

Population crash of the ortolan bunting *Emberiza hortulana* in agricultural landscapes of southern Finland

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The ortolan bunting *Emberiza hortulana* is a bird species that has shown a particularly dramatic decline during recent decades within the agricultural areas of Europe. We studied the population density changes and environment associations of the ortolan bunting within agricultural landscapes in southern Finland, from territory to landscape scale, in 1984–2002. The crash of the ortolan bunting population took place synchronously during the early 1990s in all the subpopulations, resulting in a total decrease of 72% by the end of the study period. The decline was associated with the amount of small-scale environmental heterogeneity and with agricultural practices. Bush- or tree-covered ditches and springtime non-vegetated fields (mainly spring cereal and root crops) were the habitat factors showing a clear positive effect on the occurrence of the ortolan bunting. However, the European-wide decrease of the ortolan bunting is probably also due to changes in migration and wintering areas. All these factors should be taken into consideration when planning conservation measures.

Introduction

The ortolan bunting *Emberiza hortulana* is a western Palearctic, migrant passerine species (Cramp & Perrins 1994). In most parts of Europe the species inhabits open farmlands, where sparse trees and a high diversity of arable crops are important elements (Conrads 1968, von Lang *et al.* 1990). It is undergoing one of the steepest declines of the bird species found in the agricultural areas of Europe. Its populations have diminished since the 1950s–1980s, but the timing of the decline has varied in different geographical areas (Conrads 1977, von Bülow 1990,

von Lang *et al.* 1990, Claessens 1994, Tucker & Heath 1994, Valera & Rey 1994, Bejček *et al.* 1997, Ojanen *et al.* 1997, Stolt 1997, Väisänen *et al.* 1998, Svensson *et al.* 1999, Dale 2001a, Tiainen & Pakkala 2001). Owing to this steep decline, the European conservation status of the species has been defined as vulnerable (SPEC Category 2; BirdLife International/European Bird Census Council 2000).

At the end of the 1980s the size of the Finnish ortolan bunting population was estimated to be 150 000–200 000 pairs (Väisänen *et al.* 1998), comprising the second largest population in Europe after Spain (BirdLife International/

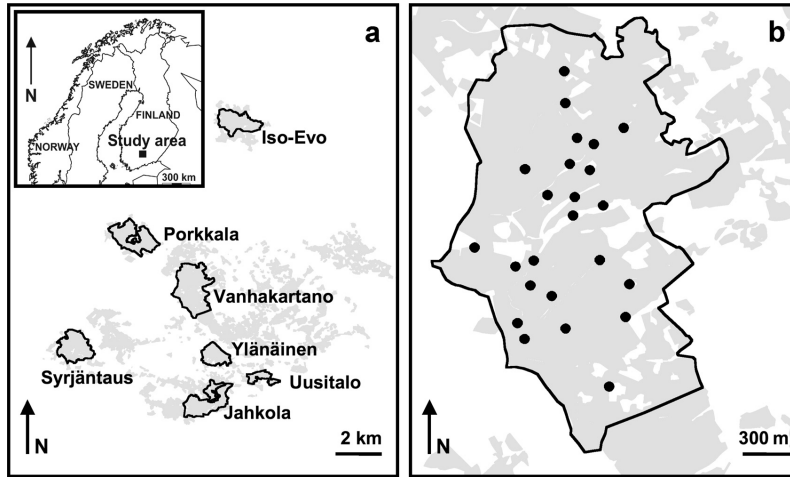


Fig. 1. — **a:** Location of the study area with the seven sub-areas delineated by a black line. The grey shading shows agricultural areas. — **b:** An example of the distribution of the ortolan bunting territories (black dots) in Vanhakartano in 1988.

European Bird Census Council 2000). The distributional history of the species in Finland is not fully known. According to sparse data from the 19th and early 20th century, the ortolan bunting bred mainly in western and northern Finland (c.f. von Haartman *et al.* 1963–1972, Lehtikoinen *et al.* 2003). It has been suggested that the Finnish population increased from the 1930s–1940s to the 1960s–1970s, with the species expanding its distribution to central and eastern Finland, and also inhabiting clear-felled areas of forest (Väisänen 1994, Tiainen & Pakkala 2001). Unfortunately there is a lack of comprehensive national census data before the 1970s, and thus the detailed history of the species remains unclear.

We know that the decline of the ortolan bunting in Finland began in the 1970s–1980s, and that it is still continuing. This is revealed by the results of two national bird atlas surveys (1974–1979 and 1986–1989) and by annual breeding bird censuses since the 1980s (Väisänen *et al.* 1998). The recent population size is estimated to be approximately 30 000 pairs (Väisänen 2001), showing that the decrease has been dramatic. The decline has been steepest in northern and eastern Finland, and less severe in western and southern Finland, the main breeding area of the species (Väisänen *et al.* 1998).

In Lammi, southern Finland, a population crash corresponding to a 54% reduction in population density took place between 1990 and 1993. Thereafter the decline continued steadily, resulting in a total decline in density of 72% between

1984 and 2002. This means that the timing of the decline was different from that observed at a national level. We studied the population trends of the ortolan bunting and the causes of the decline within this large agricultural area, using annual territory mapping census data of 1984–2002. In order to explain the changes in the ortolan bunting density and the prevailing population trend, we used a multi-scale analysis of territory density and occurrence changes, and related these to the habitat and landscape characteristics of the agricultural environment; we further related the changes to the weather conditions during the breeding season.

Material and methods

Study area

The study area is located in the municipality of Lammi in southern Finland (61°05'N, 25°00'E; Fig. 1a). The area consists of cultivated farmland, surrounded by forests, and scattered settlements. The total farmland area in this study area was 11.8 km², consisting of seven separate patches of farmland ranging in size from 0.5 to 3.1 km² (Fig. 1a).

