Ornis Fennica 80:97–110. 2003

Habitat preferences of the Skylark *Alauda arvensis* in southern Finland

Markus Piha*, Timo Pakkala & Juha Tiainen

*Piha, M. & Pakkala, T., Finnish Museum of Natural History, P.O. Box 17, FIN-00014, University of Helsinki, Finland. (*E-mail: markus.piha@helsinki.fi)*
Tiainen, J., Finnish Game and Fisheries Research Institute, P.O. Box 6, FIN-00721 Helsinki, Finland

Received 8 May 2003, accepted 11 August 2003

The agricultural environments of forest-dominated northern Europe are different from those in southern Europe. One could expect corresponding differences in the ecology of farmland birds such as the Skylark. We studied the habitat characteristics of the Skylark in an agricultural landscape of 30 km^2 in southern Finland. GIS-based methods were applied to analyse the habitat associations and distribution of Skylark territories. We found that landscape factors were associated with Skylark occurrence: the species was always present in sufficiently large patches of farmland (> 11.5 ha). Skylarks avoided forest edges, and the isolation of farmland areas also decreased the probability of Skylark occurrence. Year-round vegetative cover of fields and the amount of open ditches (ditch margins) had a positive effect on Skylark density. Set-aside regimes and buffer zones along ditches would thus be beneficial to northern Skylark populations.

1. Introduction

In recent decades, the decrease of farmland bird diversity resulting from agricultural intensification has been a major issue in agricultural conservation ecology. The Skylark *Alauda arvensis* is a farmland bird species which has undergone a steep decline in Central and Western Europe in recent decades; the population has halved since the middle of the 1970s (Tucker & Heath 1994, Wilson 1997, Siriwardena *et al.* 1998).

The main reason for the decline in Skylark populations, as suggested in many studies, is the deterioration of breeding and wintering habitats caused by intensified agricultural production (Jenny 1990, Donald & Evans 1994, Fuller *et al.* 1995, Wilson *et al.* 1996, Tucker & Dixon 1997, Chamberlain *et al.* 1999, Perkins *et al.* 2000, Donald *et al.* 2001). Various approaches have been used in seeking environmental causes for the population declines of the Skylark; for example, studies have been carried out on habitat selection, habitat-related breeding success and changes in the availability of preferred habitat types in changing agro-ecosystems (Jenny 1990, Wilson *et al.* 1997, Chamberlain & Gregory 1999, Chamberlain *et al.* 2000, Donald *et al.* 2001).

Several factors affect habitat selection by the Skylark. One of the key factors is the size of open field areas: the Skylark requires relatively large open areas, without tall vegetation or other structures (Wilson *et al.* 1997, Chamberlain & Gregory 1999). The structure of field vegetation is also important in Skylark territory selection. The vegetation should not be too high or dense, nor should there be much bare soil — a varied vegetation structure, with the inclusion of some bare patches, is probably optimal (Schläpfer 1988, Wilson *et al.* 1997). Thus, it has been proposed that the Skylark decline in the British Isles is due to the increase in autumn sown cereals at the expense of spring cereals (Wilson *et al.* 1997, Chamberlain *et al.* 2000, Donald & Vickery 2000). In Central and Western Europe Skylarks have 2–3 broods per breeding season, but the number of breeding attempts in winter cereal fields is reduced because the sward grows too high and dense in the course of the season (Schläpfer 1988, Jenny 1990, Wilson *et al.* 1997, Chamberlain & Crick 1999). Skylarks favour areas with abundant invertebrate food supplies, such as set-asides, meadows, grasslands and fields with open ditches, and breeding success is high in these habitats (Haukioja *et al.* 1985, Mehtälä *et al.* 1985, Jenny 1990, Wilson *et al.* 1997, Poulsen *et al.* 1998, Chamberlain *et al.* 2000).

For the Skylark, Northern Europe is very different from Central and Western Europe: northern Skylarks are migratory and the agricultural environment is fragmented. In Finland only 8.3% of land area is farmland. Farms and fields are small, and farmland consists of small patches usually surrounded by forest. For climatic reasons, spring crops are prevalent, unlike temperate Europe, where winter cereals are more common. Hence most agricultural land is without vegetation at the start of the Skylark breeding season.

In Central and Western Europe spring crops provide better habitats for agricultural birds than do winter cereals; this is because the vegetation has not yet become dense and high during the breeding season (e.g. Potts 1986, Chamberlain *et al.* 2000). In Finland, winter crops are beneficial for many birds: they offer vegetation in the early part of the breeding season, but the sward is still low (some 10 cm) and sparse (the main winter crop is rye *Secale cereale* with 50%–70% of winter crops; Tiainen *et al.* 2001).

Due to the climate, the Skylark is a migrant in Northern Europe (being mainly sedentary in Western Europe). The breeding season is short in Finland. Although Skylarks arrive in April, breeding does not usually start before May (von Haartman 1969). There is usually one brood (occasionally two) per breeding season, contrasting with 2–3 in temperate Europe (Delius 1965, von Haartman 1969, Cramp 1988). In Finland spring sowing usually occurs during the first breeding attempt and a high proportion of the nests are destroyed (Haukioja *et al.* 1985). However, new breeding attempts usually begin soon after a nest loss (Delius 1965, von Haartman 1969).

