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Population increase and aspects of colonization of the Tree Sparrow *Passer montanus*, and its relationships with the House Sparrow *Passer domesticus*, in the agricultural landscapes of Southern Finland

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While many farmland bird species are declining in Western Europe, the Finnish Tree Sparrow *Passer montanus* population has increased significantly during recent decades. During 1984–2002, we studied the population changes, colonization characteristics and nest sites of the Tree Sparrow in a large area of agricultural landscape within southern Finland. The study focused mainly on the local landscape level. To explain the patterns of colonization, we took into account the conspesifics of the species itself, the abundance of resources, the land use types in the agricultural area, the effects of a potential competitor (the House Sparrow *Passer domesticus*) and the amount of human impact. The Tree Sparrow population increased exponentially during the study period. The species colonized places where House Sparrows were present, but we did not observe competition between the two species. Human impact had a positive effect on colonization. The Tree Sparrow showed a strong capacity for colonization in the agricultural environment. The land use of the agricultural area did not have significant effects on colonization at the spatial scale used. The Tree Sparrow showed more diversity in nest sites than the House Sparrow.

1. Introduction

The Tree Sparrow *Passer montanus* is abundant and common in western and central Europe (Ivanov & Summers-Smith 1997). Its density is high in mid-continental Europe (Germany, the Netherlands and Belgium) contrasting with lower densities in the northern and southern parts of the distribution area (Summers-Smith 1998). In the British Isles, the numbers and distribution of the Tree Sparrow have undergone considerable fluctuations: the population has been decreasing since the late 1970s, but this decrease was preceded by a period of strong population growth, starting in the 1950s (Summers-Smith 1998). Similar changes occurred in the Netherlands, Switzerland, and Germany about the same time (Ivanov & Summers-Smith 1997). In three of the neighbouring countries of Finland – Sweden, Estonia and Russia – the Tree Sparrow is one of the most common species in agricultural and urban environments. For example, in Sweden the size of the breeding population is 400,000–900,000 pairs (Svensson *et al.* 1999). The Swedish population increased from 1975 to the early 1990s, but is nowadays regarded as stable. In Russia, the breeding population has been relatively stable during 1970–2000, and in the Baltic countries there has been a small increase over this period (BirdLife International 2004).

In Finland, the Tree Sparrow is at the northern limit of its distribution. In the mid-1990s the breeding population was estimated to be approximately 8,000 pairs (Väisänen *et al.* 1998). The population of Finnish Tree Sparrows increased exponentially in 1957–1996 (Fig. 1), and this pattern of growth is still continuing (BirdLife International 2004; R. A. Väisänen, unpublished winter census data). During this period, the Tree Sparrow expanded its distribution from former core areas in south-eastern Finland and the Åland Islands (situated between Finland and Sweden) to other parts of the country (von Haartman *et al.* 1963–1972, Väisänen *et al.* 1998). Given the abundance of the Tree Sparrow in the neighbouring countries, the spread of the species within Finland has come surprisingly late. It has been suggested that increased winter-feeding by humans may explain the population growth, but other factors that may be causing the rapid population increase are not known (Väisänen & Solonen 1997).

There is a potential competitive relationship between the House Sparrow and the Tree Sparrow (Summers-Smith 1994), but there have been no studies on the possible effect of competition on the population trends of the two species. Over the period of the Tree Sparrow's impressive population growth, the House Sparrow population in Finland has declined dramatically, by about 50% from the mid-1980s to the mid-1990s (Väisänen & Solonen 1997), and the decline is continuing (BirdLife International 2004). Indeed, the House Sparrow is reported to be in decline in many western European countries (Summers-Smith 1994, Indykiewicz & Summers-Smith 1997, Väisänen & Solonen 1997, BirdLife International 2004). The decline of the House Sparrow in Finland has been associated with changes in agricultural practices,

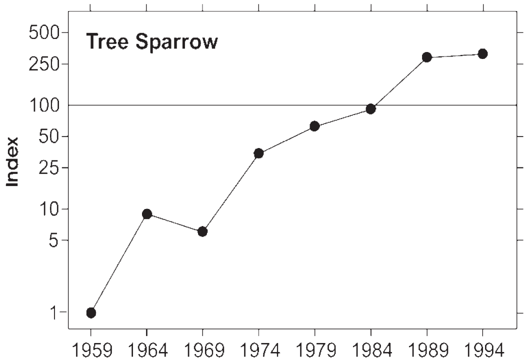

Fig. 1. Winter population index of the Tree Sparrow in Finland. Black dots show the median years of eight 5-winter periods. The densities for each period were calculated as the total numbers of individuals observed in censuses over five winters, divided by the total length of census routes. Densities were then transformed into a population index; so that the mean of the periods is 100 (after Väisänen & Solonen 1997).

and especially the decrease in the number of pastures and cattle farms that would offer good food supplies (Väisänen & Solonen 1997, Tiainen & Pakkala 2001). The decline of the House Sparrow could have positive effect on the Tree Sparrow population and could expand its range, if there is competition between the two Sparrow species.