Bird data

The territories of the ortolan buntings in the

study area were mapped annually during 1984–2002 using a two-visit mapping method, which has been shown to be an effective and reliable method for mapping ortolan buntings (Tiainen *et al.* 1985). The visits were made in May and the first half of June. Special attention was paid to simultaneous observations of singing males, to the territory locations, and to accurate estimation of territory numbers in territory concentrations. The annual numbers of territories and the positions of territory centres were then interpreted following the standards developed for studies of agricultural birds in Finland (*see* Tiainen & Pakkala 2000, Piha *et al.* 2003). Densities were calculated as the number of territories per area of agricultural land (*see* below). Furthermore, on the basis of the dominating main habitat type of each territory, we noted whether the territory was located in field area covered or not covered by springtime vegetation (*see* below). The data on territories were digitized to a GIS database, from which the occurrence of ortolan bunting territory centres in different-sized grid cells (*see* below) was determined.

The numbers of ortolan buntings were also studied over three three-year periods: 1984–1986, 1992–1994, and 2000–2002. The first period represents a phase of large population size before the decline, the second a phase of decline, and the third a phase of small population size after the decline. Owing to the non-normal distributions of the densities, we used the occurrences of the ortolan buntings within the respective periods for our grid-based analyses, rather than the density.

Spatial scales of the study

A multi-scale approach was used in our study. The occurrence of the ortolan bunting in relation to its environment within each of the three time periods was studied within grids of 100 × 100 m, 150 × 150 m, 200 × 200 m, 300 × 300 m, and 400 × 400 m. The grids covered the entire study area. In addition, we studied the density changes in seven separate sub-areas of farmland (range 0.5–3.1 km²). Overall, these scales range from territory scale to landscape scale.

Environmental data

Habitat data

Habitat data were collected in the field by identifying land-use types and by mapping land-use boundaries. The data were classified as belonging to the following five main types: (1) fields with spring tillage, not covered by vegetation in the spring (usually fields of spring cereal, potato, sugar beet, or turnip rape; rarely also sunflower, pea, vegetable garden plants, corn, onion, carrot, beetroot, or cabbage), (2) fields covered by vegetation in the spring (including ley, hay, pasture, set-aside, meadow, autumn cereal, stubble, ruderal vegetation, currant, and strawberry), (3) bush and forest patches (size ≥ 0.4 ha), (4) settlement, including farm-yards and gardens, and (5) roads. Areas were calculated for all land-use types except roads, for which length was used. The division of fields into covered *vs.* non-covered by vegetation in spring represents the situation in the first half of May, when ortolan buntings arrive at their breeding areas. In addition, the total area of cultivated land (= fields without vegetation in spring + fields covered by vegetation in spring) was used as a habitat factor.

Habitat data were digitized from the field maps into a GIS database. We used the data from 1984, 1991–1992, and 2000 that chronologically best match the data from available aerial photographs (*see* next section) for the three-year periods 1984–1986, 1992–1994, and 2000–2002, respectively.

Data on small-scale habitat elements

Data on small-scale habitat elements (point objects and linear elements, *see* below) were collected from field maps and aerial photographs taken in 1979, 1991–1992, and 2000 (aerial photographs were available from these years only). The data from aerial photographs taken in 1979 were used together with land-use data from 1984 to make the data valid for the year 1984. In addition, all other small-scale data from the aerial photographs were compared and crosschecked with the field data. Point objects included: large rocks or rock piles, single large trees and bushes,

small tree or bush islets (size < 0.4 ha), and barns. Linear elements were classified either as 'open' (short vegetation), including open field ditches and road bank ditches, or 'closed' (high vegetation, i.e. bushes or trees), including bush- or tree-covered ditches and road banks, and wood avenues. The data on small-scale habitat elements were digitized into a GIS database.

Weather data

Annual data on temperature and precipitation were collected in 1984–2002 by the weather station of Lammi Biological Station, located in the study area. Most ortolan buntings arrive in southern Finland during the first half of May (von Haartman *et al.* 1963–1972, Lehtikoinen & Vähätalo 2000), and nearly all the ortolan buntings of our study area had settled in their territories before 20 May (T. Pakkala & J. Tiainen unpubl. data). We used the number of warm (maximum daily temperature > 20 °C) days between 1 May and 20 May as a weather variable to describe the quality of the spring migration season for the ortolan bunting. In addition, we used the daily mean temperature and total amount of rain between 16 May and 31 July as weather variables to describe the quality of breeding season. Generally speaking, higher temperatures correlate positively with the early arrival and survival of migratory birds (c.f. Newton 1998, Newton 2004), and also with breeding success, whereas rainfall correlates negatively with breeding success (for the ortolan bunting: Durango 1948, Conrads 1977; for other bird species, *see e.g.* Newton 1998, Järvinen 1994, Crick & Sparks 1999, Stevenson & Bryant 2000).

Analyses

Synchrony within density and within field coverage

The levels of synchrony between the seven bunting sub-populations were studied, considering both the ortolan bunting density and the

field coverage. Time series (1984–2002) for each sub-population were first log-transformed [$\ln(x + 1)$] and detrended by differencing. The time series were then studied using a cross-correlation analysis with bootstrapping (Ranta *et al.* 1995 and Cattadori *et al.* 1999, *see also* Efron & Tibshirani 1993). Each bootstrap sample consisted of re-sampled time series selected at random. The sampling process was repeated 1000 times, and for each pair studied, the mean and standard deviations of the cross-correlation coefficients were estimated at time lag zero.

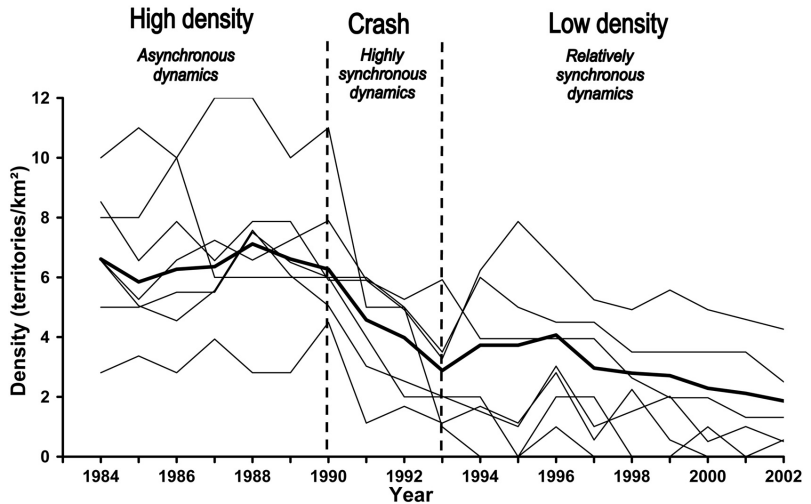
Correlation between ortolan bunting density and annual field coverage

To study the dependencies between annual changes in the ortolan bunting density and annual changes in the ratio of the springtime non-covered/covered field area of the seven farmland sub-areas, Spearman's rank correlations were calculated for the respective annual changes. The spatial scale used is considered ecologically relevant, especially when one considers the possible effects of springtime field coverage on the attractiveness of farmland as a whole to ortolan buntings arriving at their breeding grounds.