The population of Finnish Skylarks has undergone fluctuations, in contrast to the decreasing trend in Western Europe. The population grew from the 1930s to the mid-1970s, and decreased in the 1980s. In the early 1990s the population increased, but diminished again in the late 1990s. It is currently at the level of the 1980s (Väisänen *et al.* 1998, Väisänen 1999, Tiainen *et al.* 2001).

Finnish agricultural landscapes have changed considerably, with the main changes occurring during the period of intensive agriculture — the intensification began in the 1950s (Raatikainen 1986, Hanski & Tiainen 1988, Grönroos *et al.* 1997). The disadvantageous habitat changes for the Skylark have been caused by the intensification of land use and cultivation, and a shift from mixed farming to specialization in spring cereals (Tiainen 2001).

According to Tiainen (2001), the deterioration in those habitats which are important for ground-nesting passerines in Finland is due to several interrelated factors: (1) a decline in livestock farming, (2) a decline in the area of meadows, verges, and unused agricultural lands, (3) an increase in subsurface drainage, (4) simplification of crop rotation due to a concentration on cereal cultivation, (5) a decline in autumn-sown cereals (chiefly rye; the relatively small area of wheat *Triticum aestivum* has not changed markedly), (6) replacement of traditional hay fields by fertilized silage grass fields, (7) the replacement of manure by artificial fertilizers, and (8) the increased use of herbicides.

Finland joined the European Union in 1995, and thereafter the EU Common Agricultural Policy (CAP) has been applied. One aim of the second national agri-environmental programme (2000-06) is to preserve the biodiversity of agricultural ecosystems. Some of the measures in this programme will increase the area of habitats, which may be important for the Skylark. As population changes are often linked to habitat changes, relevant information regarding the habitat requirements of the Skylark and other farmland bird species is needed in order to evaluate the significance of the programme for the population development of these species.

The aim of this study was to identify the characteristics of the Finnish agricultural landscape associated with the density and territory distribution of the Skylark. The environmental factors included (1) the size and openness of farmland areas, (2) the patch configuration of farmland areas, and (3) land use of fields. The habitat characteristics were studied at two ecologically relevant scales of magnitude. First of all, we studied how individual Skylark territories were distributed within farmland areas, and which environmental factors were important for territory selection. Secondly, we studied Skylarks in relation to the wider landscape, i.e. examining the properties of farmland areas that affected Skylark distribution and density. On the basis of the results we discuss the status of the Skylark in the changing agricultural environments of Finland.

2. Material and methods

2.1. Study area

The study area is located in Lammi, Southern Finland (61°05′N, 25°00′E). The area consists of a fragmented agricultural landscape with patches of farmland ranging from 0.3 to 300 hectares; the total area of arable land studied was 29.5 km^2 (Fig. 1). The dominating crop types were spring cereals, cultivated grass and sugarbeet *Beta vulgaris* var. *altissima* (Table 1).

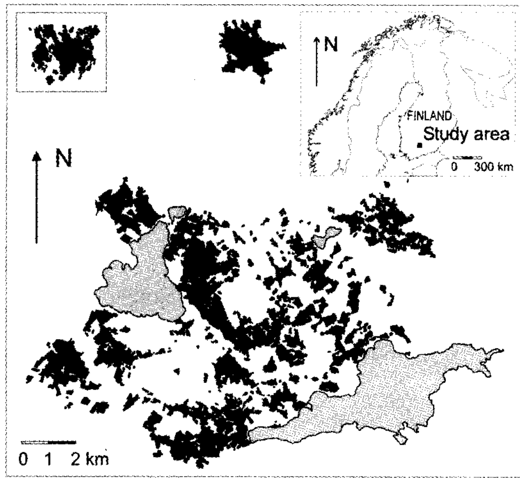

Fig. 1. The study area. The studied fields are shown in black, the white areas represent other land area (mainly forests), the grey areas are lakes. The inserted part of the study area (top left) is located ca. 20 km north of other study areas. The location of the study area is shown in the inserted picture (top right).

2.2. Bird census and habitat data

The field work was carried out in 1999. Breeding Skylarks were censused using a two-visit mapping method, which has been shown to be a reliable method for territory mapping of the Skylark (Tiainen *et al.* 1985a, Tiainen & Pakkala 2000). The first visit was made during 5–20 May and the second during 1–20 June. Special attention was paid to recording simultaneous observations of singing males, as these are important for the identification of territories. During each field-visit several observations of the same individuals were gathered; thus the interpretation of territories and the definition of territory centres were based on more than just single observations from two visits. The interpretation was made according to a standard practice developed for studies on agricultural birds in Finland (Tiainen & Ylimaunu 1984, Mehtälä *et al.* 1985, Piiroinen *et al.* 1985,

Table 1. Areas and proportions of crop types in the study area in 1999. The type "special cultivation" includes garden cultivation and some uncommon crops (e.g. carrot and strawberry).