We studied the population changes and colonization characteristics of the Tree Sparrow using long-term territory mapping data from a large area of agricultural landscape in southern Finland. The aims of the study were as follows: (1), to find explanations (besides winter-feeding) for the rapid population growth of the Tree Sparrow. (2), To study whether the land use of an agricultural and semi-urban landscape has an effect on colonization (with particular reference to the intensity of field management). (3), To study the possible competition between the Tree Sparrow and the House Sparrow and its effects on colonization. (4), To study the diversity of Tree Sparrow nest sites. Hence, in an attempt to explain the colonization success of the Tree Sparrow, we investigate the effects of conspesifics, different habitat types, resources, and potential competitor species.

2. Material and methods

2.1. The study area

The study area is located in the municipality of Lammi, southern Finland (61º05'N, 25º00'E; Fig. 2a). The area consists of a mosaic of farmland, forest, scattered settlements and a more densely inhabited area (Lammi main village with an area of 3 km²; Fig. 2b). The total area covered was 30.3 km². The population changes were studied within two separate parts of the study area: the northern (13.25 km²) and the southern area (14.00 km²), located on opposite sides of the area of Lammi main village (Fig 2b).

2.2. Bird data

Within the study area, Tree Sparrows and House Sparrows were mapped annually during 1984–2002, using a two-visit mapping census method. The method has been shown to be a reliable for mapping farmland birds (Tiainen *et al*. 1985a, Tiainen & Pakkala 2000). The two-visit mapping method used generally followed the procedures used in the mapping census of breeding land birds (Koskimies & Väisänen 1991). The first field-visit was made during 5–20 May and second during 25 May–10 June. In the case of the two Sparrow species, particular attention was paid to recording simultaneous observations of singing males, accurately estimating the pair numbers of breeding groups, and to the locations of the breeding sites of both sparrow species. As the two Sparrow species are not ordinary territorial species, we did not define any "territory centres", but rather "approximate nest sites", determined by the locations of nest sites or by the singing or alarm calls of males/pairs.

To study the colonization characteristics of the Tree Sparrow, the period 1986–2001 was divided into four 4-year periods. Within each period, the occupancy of the Tree Sparrow and the House Sparrow was determined in a 500 × 500 m grid, covering the entire study area (Fig. 2b). This local landscape scale reflects the relevant ecological scale of the two sparrow species at the territory group level. Occupancy was defined by the locations of nest sites (see above). In 1994 and 2000 the area of the main village, 3 km², was censused using a three-visit mapping method, and in 1979 by single-visit mapping. To obtain data for this area comparable with those from the agricultural environments, we used data additional to those in the mapping censuses (mainly information on nest sites).

In 2002, in addition to the mapping censuses,

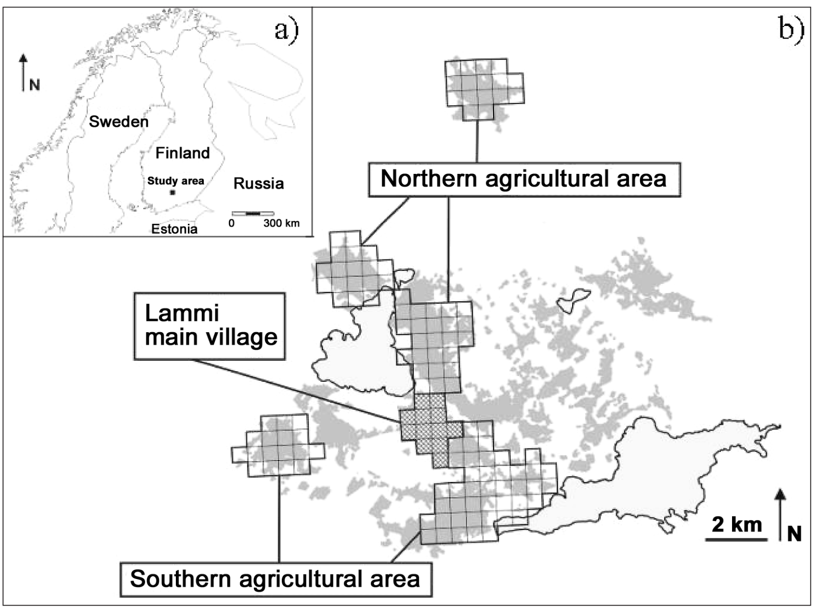

Fig. 2. a) Location (61°05' N, 25°00' E) of Lammi study area in southern Finland. b) Map of the study area. The 500 × 500 m grid shows the censused squares. The checked squares refer to the densely inhabited study area (Lammi main village; 3 km²), the unchecked squares to the agricultural study area (27.25 km²). Darker grey shading locates agricultural areas, and light grey areas are lakes.