Analyses of the relationships between occurrence, density, and environmental factors

The relationships between the occurrence of the ortolan bunting and the environmental factors were studied with forward stepwise logistic regression analysis. The dependent variable was the occurrence of the ortolan bunting territory/territories in a grid cell. The dependent variable had four response levels: 0, 0.34, 0.67, and 1, depending on whether a grid cell was occupied 0, 1, 2, or 3 times within a time-period of three years (1984–1986, 1992–1994, 2000–2002), respectively. The environmental factors described in the section 'Environmental data', i.e. habitat data and data on small-scale habitat elements, were used as the independent variables. Only the proportion (%) of field not

Fig. 2. Density changes of the ortolan bunting in the seven sub-areas during the study period 1984–2002. The thick line represents the density of the entire study area, the thin lines represent the sub-areas. The dotted vertical lines divide the time series into the three periods of high density, population crash, and low density, respectively.



covered by vegetation was used. In the case of sub-areas of different sizes, the area, length or number of each habitat factor was calculated in relation to the size of the sub-area in question. Analyses were carried out at all spatial scales for each of the time-periods. Along with traditional R^2 (= coefficient of determination of the model) we also estimated maximum rescaled R^2 , which according to Nagelkerke (1991) is often more suitable for logistic regression.

The relationships between changes in the density of the ortolan buntings and changes in the habitat factors were studied using forward stepwise linear regression models. Grid cells that never had been occupied by the ortolan bunting during the entire study period were removed from the analyses. Thus, the numbers of grid cells were 297, 182, 161, 101, and 66 at the respective scales of 100 m, 150 m, 200 m, 300 m, and 400 m. The dependent variable in the models, i.e. the change in the density of the ortolan bunting, was calculated as the difference in the average number of territories between the first and second, and between the second and third period. The analyses were carried out for all the spatial scales. In both of the analyses mentioned above we also calculated all the pairwise correlations between the habitat factors for all the spatial scales, in order to discover possible interactions that might affect the interpretation of the results.

Correlation between ortolan bunting numbers and weather variables

To study the dependencies between annual changes in the ortolan bunting numbers and annual changes in the weather, Pearson's correlations were calculated between detrended time-series for the ortolan bunting of the entire study area and the following variables; (i) mean daily temperature (breeding season), (ii) total rainfall (breeding season), and (iii) number of warm days (migration period). In investigating dependency between weather and breeding success, correlations were calculated with a lag of one year for both weather variables, since any effects on breeding success can be expected to be observed in the population numbers of the following year.

Results

Population densities and trends

A strong downward trend in the ortolan bunting population density was detected, with a total decrease of 72% during the study period (Fig. 2). The total numbers of territories decreased, from 74–78 (1984–1986) to 22–27 (2000–2002). The magnitude of the decline differed between the sub-areas, as did the mean density at the beginning of the study period, i.e. before the decline

(Table 1). The magnitude of the decrease within each sub-area showed a clear negative correlation with the mean density at the beginning of the study period, although this association was not statistically significant ($r_{s[5]} = -0.429$, $p = 0.34$). However, the magnitude of decrease showed a significant negative correlation with the size of the sub-area ($r_{s[5]} = -0.811$, $p = 0.03$). Furthermore, the mean density at the beginning of the study period showed a negative, but statistically insignificant correlation with the size of the sub-area ($r_{s[5]} = -0.306$, $p = 0.51$; Table 1).

Over the whole study period, the densities of the ortolan bunting were significantly higher in field areas not covered by vegetation in spring than in field areas covered by vegetation in spring (Fig. 3a), the difference being largest during the phase of low population density in 1994–2002 as compared with the phase of high population density (1984–1989) or with the phase of population crash (1990–1993) (paired t -test: 1984–1989: $\bar{d}_{\text{non-covered}} = 9.00$ territories/km², $\bar{d}_{\text{covered}} = 6.72$ territories/km², $t_5 = -3.48$, $p = 0.018$; 1990–1993: $\bar{d}_{\text{non-covered}} = 6.56$, $\bar{d}_{\text{covered}} = 4.61$, $t_3 = -3.61$, $p = 0.037$; 1994–2002: $\bar{d}_{\text{non-covered}} = 4.74$, $\bar{d}_{\text{covered}} = 1.56$, $t_8 = -11.17$, $p < 0.001$).

Synchronies within density changes and within field coverage patterns

Overall, no strong synchrony between the sub-areas was detected in respect to the density changes ($\bar{r}_s = 0.141$; one-sample t -test: $H_0: \rho = 0$, $t_{20} = 3.16$, $p = 0.005$). Only three pair-wise correlations, all positive, out of 21 were significant

($p < 0.05$). The level of synchrony was not associated with the distance between the sub-areas ($r_{s[19]} = -0.170$, $p = 0.46$).

When the study period was divided into three sub-periods, differences in synchrony patterns could be detected (see Fig. 2). During the high-density phase in 1984–1989 the density changes in sub-areas were asynchronous ($\bar{r}_s = -0.041$; one-sample t -test: $H_0: \rho = 0$, $t_{20} = -0.40$, $p = 0.69$). In 1990–1993 the pattern was different: the decline was strongly synchronous in all the sub-areas ($\bar{r}_s = 0.786$, $t_{20} = 20.58$, $p < 0.001$). During the low-density phase in 1994–2002 the density changes between the sub-areas continued to be synchronous, although the synchrony was not as strong as during the previous period ($\bar{r}_s = 0.432$, $t_{20} = 7.96$, $p < 0.001$). The mean level of synchrony between the three periods differed significantly (one-way ANOVA: $F_{2,60} = 34.79$, $p < 0.001$). In pair-wise *a posteriori* comparisons the mean level of synchrony was significantly different in each of the time periods (Tukey's test: $p < 0.002$ in all comparisons).