Crop type	Area (ha)	% of cultivated area
Spring cereal	1349	45.7
Cultivated grass	460	15.6
Sugar beet	368	12.5
Set-aside	235	7.9
Potato	128	4.3
Pasture	124	4.2
Plough (fallow)	87	2.9
Turnip rape	39	1.3
Special cultivation	24	0.8
Winter cereal	22	0.7
Missing information	118	4.0
Total	2954	

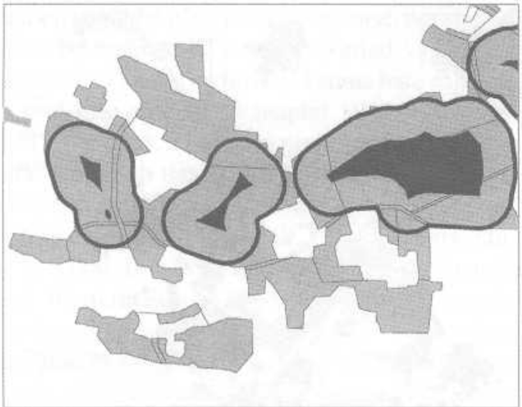

Fig. 2. Formation of open farmland areas (OFA). First, we selected central farmland areas (black areas), which were at least X metres from the forest and settlement edges. The grey areas represent fields and other open habitats (roads, open ditches, etc.), the white areas are forests and settlements. Then we buffered X metres towards the edges from the central areas. These buffers (thick black line) were used as borders of OFAs.

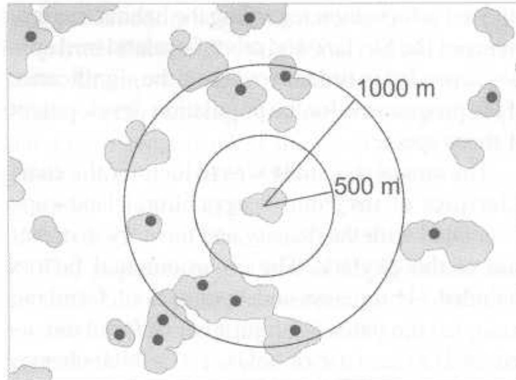

Fig. 3. Isolation measures of OFAs. First, two circles with radii of 500 and 1000 metres from the centre of the OFA were formed. Then the total numbers of OFAs and skylark territories within (or intersecting) the circles were calculated. The centre-OFA was not included. In this example the values of the isolation measures are: number of skylark territories within a radius of 500 m = 0 and within a radius of 1000 m = 6, number of OFAs within a radius of 500 m = 1, OFAs within a radius of 1000 m = 7. The grey areas represent OFAs; the black circles are Skylark territories.

Tiainen *et al.* 1985b, Pakkala *et al.* 1986, Tiainen & Pakkala 2000). The positions of the 267 identified Skylark territory centres were stored in a GIS database. The boundaries and land-use of the fields studied were mapped and classified within various land-use categories during field visits (Appendix). These data were digitized and stored within a GIS database. Note that over-winter vegetation means that the field is vegetated from autumn to the following growth period, though covered by snow in winter.

2.3. Habitat and landscape analysis

2.3.1. Habitat factors: territory level

The habitat composition of the Skylark territories was studied by comparing the territories with control areas where there were no territories. 267 control points, equal to the number of Skylark territories, were selected. The selection of these points was random, but done in such a way that their distance from the nearest Skylark territory centre and from any other control point was at least 100 m. For every territory centre and control point a buffer zone circle with a radius of 50 m was set out. The 50 m radius was based on an observation that the minimum distance of two adjacent Skylark territories in the study area was approximately 100 metres. In the present study, this circle is referred to as a territory. The control areas and their centres are referred to as random territories, and their centres are referred to as random points.

The areas of different land use types within Skylark and random territories were then measured using the GIS. The classification of land use types was based on the ecological similarity of the types (see Appendix). It should be noted that the areas of land use types within circles are not independent of each other. To eliminate this dependence, composite transformations (amount of land use type = ln(proportion of land use type/proportion of spring cereal)) were used (see Aitchison 1986, Aebischer *et al.* 1993) and zero proportions were replaced by 0.001, which was an order of magnitude smaller than the smallest proportion observed. The land use type diversity of the Skylark and random territories (Shannon-Wiener-index; see Krebs 1989) was also calculated. The position of the Skylark and random territories in relation to the forest edge was meas-

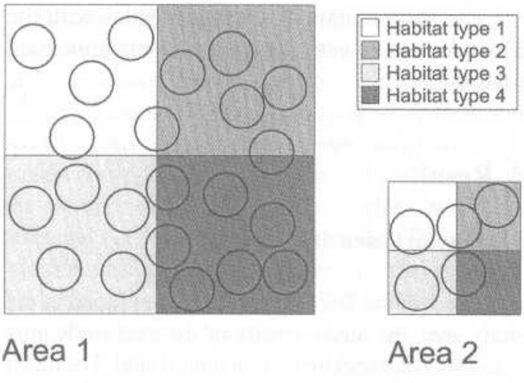

Fig. 4. The Shannon-Wiener-diversity of habitat types and the amount of verges (m) of each OFA were measured using circles formed inside the OFAs. In this example the two areas have the same habitat diversity if the diversities are calculated using habitat proportions. However, if the diversities are calculated on the territory scale (circles), the mean diversity of the smaller area is considerably greater than that of the larger area. By this method, habitat diversity and the amount of verges are linked on a relevant ecological scale i.e. the core area of the Skylark territory.

