting density correlated differently with *Road* and *Track* ($r_{density \times road} = 0.25$, $P < 0.001$; $r_{density \times track} = -0.07$, ns). Grassy margins are important sources of invertebrate food (Wilson et al. 1999, Brickle & Harper 2000), but are susceptible to accidental pesticide spraying and other farming activity. This damaging effect is probably larger on boundaries between fields than edges along public roads. *Road verges* also reflected farmland composition. The network of roads (but not of tracks) was denser in farmland with many farms and smallholdings, smaller fields and higher crop diversity (e.g., $r_{road \times tilled\ land\text{-}d} = 0.31$, $P < 0.001$).

No other parameters describing grassy habitats were significantly and positively correlated with Corn Bunting density, nor were they included in the regression model. In fact, *Permanent pasture* was strongly negatively correlated with density (Table 2). Permanent grasslands, depending on grazing pressure and fertilizing, evolve dense and less diverse grass swards less suitable for seed-eating birds (Wakeham-Dawson & Smith 2000). All *Permanent pasture* was wet, grazed land often adjacent to bogs, scrubs and hay fields, forming large areas unsuitable for breeding Corn Buntings. The partial correlations of Table 2 indicated a (non-significant) positive preference for *Temporally grazed* (typically non-humid areas). Field sizes of *Temporally grazed* were fairly small (on average 0.8 ha) and thus potentially attractive to the Corn Buntings, similar to the ungrazed grassy habitats (Fig. 3).

It is not expected that Corn Bunting density would correlate strongly with area of grassy field types, since area of grassland intrinsically constrain the area of tilled land, which is considered the species' main habitat. Smaller fields of ungrazed grassland scattered in the farmland may nevertheless be important to breeding Corn Buntings for foraging and nesting (Fig. 3). Though Corn Buntings most often nest in cereals (frequently close to field margins), they also regularly use ungrazed fields (set-aside, hay, weedy areas etc), grass margins and bramble, while nests are seldom reported from grazed or improved grassland (Cramp & Perrins 1994, Gillings & Watts 1997, Hartley & Shepherd 1997, Brickle & Harper 2000). Møller (1983a) and Brickle & Harper (l.c.) found grassy field margins to be more common near nests than expected by chance. Field margins and ungrazed grassland are rich in invertebrates used in feeding chicks, and relative to their availability they are heavily used for foraging (Fischer & Schneider 1996, Watson & Rae 1997, Brickle & Harper 2000, Brickle et al. 2000).

Soil type

Several authors have noted soil type preferences by Corn Buntings, though no detailed studies have been made on this issue. In the British Isles there appears to be an affinity for light soils, particularly chalk and limestone, while clay soils seem less favoured (Shrubb 1997, Gillings & Watt 1997). In contrast, range contractions in northern Germany has confined the species to more fertile soils (Busche 1989), in some cases heavy clay and calcareous soils (Tennhardt 1995). Of the three sandy soil types present in north-eastern Djursland, there was a greater abundance of Corn Buntings on the clayey one; a soil that most likely was influenced by the limestone underground. In the study area there were no heavy clay soils, but on a national scale the decline of the Corn Buntings since the 1970s appears to have been most severe on the more fertile soils of south-eastern Denmark, where the species has disappeared from many places (Grell 1998). It seems that the species' distribution in Denmark in relation to soil type follows the same pattern as in Britain.

However, soil type influences the above-ground environment in many aspects, so it is hard to interpret the ecological mechanisms behind an association between soil type and bird density. The distribution of agricultural systems is affected by soil type, as is the timing of changes in these systems. On the fertile soils of south-eastern Denmark mixed pastoral agriculture in general was converted to intensive arable farming earlier than elsewhere (Fox 2004). Wilson et al. (1997) suggested that heavy clay soils were less suitable for nesting, because they tended to be wetter in April and May. The topic clearly needs further investigation.