As with the density changes, some synchrony was detected in the field coverage changes between the sub-areas over the entire study period, even though the synchrony was not strong ($\bar{r}_s = 0.355$; one-sample t -test: $H_0: \rho = 0$, $t_{20} = 7.30$, $p < 0.001$). Nine pair-wise correlations, all positive, out of 21 were significant ($p < 0.05$). The level of synchrony did not depend on the distance between the sub-areas ($r_{s[19]} = 0.038$, $p = 0.87$).

Once again, when the study period was divided into three sub-periods, a pattern sim-

Table 1. Field areas, mean densities and density trends of the ortolan bunting in the seven sub-areas of the study area.

Name of sub-area	Size (km ²)	Mean density before decline (1984–1986; territories/km ²)	Change in density (%) during the study period (1984–1986 vs. 2000–2002)
Vanhakartano	3.1	7.7	–40.3
Jahkola	2.0	5.4	–87.0
Porkkala	2.0	5.2	–36.5
Syrjäntaus	1.8	3.0	–93.3
Iso-Evo	1.5	4.5	–66.7
Yläinäinen	1.0	10.3	–97.1
Uusitalo	0.5	8.7	–100.0

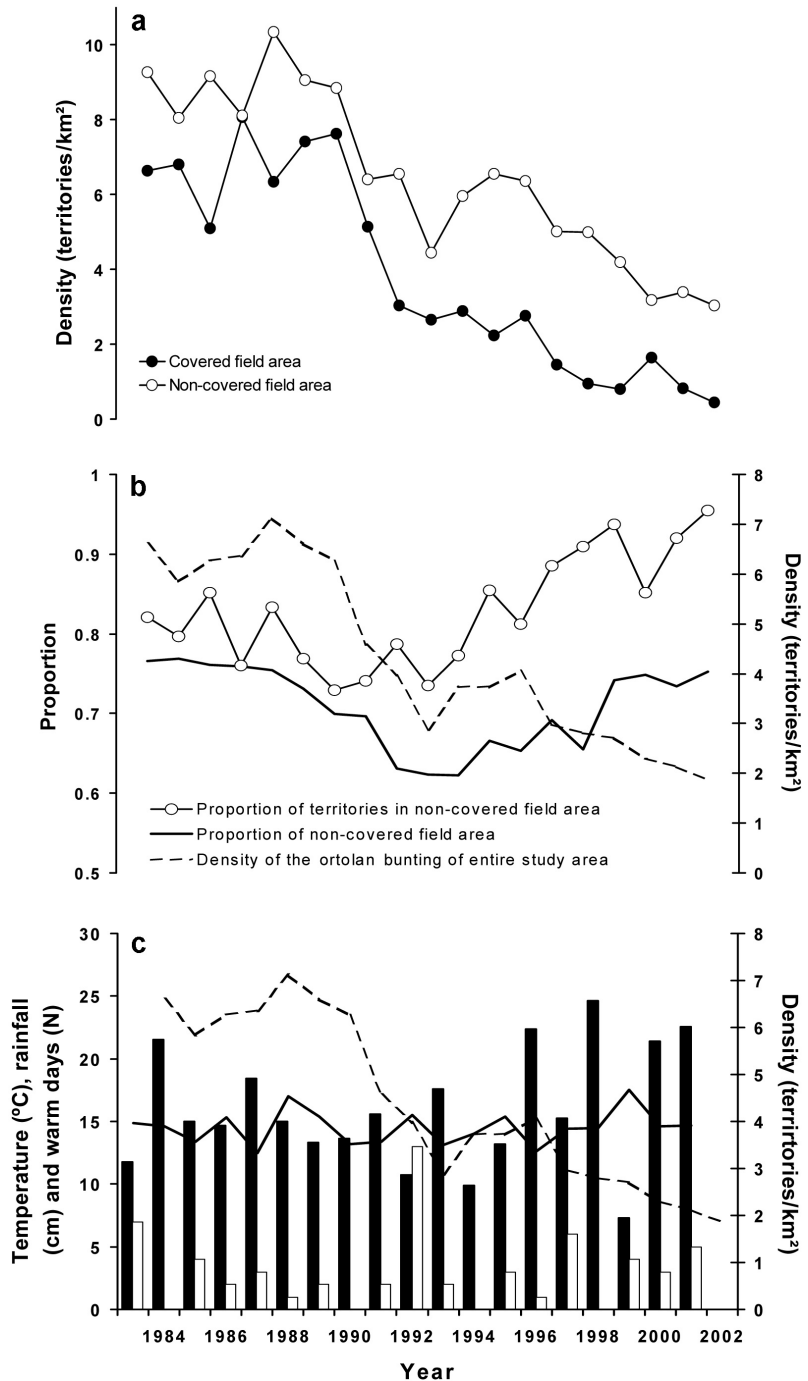


Fig. 3. — **a:** Density of the ortolan bunting in field areas not covered by springtime vegetation and in field areas covered by springtime vegetation 1984–2002. — **b:** The proportion of springtime non-covered field area and the proportion of ortolan bunting territories located in this field type 1984–2002 (left vertical axis). The ortolan bunting density of the entire study area is also shown (right vertical axis). — **c:** Number of warm days (white bars) between 1 and 20 May; also annual daily mean temperature (solid line) and total rainfall (black bars) between 16 May and 31 July at Lammi in 1983–2002. The ortolan bunting density for the entire study area is also shown (dashed line).

ilar to that observed in the density changes could be detected. During the high-density phase 1984–1989 the field coverage changes between sub-areas were asynchronous ($\bar{r}_s = -0.095$; one-sample t -test: $H_0: \rho = 0$, $t_{20} = -0.93$, $p = 0.36$).

During the population crash 1990–1993, the field coverage changes were strongly synchronous in all sub-areas ($\bar{r}_s = 0.671$, $t_{20} = 12.02$, $p < 0.001$). During the low-density phase 1994–2002, the field coverage changes between the sub-areas

continued to be synchronous, although the synchrony was not as evident as during the previous period ($\bar{r}_s = 0.245$, $t_{20} = 3.36$, $p = 0.003$). The mean level of synchrony between the three sub-periods differed significantly (one-way ANOVA: $F_{2,60} = 23.58$, $p < 0.001$). In pair-wise *a posteriori* comparisons the mean level of synchrony was significantly different in each of the time periods (Tukey's test: $p \leq 0.001$ in all comparisons).