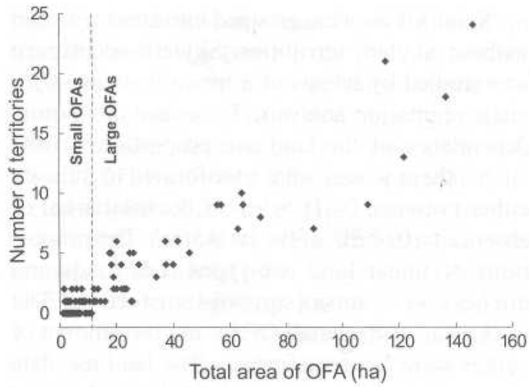

Fig. 5. The relationship between total area of OFA (ha) and number of Skylark territories.

ured as the distance (m) of the territory centres from the nearest edge or islet containing a forest or settlement. The most important factors associated with the presence of a Skylark territory were sought out using a forward stepwise logistic regression analysis. It is possible that important environmental factors did not enter the stepwise model, due to correlation with factors selected in the model. For this reason, we also studied the importance of these variables using univariate logistic regression.

2.3.2. *Habitat factors: landscape level*

The patches of farmland in the study area were divided into separate open farmland areas using a special buffering procedure. The idea was to define areas that include an open area (defined below), and by this means to exclude all the other areas from the analysis. First of all we selected those farmland areas that contained areas at least X metres from the forest and settlement edges. A buffer zone of X metres was set out around these central areas (black areas in Fig. 2). As a result we obtained the borders of open farmland areas (OFAs) (thick black line in Fig. 2). The procedure was carried out using 100, 90, 80, 70, 60 and 50 m radii. The 60 metre radius was the smallest to include at least 95% of the Skylark territories and hence was the one we chose. Using this method, 156 OFAs were formed.

For each of the 156 OFAs we measured (in GIS) the Skylark density and following environmental factors: total area (ha), proportion of different land use types (classification in the Appendix), coordinates of the centre of the OFA, and isolation measures (Fig. 3). For measuring the amount of verges (m) and land use diversity (Shannon-Wiener index; see Krebs 1989), we created 3000 random circles (radius 50 m) inside the OFAs. After this we chose those 579 circles which were entirely inside the OFAs and which did not intersect each other. All the borders between different land use areas (except forest edges and edges between open farmland and settlement) were defined as verges. The mean values of the circles were calculated for each OFA (see Fig. 4). In addition we defined a shape measure for every OFA, which was calculated by dividing the total area (ha) by the square of its circumference. This measure represents the amount of open area in relation to the amount of edge; round and straight-edged OFAs get high values from this shape measure index.

The OFAs were grouped into small (< 11.5 ha; n = 113) and large OFAs (> 11.5 ha; n = 43). Note that above the 11.5 hectare value, OFAs were always occupied by one or more Skylarks (see Fig. 5).

Small OFAs were grouped into areas with and without Skylark territories. Skylark occurrence was studied by means of a forward stepwise logistic regression analysis. To reduce the mutual dependence of the land use proportions of the OFAs, these values were transformed to indicate either presence (= 1; > 5% of the total area) or absence (= 0; < 5% of the total area). The proportions of linear land use types (i.e. roads and ditches) were arcsin[sqrt(x)]-transformed. The total areas of the small OFAs and the amount of verges were log-transformed. The land use data were incomplete in one small OFA and that area was discarded from the analysis.

The associations of the properties of large OFAs with Skylark density were studied by means of a forward stepwise regression analysis. Composite transformations (see 2.3.1.) were used for the following land use types: (1) grasslands, (2) broad-leaved, (3) other vegetation cover, (4) other ploughed, (5) other open areas and (6) bushes (zero proportions were replaced by 0.0001, which was an order of magnitude smaller than the smallest proportion observed). The proportions of linear land use types, i.e. open ditches and roads were arcsin[sqrt(x)]-transformed. The total area (ha) and the amount of verges (m) were log-transformed. Two large OFAs lacked more than 30% of land use data and were therefore discarded from the analysis.

The associations of single variables with the Skylark density were also studied using univariate regressions.

3. Results

3.1. Skylark density

In respect of the 267 Skylark territories found in the study area, the mean density of the total study area was 9.0 territories/km^2 of agricultural land. The mean density in OFAs was 11.6 territories/km^2. The mean density in large OFAs (13.4 territories/km^2) was significantly higher than that in small OFAs (6.3 territories/km^2; two-sample t-test, $t_{151} = 8.667$, $P < 0.001$). The Skylark density in large OFAs was not dependent on the OFA area ($r_s = 0.072$, df = 39, $P > 0.1$).