Song posts

The song post type *Overhead wire* was included in the regression model, though it did not correlate significantly with density (r = 0.07, ns). Birds singing from overhead wires have a high visibility, potentially leading to a relatively higher frequency of registration. But this source of error was minimized by the limitation of survey area to 300 meters distance from the registration route. An analysis of the male Corn Buntings' use of song posts showed a clear preference for overhead wires (Lilleør in press). Since *Overhead wire* did not correlate significantly with any other parameters, it can be concluded that accessibility of preferred song posts was a factor to the male Corn Buntings in establishing a territory.

No other preferred song post types were significantly and positively correlated with Corn Bunting density in a way that could establish if the relationship was specifically due to their attractiveness as song posts, or merely reflected that they were indicators of a certain farmland structure.

Population changes in Denmark

The recent dramatic decline in the Danish population of Corn Buntings has been documented since late 1970s (Heldbjerg 2005), and has resulted in a range contraction especially in south-eastern Denmark (Grell 1998). It has been suggested that the increase in autumn-sown crops and the associated reduction in area of stubble fields were a major cause of the decline (Grell l.c.). But Fox (2004) found no indication that any of several investigated changes in agricultural practice, including the switch from spring- to autumn-sown crops, had affected the population trend in Corn Buntings during 1983-2001. However, while this would be the case when only considering the overall population trend in this period, it seems more reasonable to separate the period into two: a period of decline until 1993, and a period of increase hereafter. The population decline coincided well with the increase in the area of winter wheat and a corresponding decrease in spring barley (data from StatBank Denmark, www.dst.dk), supporting the stubble hypothesis. But in the same period there was also a decrease in the area of fodder beets and rotational grassland, crops characteristic of a mixed pastoral farming system.

It is likely that the period of decline was initiated by at least two changes in the Danish farmland. First, the shift to autumn-sown cereals whereby the stubble field area decreased, partly eliminating an important food source to the wintering birds. It is commonly recognized that the disappearance of stubble is a key factor in the decline of the Corn Bunting (Donald & Evans 1994, Donald & Forrest 1995, Mason & Macdonald 2000). Second, the abandonment of traditional, mixed farming with its mosaic of small fields of autumn- and spring-sown crops, grassland and fodder crops in favour of modern, intensified and specialized agriculture, which deteriorated the farmland as a breeding habitat.

The present analysis clearly points towards a preference for a traditional, mixed farmland, showing that Corn Buntings prefer an intensively managed farmland of high crop-diversity with many fields and tend to avoid a monotone landscape with fewer fields. This was established both by the principal component analysis (Fig. 4) and the multiple linear regression (Table 4). Several of the parameters in the regression model could also be interpreted as reflecting traditional mixed farming. Both *Beet* and *Mixed spring barley/pea* could be viewed as associated with livestock farming, and *Road verge* was much more common in farmland with many farms and smallholdings, since more settlements inevitably require more roads. *Temporally grazed*, though not included in the model, correlated significantly with the crop diversity index *Tilled land-d* ($r = 0.27$, $P < 0.01$). This field type was a central element in the formerly widespread mixed pastoral agriculture. Finally, barley is frequently recorded associated with less intensive farming systems (Ward & Aebischer 1994, Donald 1997, Gillings & Watt 1997) though this may not be the case in Denmark, where the crop often is grown as fodder to pigs.

An association between Corn Bunting and mixed farming has been documented in several studies (and in Denmark suggested by Møller 1983b). Ward & Aebischer (1994) found higher densities of Corn Buntings on farms with traditional rotations than on more specialized farms, and densities were correlated with abundance of caterpillars (Aebischer & Ward 1997). Gillings & Watt (1997) showed a positive correlation between density and crop diversity and related this to the structure of farms. Breeding performance has likewise been shown to be higher in mixed farming compared to purely arable farming (Siriwardena et al. 2000). However, some studies have failed to correlate density with crop diversity (Donald & Forrest 1995, Mason & Macdonald 2000). Mixed farming provides a high abundance and diversity of seed foods among intensive farming systems (Wilson et al. 1999), and is considered beneficial to several farmland bird species (Evans 1997, Siriwardena et al. 2000, 2001). The mosaic of crops and field boundaries also provide a variety of nesting possibilities throughout the breeding season.