Field coverage and density changes

The correlation between the ortolan bunting density and the proportion of springtime non-covered field area for the whole study period was positive, although not statistically significant ($r_{s[17]} = 0.340$, $p = 0.15$; Fig 3b). At the sub-area scale, considering the study period as a whole, the proportion of springtime non-covered field area correlated non-significantly with the density ($r_{s[17]} = 0.164$, $p = 0.51$). However, the correlation was significant in two sub-areas out of seven, i.e. those of Ylämäinen and Jahkola ($r_{s[17]} = 0.63$, $p = 0.004$ and $r_{s[17]} = 0.61$, $p = 0.005$, respectively). These two areas are among the four sub-areas in which the decline has been steepest (see Table 1).

However, when the correlations between the ortolan bunting density and the proportion of springtime non-covered field area were examined using the sliding averages of five-year periods, differences between different segments of the study period were revealed. At the beginning of the study period the correlation coefficients of the sliding five-year periods (the median years being 1986–1989) ranged from -0.83 to 0.69 , with p values between 0.08 and 0.97 . During the following time period, i.e. that of the population crash (median years 1990–1993) the correlations were stronger and clearly positive, ranging from 0.77 to 0.95 , with p values between 0.13 and 0.01 . After the crash (median years 1992–2000) the correlations were again weaker and non-significant, ranging from -0.66 to 0.54 with p values between 0.85 and 0.23 .

The proportion of all ortolan bunting territories in field areas not covered by springtime vegetation was high throughout the study period — between 73% and 95% — with the proportion increasing after the population crash, indicating

even higher preference for this habitat type (Fig. 3b).

Habitat changes during the study period

Over the total study period 1984–2002, the total area of cultivated field increased from 8.9 to 9.2 km². The proportion of springtime non-covered field area decreased during the first half of the study period but then increased again to its previous level during the second half of the study period (see Fig. 3b). This pattern was mostly caused by the Finnish national set-aside scheme, a measure which obliged cereal-dominated farms to leave (in 1991–1994) at least 15% of their field area as vegetated set-aside. During the study period the lengths of open linear elements (open ditches, open road bank ditches and road banks) remained roughly unchanged (60.6 km in 1984–1986; 58.8 km in 1992–1994; 60 km in 2000–2002). However, there was a 30.5% decrease in the length of closed linear elements, i.e. bush- or tree-growing ditches and road banks, and wood avenues (the lengths totalled 34.2 km in 1984–1986, 29.2 km in 1992–1994, and 23.8 km in 2000–2002). Even though the differences were not statistically significant (sub-area scale: one-way ANOVA: $F_{2,18} = 1.99$, $p = 0.17$), this roughly 30% decrease in the length of the closed linear elements during the study period is notable in an ecological context. It indicates an important change in the landscape, with ditches being mostly replaced by sub-surface drainage.

The total number of all point objects remained relatively stable during the overall study period (1984–1986 = $24.8/\text{km}^2$; 1992–1994 = $26.1/\text{km}^2$; 2000–2002 = $26.8/\text{km}^2$). Among the point objects, the number of single large trees or bushes and small tree or bush islets (< 0.4 ha) increased by 17% from the mid-1980s to the early 2000s. The increase resulted mainly from an actual decrease in bush- and tree-growing ditches, with the particular feature that not all the vegetation had been removed, and that some single trees or bushes had been left untouched. In other words, some of the closed linear elements were transformed to point objects. The total area of bush and forest patches (≥ 0.4 ha) decreased by 7.4% (0.68 km² to 0.62 km²) during the

study period. The figures for the length of roads (45.8–47.1 km) and the total area of settlements (0.44–0.5 km²) remained fairly stable throughout the study period.

Pair-wise correlations between habitat factors

The various habitat factors and their spatial patterns are not independent of each other. Multi-scale correlation analysis revealed three statistically significant ($p < 0.05$) and ecologically relevant pairs of correlating habitat factors. These were: (1) the proportion of springtime non-covered field and the total area of cultivated field (at all spatial scales and in all time periods; range of r_s : 0.516–0.800), (2) the length of the closed linear elements and the area of forest and bush patches (≥ 0.4 ha; at all spatial scales and in all time periods, except in the last two periods when not occurring at scales > 150 m; range of r_s : 0.294–0.461), and (3) the length of the open linear elements and the length of roads (at all spatial scales and in all time periods; range of r_s : 0.366–0.521).

Important habitat factors at different spatial scales

Various habitat factors had a significant positive effect ($p < 0.05$) on the occurrence of the ortolan

bunting and thus entered the stepwise logistic regression models (Table 2). The coefficients of determination of the models increased with the spatial scale (Fig. 4). Partly owing to a relatively large proportion of unoccupied grid cells at the smallest grid sizes, the explanatory power was rather small at the territory scales (100–150 m). The explanatory power of the models was strongest during the second sub-period, i.e. during the population crash. There was variation in the importance of various habitat factors that depended on the spatial scale and time period. However, two factors, namely the proportion of springtime non-covered field and the length of closed linear elements (i.e. bush- or tree-covered ditches and road banks and wood avenues) seemed to be the most important habitat features explaining the occurrence of the ortolan bunting, since they were significant throughout the spatial continuum and within all the time periods (Table 2).

The other habitat factors did not show as clear a pattern as the two factors mentioned above: only the density of point objects (large rocks or rock piles, single large trees and bushes, small tree or bush islets (size < 0.4 ha), and barns) and the length of open linear elements (open field ditches and road bank ditches) were significant throughout the study period, though only at territory scale. The importance of the area of bush and forest patches at the territory scale most probably has some ecological relevance. It is also worth remembering that this

Table 2. The results from the logistic regression analyses of the occurrence of the ortolan bunting at the different spatial scales and in the different time periods. Statistically significant ($p < 0.05$) effects of the different habitat factors are indicated with black dots. Read from left to right, the dots represent time periods of 1984–1986, 1992–1994 and 2000–2002, respectively. Short lines indicate statistically insignificant effects of the habitat factors, following the same order as the black dots.