3.2. Location and habitat composition of Skylark territories

Skylark territories were located significantly further from the nearest forest or settlement edge than random territories (Mann-Whitney U-test, $Md_{SKYLARK} = 79.9$ m, $Md_{RANDOM} = 26.3$ m, U = 60095, $P < 0.001$). The most important variables associated with the presence

Table 2. Variables in the forward stepwise logistic regression analysis of Skylark territory occurrence. The total amount of variation in territory occupancy explained by the model was 31.6% (McFadden's Rho-squared). Variables entered the model if P < 0.05.

Variable			Cumulative % of variation explained
In the model:	Coefficient	P	
Constant	–7.191		
Distance from forest or settlement edge	4.348	<0.001	29.5
Amount of broad-leaved crops*	–0.096	0.008	30.4
Amount of other vegetation cover -land use type*	0.175	0.006	31.0
Amount of roads*	–0.112	0.042	31.6
Not in the model:	Score	P	
Amount of grassland*	1.722	0.189	
Amount of bush*	1.819	0.177	
Amount of other ploughed -land use type*	0.158	0.691	
Amount of other open area*	2.403	0.121	
Habitat diversity	0.707	0.400	

* ln(proportion of land use type/proportion of spring cereal)

of Skylark territories (see Table 2) were the distance from the nearest forest or settlement edge, the amount of broad-leaved crops (potato *Solanum tuberosum*, sugarbeet and turnip rape *Brassica rapa oleifera*) and roads (negative correlations). The amount of other vegetation cover -land use type correlated positively with the presence of Skylark territories, while other variables did not enter the stepwise model (Table 2). In addition, univariate models showed that the amount of bush had a significant negative correlation with the presence of Skylark territories.

3.3. Analyses of open farmland area (OFA) characteristics

263 (98.5%) of the 267 Skylark territories were located in open farmland areas (OFAs) which contained at least some area further than 60 m from the forest edge (see Fig. 2). The total number of Skylark territories inside and outside the OFAs differed significantly from that expected on the basis of random distribution (goodness-of-fit test, $\chi^2_1 = 72.25$, $P < 0.001$). The area of the OFA affected Skylark occurrence (Fig. 5). It was for this reason that the OFAs were divided into two groups, as mentioned previously: small OFAs (< 11.5 ha; n = 113) and large OFAs (> 11.5 ha; n = 43). The division was based on the observation that there were Skylark territories in all OFAs larger than 11.5 hectares.

A forward stepwise logistic regression of the *small* OFAs (25 Skylark OFAs and 87 non-Skylark OFAs; Table 3) revealed that the probability of Skylark occurrence increased as the farmland area increased. Isolation decreased the probabil-

Table 3. Variables in the forward stepwise logistic regression analysis of the occurrence of the Skylark in small OFAs. The total amount of variation in Skylark occurrence explained by the model was 29.5% (McFadden's Rho-squared). Variables entered the model if P < 0.05.

Variable			Cumulative % of variation explained
In the model:	Coefficient	P	
Constant	–8.053		
Area	6.987	<0.001	12.8
Number of Skylark territories** within a radius of 500 m	0.367	0.020	20.3
Number of OFAs** within a radius of 1000 m	0.254	0.021	24.6
Presence of broad-leaved crops	–1.762	0.020	29.5
Not in the model:	Score	P	
Shape of the OFA*	2.665	0.103	
Number of Skylark territories** within a radius of 1000 m	0.141	0.708	
Number of OFAs** within a radius of 500 m	0.364	0.546	
Habitat diversity	1.959	0.162	
Presence of spring cereal	0.055	0.814	
Presence of other open area	0.270	0.603	
Presence of other vegetation cover -land use type	0.825	0.364	
Presence of other ploughed -land use type	0.070	0.791	
Presence of grassland	0.298	0.585	
Proportion of open ditches	0.242	0.623	
Proportion of farm roads	0.658	0.417	
Presence of bush	0.796	0.372	
Amount of verges in OFA	0.428	0.513	
Proportion of roads	0.948	0.330	
x-coordinate of the OFA centre	0.014	0.906	
y-coordinate of the OFA centre	0.753	0.385	

* Area/circumference^2

** Information on the OFA concerned not included ity of occurrence; both the Skylark number within a radius of 500 m and the OFA number within a radius of 1000 m were associated with an increased probability of occurrence (c.f. Fig. 3). The probability of occurrence of Skylarks was smaller in farmland areas where broad-leaved crops were present. In univariate regressions of other variables, the presence of other vegetation-covered fields correlated positively with Skylark occurrence. Other isolation measures correlated negatively.

The factors associated with Skylark density in *large* OFAs were studied using a forward stepwise regression analysis (Table 4). The most important factors were the proportion of open ditches and the amount of grasslands, both of which correlated positively with Skylark density. The amount of broad-leaved crops had an almost significant negative correlation with Skylark density. Other environmental factors did not have significant associations with Skylark density. Similarly, these factors were not significantly associated with Skylark density in univariate regression analyses.