The Danish Corn Bunting population has partly recovered within recent years, though it is still considerably below the levels of the 1970s (Heldbjerg 2005). The increase began in 1994, coinciding with the introduction of set-aside the year before. However, in the UK Corn Bunting has failed to recover despite the set-aside scheme (Gregory et al. 2004), and it was not possible to demonstrate a relationship between Corn Bunting density and *Set-aside* in the present study, although another type of small-scale grassy habitat, *Road verge*, was included in the regression model (Table 4). So, even if set-aside is an important foraging habitat for several bird species both in winter and in summer (Donald & Evans 1994, Wilson et al. 1996, Buckingham et al. 1999, Henderson & Evans 2000, Henderson et al. 2000), and other studies have found higher Corn Bunting densities and breeding success on set-aside than in the arable land (Fischer & Schneider 1996), it would seem that the value of set-aside for breeding Corn Buntings is a complex issue.

The present results has, in accordance with other studies, demonstrated that farmland with a high crop diversity is favoured by Corn Buntings, more so than any specific crop type. This suggests that the shift from traditional mixed farming towards a specialized and intensified farming practice has been a key factor in the decline of the species in Denmark, but leaves the recent population increase unexplained. The data also indicated that a limited amount of ungrazed grassy habitat within arable farmland is beneficial to Corn Buntings.

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Resumé

Habitatvalg af Bomlærke *Miliaria calandra* i et dansk landbrugsområde
Fordelingen af Bomlærke-hanner *Miliaria calandra* blev kortlagt i et 28 km^2 intensivt dyrket agerlandsområde i NØ-Djursland. Samlet var bestandstætheden 8.8 territorier km^{-2}, men med stor lokal variation. Området blev opdelt i et net af 0,5×0,5 km kvadrater (0.25 km^2), og den højeste territorietæthed i et kvadrat var 23.9 territorier km^{-2}. Med anvendelse af Principal Component Analysis (PCA) og lineær multipel regression blev fuglenes fordeling analyseret i forhold til udbredelsen af afgrøder, læhegn, jordtyper samt andre relevante elementer i landskabet. Fuglene havde de største tætheder på den mest frugtbare jord, mens de var helt fraværende på humusjord og i skov. Der var en klar positiv sammenhæng mellem bestandstætheden og arealet af intensivt landbrug under plov, mens fuglene undgik store græsklædte områder (enge). I det intensivt dyrkede land var der stærk præference for områder med mange marker og høj afgrødediversitet. Vinterraps, roer og en blandingsafgrøde med vårbyg og ærter var særligt foretrukne, mens rug blev klart afvist. Hvede- og vinterbygarealerne korrelerede også signifikant med bomlærketætheden, men sammenhængen med disse vidt udbredte afgrøder skyldtes snarere en præference for det dyrkede land i sig selv end for den specifikke afgrøde. De største bestandstætheder fandtes i områder, hvor 1-5% af landskabet bestod af små ugræssede "fristeder", såsom markskel, vejkanter, brakmarker og små høenge.

På baggrund af resultaterne fra NØ-Djursland og erfaringer fra udlandet diskuteres mulige årsager til den kraftige bestandsnedgang i Danmark frem til 1993 og den efterfølgende fremgang. Ændringen i landbrugets struktur fra traditionelt brug med husdyrhold, foderafgrøder og planteavl til specialiserede og intensificerede landbrug har efter alt at dømme været en hovedfaktor bag artens tilbagegang, mens den senere fremgang ikke uden videre lader sig forklare ud fra denne undersøgelse.

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