Variable	Scale				
	100 m	150 m	200 m	300 m	400 m
Proportion of springtime non-covered field	•••	•••	•••	•••	•••
Length of closed linear elements	•••	•••	•••	•••	•••
Length of open linear elements	•••	••	••	••	••
Density of point objects	•••	••	••	••	••
Area of bush and forest islets (> 0.4 ha)	••	••	••	••	••
Length of roads	•••	••	••	••	••
Area of cultivated land	•••	••	••	••	••
Area of settlement	•••	••	••	••	••

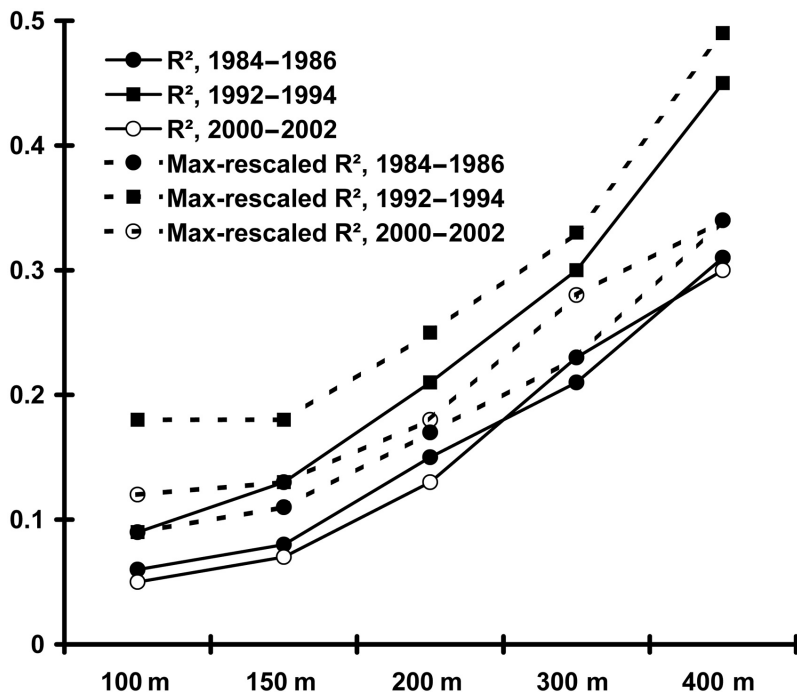


Fig. 4. Coefficients of determination for the logistic regression models of the ortolan bunting occurrence at different spatial scales and time periods. In each case, only variables with a statistically significant effect ($p < 0.05$) are included in the model (see Table 2 and text for details).

habitat factor correlated strongly with the length of closed linear elements (see the previous section), meaning that these two habitat elements commonly occurred in the same areas. The area of cultivated land becomes significant at the landscape level during the low-density period.

Changes in habitat factors and territory numbers between time periods

We analysed the effects of changes in habitat factors that would explain changes in ortolan bunting territory numbers over the three sub-periods. The coefficients of determination for the multiple linear regressions were small, ranging from 0.04 to 0.12. Thus, only few habitat variables appeared to be statistically significant ($p < 0.05$) in the models. Between 1984–1986 and 1992–1994, the decrease in the area of large bush and forest patches and the increase in the length of roads explained significantly ($p = 0.001$ for both) the decrease in the number of ortolan bunting territories. Between 1992–1994 and 2000–2002, the increase in the length of open ditches and similar features was signifi-

cant at grid sizes of 100, 200, and 300 metres ($p < 0.001$, $p = 0.012$, and $p = 0.016$, respectively).

Weather related to density changes

The more warm days there were in the Lammi region during the migration season of the ortolan bunting, the smaller was the density of the species in the breeding season ($r_{17} = -0.526$, $p = 0.02$). However, the spring of 1993 was exceptionally warm, having 13 warm days out of 20, while in the other study years the number of warm days ranged between zero and seven. If the spring of 1993 is excluded, the significance of the correlation disappears ($r_{16} = -0.18$, $p = 0.475$). The ortolan bunting density did not correlate significantly with the weather conditions of the previous year's breeding season (Fig. 3c; mean daily temperature: $r_{17} = 0.054$, $p = 0.82$, $df = 17$; total rain amount: $r_{17} = -0.002$, $p = 0.99$). In particular, there seemed to be no connection between the weather conditions of the breeding season and the start of the steep population decline.

Discussion

Density changes and trends

The population dynamics of a bird species involve a combination of long- and short-term changes caused by a mixture of demographic and environmental factors (e.g. Wiens 1989, Newton 1998). In the case of the ortolan bunting in southern Finland, our study period was preceded by a phase of increase from the 1930s to the 1970s, continuing until at least the early 1980s (Väisänen *et al.* 1998). Within our study area in particular, the ortolan bunting densities in the period 1936–1939 (Soveri 1940) were only about 35% of the densities observed during the early 1980s (Tiainen & Pakkala 2001). The reasons for this population increase are not understood (c.f. Väisänen *et al.* 1998, Tiainen & Pakkala 2001). It has been suggested that the population increase in Finland before the 1970s was caused by an increase in the total area of arable land (an increase of about 30% between the 1920s and the 1970s (Soininen 1974)), and by a simultaneous increase in the large open areas of farmland suitable for the ortolan bunting (Väisänen 1994). It should also be noted that alkyl mercury, a notoriously toxic substance (Otterlind & Lennerstedt 1964, Swanberg 1976), was never used as a seed coating in Finnish agro-ecosystems (unlike for example in Sweden) and that it was actually banned in Finland as early as 1967 (Suominen 1967, Markkula *et al.* 1990). This may have contributed to the population trends of the ortolan bunting: instead of a population increase, as in Finland, the Swedish population went into decline as early as the 1950s (Svensson *et al.* 1999).

The first part of the study period, 1984–1989, was characterized by high ortolan bunting densities, 6–7 territories/km², and small annual density changes. These changes were asynchronous between the different sub-areas. According to the Finnish national field bird survey of 1984 (Piironen *et al.* 1985), these densities were higher than the average density of 4–5 pairs/km² observed in the agricultural areas of southern and central Finland. The densities of 10–12 territories/km² in some of the sub-areas of our study area were

comparable to the densities found in the large field areas of Ostrobothnia in western Finland. The mean densities there were 9 pairs/km² in 1984 (Piironen *et al.* 1985) and in the best locations commonly 10–20 pairs/km² (Väisänen *et al.* 1998).