4. Discussion

4.1. Landscape characteristics and Skylark occurrence

We found that the landscape characteristics of agricultural areas (size, openness and isolation) are strongly associated with Skylark distribution. It is assumed that the original habitats of the Skylark were on the open steppes of Asia, which is reflected in the ecology of the species in agricultural environments (cf. Pätzold 1983, Wilson 1997). Landscape characteristics are of particular importance in Finland where the agricultural landscape consists of relatively small patches of farmland.

Table 4. Variables in the forward stepwise regression analysis of the density of the Skylark in large OFAs. The total amount of variation in Skylark density explained by the model was 28.6% (coefficient of determination = r^2); variables entered the model if $P < 0.05$.

Variable			Cumulative % of variation explained
In the model:	Standardized Coefficient	P	
Amount of grassland*	0.412	0.005	17.6
Proportion of open ditches	0.332	0.020	28.6
Not in the model:	Partial correlation	P	
Amount of broad-leaved crops*	–0.290	0.073	
Habitat diversity	–0.109	0.509	
Shape of the OFA**	0.056	0.736	
Amount of other open area*	–0.048	0.770	
Amount of other vegetation cover -land use type*	–0.071	0.667	
Amount of other ploughed -land use type*	0.009	0.954	
Area	–0.063	0.705	
Proportion of farm roads	0.036	0.828	
Amount of bush*	0.168	0.308	
Amount of verges	–0.198	0.228	
Proportion of roads	–0.050	0.765	
x-coordinate of the OFA centre	0.137	0.406	
y-coordinate of the OFA centre	0.039	0.813	

* ln(proportion of land use type/proportion of spring cereal)

** area/circumference^2

According to our results, Skylarks in Finland usually occur in patches of farmland which are larger than 11.5 hectares. The density was lower in small OFAs than in large ones, but in our study, density was not dependent on the area of the OFA beyond the 11.5 hectare threshold. Similar density patterns have also been found in previous Finnish Skylark studies (Piiroinen *et al.* 1985, Tiainen *et al.* 1985b, 2001). Forest edge avoidance may be an adaptation to increased nest predation close to edges. Forest edges are preferred by nest-predators such as the Hooded Crow *Corvus corone*, Magpie *Pica pica*, Jackdaw *Corvus monedula*, Red Fox *Vulpes vulpes* and Raccoon Dog *Nyctereutes procyonoides* (e.g. Andrén 1992, Huhta *et al.* 1996, Smedshaug *et al.* 2002). Predators have been shown to affect the distribution of bird territories in farmland landscapes (Suhonen *et al.* 1994, Yanes & Oñate 1996, Hromada *et al.* 2002, Tryjanowski *et al.* 2002). The effects of different forest-field edge types on Skylark occurrence were not examined in this study, but the height and density of edge forests can have a considerable effect on the spacing of Skylark territories, especially in small and fragmented patches of farmland (c.f. Chamberlain & Gregory 1999).

The size of farmland patches is probably an important factor for territory selection when Skylarks arrive in breeding areas. Large patches of farmland may be more attractive than small ones. In large farmland areas, it is easier for Skylarks to place the territories both further from the forest, and settlement, edges and in preferred habitats. In this study we also found that isolation decreased the probability of Skylark occurrence in small patches of farmland: both the number of surrounding OFAs and the number of surrounding Skylark territories affected the occurrence in small OFAs. Social factors may affect territory selection: the presence of other territories can induce the Skylarks to establish a territory in an already colonized area (c.f. Kodrick-Brown & Brown 1984, Searcy & Andersson 1986, Hedenström 1995).

4.2. Agricultural factors and Skylark occurrence

We found that the over-winter vegetation of fields was an important factor associated with Skylark occurrence and density. The amount of grasslands was the most important factor determining Skylark density in large OFAs. It has been shown that many breeding bird species of open farmland areas, such as the Corncrake *Crex crex*, Grey Partridge *Perdix perdix* and Curlew *Numenius arquata*, need vegetation cover for a successful breeding, and the Skylark is no exception (Potts 1986, Stowe *et al.* 1993, Grant *et al.* 1999, Schäffer 1999). Fields with over-winter vegetation (i.e. cultivated grass, pasture, winter cereal and set-aside) offer better protection for nests and foraging than ploughed fields (e.g. spring cereal, sugar beet and potato). The results of our study imply that in the Finnish agro-ecosystem it is rather the absence than the excess of vegetation which limits Skylark occurrence. Grasslands constitute a major part of the arable area with over-winter vegetation in Finland. It can therefore be suggested that at the time of Skylark arrival, grasslands are preferable habitats for territory establishment compared to bare soil.

We also found that Skylarks avoided sugar beet, potato and turnip rape areas. Moreover, other vegetation cover -land use type was more abundant in the territories than expected. In large OFAs the Skylark density was negatively correlated with the proportion of sugar beet, potato and rape areas. Correspondingly, in the small OFAs with Skylark territories there were fewer sugar beet, potato and turnip rape fields than in the areas without territories. There are markedly fewer invertebrates and weeds in heavily managed and sprayed sugarbeet, potato and turnip rape fields than in leys and set-asides (Aebischer 1990, Poulsen *et al.* 1998, Salonen *et al.* 2001, Kinnunen *et al.* 2001, Hyvönen *et al.* 2003). Skylarks eat both weed seeds and invertebrates, but the invertebrates are more important, and are in fact a basic requirement for nestlings (Poulsen 1995, Poulsen *et al.* 1998). In addition, regular and frequent agricultural practices destroy a high proportion of nests (Haukioja *et al.* 1985).

In our study we found that Skylark density was higher in large OFAs with a high proportion of open ditches. In small OFAs a similar dependence was not detected, but in small OFAs the quantities of open ditches were low and the Skylark occurrence was more likely to be affected by landscape factors. Areas with open ditches provide safe nest places and an abundant invertebrate and weed food supply for breeding birds (see Tiainen & Pakkala 2001). Open ditches have been observed to increase the abundance and species number of agricultural birds in many studies (e.g. Haukioja *et al.* 1985, Mehtälä *et al.* 1985, see also Arnold 1983). It can be assumed that the relative significance of ditches and especially their margins has recently increased in Finland, mainly because of the adoption of the first national agri-environmental support scheme in 1995. One of the measures of the scheme was an establishment of 1 m broad margins along all larger ditches and at least 3 m broad shelter beds along other waters in farmland. Though narrow, these margins and shelter beds provide considerably more grassy habitat and safe nest sites for Skylarks than did fields before 1995; prior to this date the ditch margins were usually only 0–0.2 metres in breadth.

The territories contained less roads than the control points, but the amount of roads of the total area of the OFAs did not affect Skylark density. Roads increase disturbance (e.g. Meunier *et al.* 1999); it can also be suggested that they are lacking in food provision, and that they offer potential pathways for mammalian predators. Thus the avoidance of roads is expected. The amount of other open areas (patches of non-cultivated habitats) was not observed to affect Skylark occurrence; this was probably due to the scarcity of these habitats in the study area.

Habitat diversity and the amount of verges between fields have been found to increase Skylark density (Schläpfer 1988, Chamberlain *et al.* 1999, 2000). However, in this study neither the habitat diversity nor the abundance of verges were observed to affect Skylark occurrence on either the territory or landscape level. This is a result which needs further investigation.

The effects of the surrounding landscape and the local habitat on Skylark occurrence are not completely distinguishable from each other. For example, the crop composition of small and isolated patches of farmland may differ from that of large ones. Moreover, within large patches of farmland, crop composition and patch configuration may be different in the central and the marginal parts of the farmland area. These interactions complicate the interpretation of habitat associations.

4.3. Conclusions

The changes in agricultural environments that have occurred during recent decades have decreased the amount of preferred habitats, and it has been observed that the Finnish Skylark population has responded to these agricultural changes (Tiainen *et al.* 2001).

The change from mixed farming system to specialized farming has been the major change in Finnish farmland in recent decades (Tiainen & Pakkala 2000, Tiainen 2001). In particular, the decrease in the area with plant coverage in early springtime (leys, pasture and winter cereals) has created a harsh agricultural environment for Skylarks. Set-asides could partly compensate for the population losses caused by the decline in dairy farming (see Norrdahl 1990, Tiainen *et al.* 2001). However, the number of set-asides has decreased during the late 1990s (see Tiainen 2001).

According to our results, the intensification of agricultural land use affects Skylark abundance. Fields with open ditches have drastically decreased in Finland as a result of subsurface drainage (Tiainen 2001), and this has generally had a negative effect on Skylark density (Haukioja *et al.* 1985, Mehtälä *et al.* 1985). On the other hand, the intensification of land use may also have had beneficial effects on the Skylark population due to the fact that cultivation of forest patches has increased the mean size of patches of farmland (Norrdahl 1990, Tiainen *et al.* 2001). Nevertheless, increases in field parcel size over recent decades have been shown to be disadvantageous to Skylarks (Schläpfer 1988, Jenny 1990).

Finally, our results show clearly that the habitat preferences of the Skylark are characteristic of Finnish farmland landscapes. Further studies are needed to find out the importance of landscape and land-use changes for the short- and long-term dynamics of Finnish Skylark populations.

Acknowledgements: We would like to thank Jyrki Holopainen, Henna Piha, Jarmo Piiroinen and Ville Vepsäläinen for their comments on this manuscript. Thanks are also due to Jukka Jokimäki, Danaë Stevens and two anonymous reviewers for valuable comments, which improved this paper, and to Donald Adamson for improving the English. We are grateful for the support and good working facilities of Lammi Biological Station. Financial support by the Maj and Tor Nessling Foundation (to MP) is gratefully acknowledged. This study is part of the following projects: "Biodiversity in agricultural environments" which fell within the Finnish Biodiversity Research Programme of the Academy of Finland (1997–2002), "Biodiversity effects of the national agri-environmental support scheme" (2000-06), and "Biodiversity indicators of farmland" (2003-06), all financed by the Ministry of Agriculture and Forestry.