At the beginning of the 1990s the pattern changed dramatically, with a major and rapid decline taking place simultaneously throughout the study area. This resulted in a decrease of about 50% in the total population during 1990–1994. The high level of synchrony in the decline involves correlated environmental factors (e.g. May 1973, Hanski 1991), and the decline also coincides with a population decline in southern Finland as a whole (c.f. Väisänen *et al.* 1998). It may be that in northern and eastern Finland, which are marginal areas in the distribution, the population decline started earlier, possibly in the late 1970s or early 1980s. This is supported by the contraction of the distribution area, which took place between two national bird surveys: that of 1974–1979 and that of 1986–1989 (Väisänen *et al.* 1998).

As a result of the decline, local subpopulation extinctions took place in two of the sub-areas of the study area. In two other sub-areas, ortolan bunting densities have been very low since the decline. The magnitude of the decline within a sub-area was negatively associated with the density and size of the sub-area before the decline. This finding underlines the importance of landscape structure: in our study area the population has been concentrated in three large sub-areas since the decline.

Ortolan bunting territories are typically located in small concentrations. The species may feed in groups during the breeding season and even tolerate conspecifics near the nest site (Durango 1948, Cramp & Perrins 1994). These social aspects of the ortolan bunting's behaviour may have an impact on its population dynamics. Singing males on a particular patch of farmland can attract other males to the same patch, and this can lead to an aggregated distribution pattern, one which is only partly determined by habitat structure and quality. In our study area, several territory concentrations or breeding groups persisted in traditional places for years. By con-

trast, locations of single territories were more variable (T. Pakkala & J. Tiainen unpubl. data). In a declining population, the density changes observed depend also on the persistence of the breeding groups. The observed negative association between the density and the magnitude of the decline could indicate that large breeding groups may be better “buffered” against factors affecting density changes. However, if an entire breeding group disappears, it may be difficult for the species to re-establish itself in that location, especially if regional densities are low.

Since the major decline, population densities have been low, averaging 2.8 territories/km² in 1995–2002. This decrease has continued in all of the sub-populations in the study area, with the changes in density occurring more or less simultaneously. The decline is continuing in Finland as a whole (Väisänen 2001), implying that at least part of it is due to large-scale factors.

The role of field coverage

The ortolan bunting is a ground feeder and breeder. In arable land the nests are usually located in cereal fields or in root crop fields (Cramp & Perrins 1994, Tucker & Heath 1994), and in Finland often in ditch banks and in field edges (Haukioja *et al.* 1985, Norrdahl 1990; T. Pakkala unpubl. data). Our results show that the area of field growing spring cereal, root crops, etc. (i.e. field not covered in springtime) had a positive effect on the occurrence of the species at all spatial scales and throughout the study period. Moreover, the densities in our study area were significantly higher in field areas not covered by vegetation in spring as compared with those with vegetation. We do not know the precise ecological reasons for the pattern observed for non-covered fields. It is possible that prey availability is better for the ortolan bunting in short vegetation than in tall and dense vegetation. Unfortunately, there are no detailed studies on this matter. The main distributional area of the ortolan bunting is in the east and south of Europe, mainly in dry and open landscapes (Cramp & Perrins 1994). The adaptation of the species to these environments is probably reflected in its habitat preferences in the north.

Up until 1998, we observed a strong positive correlation between the ortolan bunting density and the area of fields not covered by vegetation in the spring. However, after 1998 the decline of the ortolan bunting continued in spite of an increase in the area of non-covered field. Although in our study area the covered field type was always less abundant than the non-covered type — i.e. the type that contained the major part of the ortolan bunting population — the changes in field cover patterns may have played at least some role in accelerating the ongoing declines of sub-populations.

The importance of habitat diversity and habitat changes

Various studies have shown that the general intensification of agriculture, and especially an increase in the area of low-diversity cereal-dominated monocultures, has been responsible for declines in species richness and in the population densities of many bird species in Europe since the mid-20th century (Møller 1983, Robertson & Berg 1992, Tucker & Heath 1994, Fuller *et al.* 1995, Siriwardena *et al.* 1998, BirdLife International/European Bird Census Council 2000, Tryjanowski 2000, Tiainen & Pakkala 2001, Kujawa 2002, Piha *et al.* 2002, Rintala *et al.* 2003). In Finland too, the agricultural environment has changed radically since the 1950s, when the process of intensification began (Raatikainen 1986, Hanski & Tiainen 1988, Tiainen 2001, Tiainen 2004). The main changes involved are: a shift from predominantly dairy farming to spring cereal-dominated farming, increases in the average size of farms and in the specialization of farms, an increase in subsurface drainage, an increase in the use of fertilizers, and an increase in the use of pesticides (continuing until the late 1970s; Tiainen 2001).

The main explanation offered for the Europe-wide decline of the ortolan bunting is the loss of suitable habitat in the breeding areas, this in turn being due to changes in agricultural practices and in the landscape (von Lang *et al.* 1990, Stolt 1974, Claessens 1994, Tucker & Heath 1994, Dale 2001a, Gofawski & Dombrowski 2002). In addition, the amalgamation

of fields, a loss of hedges and single trees, and increased human disturbance are believed to threaten ortolan bunting populations (Tucker & Heath 1994). It has been shown that tree or bush islets, single large trees, wood avenues, orchards, hedgerows, barns, stone piles, stone walls, and electricity lines and poles are important for the ortolan bunting, since they provide song posts and perching sites, and also feeding places (as sources of insects) and breeding places (Stolt 1988, von Lang *et al.* 1990, Tucker & Heath 1994, Kujawa & Tryjanowski 2000, Tryjanowski 2001, Goławski & Dombrowski 2002).

Our results show clearly that the ortolan bunting is associated with bush and tree-growing ditches and other vegetated linear landscape elements, i.e. features which provide structural and biological diversity in otherwise relatively open field areas. In our study area these elements were also linked to the presence of bush and forest patches. Thus, our results support the opinion that habitat heterogeneity is important for the ortolan bunting, from the territory scale to the landscape scale. Our results strongly suggest that there was a connection between a decrease in closed linear landscape elements and the decline of the ortolan bunting. Ditch banks provide breeding, feeding and singing places for the species in Finland (Haukioja *et al.* 1985, Norrdahl 1990; T. Pakkala & J. Tiainen unpubl. data).