Selostus: **Kiurun esiintymiseen vaikuttavat elinympäristötekijät eteläsuomalaisessa maatalousympäristössä**

Kiurun elinympäristö ja elinolosuhteet ovat Suomessa erilaiset verrattuna Länsi- ja Keski-Eurooppaan. Suomessa peltoaukeat ovat yleensä pieniä ja useimmiten metsien ympäröimiä. Suomessa kevätviljat ovat viljelykasveista runsaimpia, kun taas Keski- ja Länsi-Euroopassa viljellään enemmän syysviljoja. Lisäksi kiuru on Suomessa (ja Keski-Euroopan itäosissa) muuttolintu.

Tutkimme, mitkä peltomaiseman ominaisuudet ovat tärkeitä kiurun esiintymiselle suomalaisessa maatalousympäristössä. Selvitimme kiurureviirien habitaattikoostumusta suhteessa tarjolla olevaan, peltoaukean minimialavaatimusta, reunavaikutusta sekä peltoaukean habitaattikoostumuksen ja kiurutiheyden välistä suhdetta. Maastotyö tehtiin vuonna 1999 Etelä-Suomessa Lammin kunnan peltoaukeilla peltopinta-alaltaan lähes 30 km^2:n suuruisella tutkimusalueella (kuva 1). Kiurureviirien (n = 267) sijainnit määriteltiin kartoitusmenetelmällä; lisäksi selvitettiin peltoalueiden viljelylohkojen rajat ja maankäyttö (taulukko 1, liitetaulukko). Tarkastelusta poistettiin peltoaukeita yhdistävät kapeikot kuvan 2 esittämällä menettelyllä; näin muodostuvia peltoaukeita oli yhteensä 156. Peltoaukean eristyneisyys mitattiin ympäristössä olevien muiden aukeiden ja näillä olevien kiurureviirien lukumäärän avulla (kuva 3). Aineiston käsittelyssä hyödynnettiin paikkatietojärjestelmiä.

Tutkimuksessa havaittiin, että yli 11.5 ha:n suuruisilla peltoaukeilla oli aina kiuruja (kuva 5). Kiurutiheys oli suurilla peltoaukeilla (> 11.5 ha) keskimäärin 13.4 paria/km^2 ja pienillä (< 11.5 ha) 6.4 paria/km^2. Kiurureviirien habitaattikoostumus mitattiin käyttämällä tulkitun reviirin keskipisteen ympärille muodostettua ympyrää (kuva 4); koostumusta verrattiin satunnaisesti valittuihin ympyröihin. Kiurut välttivät metsän ja asutuksen reunavyöhykkeitä. Lisäksi reviirien sijainti korreloi negatiivisesti perunan ja sokerijuurikkaan ja positiivisesti ylivuotisen kasvillisuuden määrän kanssa (taulukko 2). Suurilla peltoaukeilla nurmen ja ojien (suojakaistojen) määrä korreloivat positiivisesti kiurutiheyden kanssa (taulukko 4). Pienillä aukeilla, joista kiuruja pesi vain vajaalla neljänneksellä, tärkeimpiä selittäjiä olivat aukean koko, sokerijuurikkaan ja perunan määrä sekä aukean eristyneisyys muista peltoaukeista (taulukko 3).

Suomen kiurukannan on aiemmin esitetty vaihdelleen 1960-luvun jälkeen siten, että pellonvaraustoiminnan aikana 1970-luvulla ja viherkesannoinnin aikana 1990-luvulla se kasvoi, mutta palautui entiselle tasolle näiden toimintojen hiipuessa. Tulokset tukevat hypoteesia, jonka mukaan Suomen EU-jäsenyyden aikana peltoalueiden lisääntynyt keväinen kasvipeitteisyys sekä ojien suojakaistat ovat korvanneet karjatalouden pitkäaikaisesta väistymisestä seurannutta peltolohkojen välisen vaihtelun vähentymistä.

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Appendix. Classification of the land use of the fields in the study area. Land use classes "Territory" and "OFA" refer respectively to the classifications used in the habitat analyses of Skylark territories and the landscape analyses of open farmland areas (OFA).

Land use type		Subtype
Territory	OFA	
Without over-winter vegetation, tilled in spring:		
Spring cereal	Spring cereal	Spring sown cereal
Broad-leaved	Broad-leaved	Sugar beet Potato Turnip rape
Other ploughed	Other ploughed	Ploughed fallow Vegetable Pea Parsley Carrot Onion Other spring-sown crop
With over-winter vegetation:		
Grassland	Grassland	Cultivated grass, ley Grassy set-aside Pasture Meadow
Other vegetation cover	Other vegetation cover	Winter cereal Strawberry Rhubarb Stubble Other autumn-sown crop
Non-arable:		
Other open area	Other open area	Open non-used habitat patch
	Open ditch (with bank)	Open river (with bank) Open ditch (with bank)
Bush	Bush	Bushy river Bushy non-used habitat patch Bushy set-aside Bushy ditch Bush Sapling stand Garden
Forest and settlement	Forest and settlement	Settlement Forest Forest-bordered river Forested non-used habitat patch Forested set-aside Forest-bordered ditch
Road	Farm road	Farm road (not in intensive use)
	Road	Drivable road (in moderate or intensive use)