In addition, the presence of open field and road bank ditches was important for the species at the territory scale, but not at other spatial scales, and not throughout our study period. This suggests that these open ditches are of lower quality from ortolan bunting's point of view: they do offer nest sites, but do not usually provide many song-posts or sources of food. Moreover, during the study period the amount of open ditches remained relatively stable, even during the population crash of the ortolan bunting.

Small-scale habitat elements (e.g. small bush islets, single large trees, barns, and large rocks) had a significant positive effect on ortolan bunting occurrence at the three smallest spatial scales, except during the last time period, when these elements were significant only at the smallest (territory) scale. The observed lack of significance throughout the whole spatial and temporal continuum might be due to the low importance of

these small-scale elements as compared with e.g. closed linear elements. Yet a more likely explanation may be the changes that have taken place in the various habitat elements during the study period: aggregations of small-scale elements are often located in field areas where larger bush islets and ditches have been removed. Thus they are actually remnants of a previously better habitat for the ortolan bunting.

No clear relationships were found between the changes in the various habitat factors and the changes in the number of ortolan bunting territories during the three sub-periods representing the different population phases. We would suggest that this pattern is due to two main factors that are intermingled with each other: (1) the observed large decline of the ortolan bunting was the result of several co-operating environmental factors and was only in part due to habitat factors in the breeding area (*see* next section); (2) the habitat measures and the measurement design probably registered the variation in space better than the variation in time; it may be that the effects of single habitat factors on the ortolan bunting are not effectively captured in analyses which use averaged measures from longer time periods instead of annual data. However, according to our field observations, the disappearance of the ortolan bunting from some sub-areas seemed to be connected to changes in factors present within the core areas of territory concentrations.

Other possible reasons for the decline

Several reasons have been put forward as possibly contributing to the decline of the ortolan bunting in Europe, with the emphasis on various environmental factors in the breeding, migrating and wintering areas. Conrads (1977) suggested that losses during migration or in the wintering areas could be more important than changes in suitable habitats — a view expressed also by von Bülow (1990). Unfortunately, little is known of the ortolan bunting in its wintering areas in sub-Saharan Africa (Cramp & Perrins 1994, Stolt 1997), and the same is true of the migration behaviour of the species (c.f. Zink 1985, Yosef & Tryjanowski 2002). One factor connected to the decline might be droughts in the migrating

or wintering areas (e.g. in the Sahel, northern Africa), but we do not know how far these might have affected the ortolan bunting populations (Stolt 1993). The return to the breeding area in the spring takes place on a broader front than in the autumn, suggesting a loop migration. It has been observed that in Eilat, Israel, 98% of the ortolan buntings ringed during migration are caught in the spring (Yosef & Tryjanowski 2002). In the small Norwegian population (less than 200 pairs remaining in the late 1990s) female-biased natal dispersal has been linked to the ongoing decline (Dale 2001b). More than fifty years ago, Spaepen (1952) pointed out that ortolan buntings are hunted during migration. Claessens (1994) estimated the annual number of individuals killed by hunting in France at 50 000.

Brood losses due to precipitation have been suggested (Durango 1948, Conrads 1977) as a factor contributing to the decline, as well as decreased productivity of offspring due to the use of pesticides or other toxic substances, for example alkyl mercury (Otterlind & Lennerstedt 1964, Swanberg 1976). The use of toxic substances in migrating and wintering areas may also have impact on the ortolan bunting populations. In sub-Saharan Africa, there has been a 15-fold increase in the total import of pesticides and a five-fold increase in the use of fertilizers between the early 1960s and the early 2000s. The import of herbicides and insecticides has also increased during this period (<http://faostat.fao.org/faostat/collections?subset=agriculture>). Naturally, reliable site-specific information on illegal trade of widely banned toxic substances — such as alkyl mercury — is not available. The increasing use of pesticides in wintering areas and stopover sites of Eurasian–Afrotropical migrants can directly cause deaths of birds (for a review, *see* Newton 2004).

Our study did not reveal any unambiguous connections between climatic or weather factors (number of warm days or mean temperature, and precipitation) and density changes during the migration and breeding seasons; nor was any connection observed between these weather factors and the start of the major decline. The possibility of a negative relationship between warm weather during the migration period and

the density of the following breeding season was somewhat surprising. Warm weather in May — which is often associated with high pressure systems — may lead to migration being prolonged further north and thus result in lower densities in southern Finland.

Ultimately, however, the density changes observed within our study area are due to changes in the natality and mortality of the ortolan bunting population, and appear to be also due to immigration and emigration patterns within a wider geographical region. We do not know how these basic parameters have changed during our study period. It is often supposed that major changes in population sizes are linked to some major, or at least visible environmental changes, but it has been known for a relatively long time that quite small changes may cumulatively have large effects on the dynamics of non-linear, complex systems (*see e.g.* Lorenz 1963, May 1976). This could apply to the population dynamics of the ortolan bunting also. However, the translation of environmental variation into biological processes is far from straightforward (c.f. Laakso *et al.* 2001).

Implications for conservation

According to Tucker and Heath (1994) the ortolan bunting needs urgent conservation measures that would address the main requirements of the species; these measures include the maintenance or development of non-intensive farming, high crop diversity and low levels of pesticide use, plus the maintenance of trees.

Our results underline the importance of multi-scale habitat diversity for the ortolan bunting. In order to preserve suitable habitats of the species, attention should be given to the maintenance of several kinds of habitat features. As far as possible, one should avoid the ‘cleaning up’ of vegetated ditch banks, bush and tree islets, and small-scale habitat elements, e.g. single large trees or barns. Special attention should be paid to those agricultural areas that still contain large and viable territory concentrations.

Preventing the loss of suitable and high-quality habitat in breeding areas would be a good step forward, but if we are to set out reliable quantita-

tive scenarios for maintaining sustainable populations of the ortolan bunting — as well as a number of other agricultural bird species — we should have a clearer idea of the causal relations between environment and habitat structures and the population dynamics of the species.

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