Table 1. Range (minimum to maximum) of land-use types in the study area across 500 × 500 m squares, during the study period 1986–2001. For agriculture and settlements, the range in the size of the area is given (in km²), whereas for ditches and roads, the range in length is given (in km). See text for further details

Land-use type	Range	
Managed tilled fields	5.31–9.13	km²
Managed rotational grasslands	2.24–2.70	km²
Non-managed or extensively managed fields	0.64–1.66	km²
Forest and bush patches	1.78–1.85	km²
Settlement and farmyards	3.29–3.57	km²
Surrounding land	12.98	km²
Open ditches	18.6–20.2	km
Roads	58.4–60.7	km

nest-site data on both sparrow species were collected in the core areas of the Tree Sparrow population. Only confirmed nest sites were included, and these were grouped into three categories (buildings, nest-boxes, and the horizontal open metal tubes of electricity poles).

2.3. Environmental data

Data on the habitats of the study area (Table 1) were collected in the field by defining on maps the land use type and boundaries of each field parcel and other habitat area. The data were classified as belonging to the following categories: 1) managed tilled field (mainly spring cereal, potato, sugar beet, or turnip rape; rarely also sunflower, pea, vegetable garden, corn, onion, carrot, beetroot, and cabbage), 2) managed rotational grassland (including ley, pasture, and hay), 3) non-managed or extensively managed field (including set-aside, meadow, and unused open habitat patches), 4) bush and forest patches (including ditches with bush and tree lines) within the boundaries of farmland and Lammi main village, 5) settlement, including farm yards and gardens, 6) surrounding land (including mostly forest surrounding the field area and Lammi main village; i.e. land that is not a suitable habitat for the Tree Sparrow), 7) open ditches (i.e. with no bushes or trees), and 8) roads. Data were digitized from the field maps to a GIS-database. The areas (km²) of the land use types were calculated, except in the case of open ditches and roads, which were calculated as lengths (km). In the calculations, the averages over four years were used for each of the four 4-year periods.

The total number of buildings within each 500 × 500 m square was calculated from the topographic database of the National Land Survey of Finland. We used this variable as a measure of general human impact, one which would describe the potential amount of nest sites and winter-feeding. The number of livestock and horse farms in each 500 × 500 m square was calculated using the locations of farm buildings, based on the information in the topographic database and in our field data.

2.4. Analysis of the colonization characteristics of the Tree Sparrow

To study the characteristics of the colonization events of the Tree Sparrow in the 500 × 500 m squares we used forward stepwise logistic regression analysis. During the period 1986–2001, 54 squares were colonized. For each 4-year time period, as many non-colonized squares were randomly selected as there were actual colonized squares. Each square occurred in the model only once; thus the data sets for each time-period were independent of each other. The colonizations were explained by the following variables (with an explanation given in brackets).

1) Presence/absence of the Tree Sparrow in some of the adjacent squares (colonization of a square may be affected by the presence/absence of conspesifics in the surrounding squares).
2) Presence/absence of the House Sparrow in the square (House Sparrow is a potential competitor of the Tree Sparrow (Summers-Smith 1994), which may affect colonization).
3) Number of livestock farms in the square (livestock farms and their pastures are probably important food resources of the Tree Sparrow, c.f. Tiainen & Pakkala 2001).
4) Number of buildings in the square (this variable reflects human influence and is expected to have a strong positive correlation with the amount of winter-feeding places and nest-

boxes, because these human-built and human-maintained resources usually occur in the proximity of human settlement).

5) Area of managed tilled fields in the square (this, and the next two variables, describe the agricultural land use of the study area by a rough classification of cultivation types. The intensivity of agricultural management practices is the basis of this classification, since it is known from previous studies that the declines in farmland birds are mainly due to agricultural intensification, see also the Discussion section).
6) Area of managed rotational grasslands in the square (this habitat type differs from the previous habitat type, being less intensively managed (c.f. Pitkänen & Tiainen 2001). Grasslands have over-winter and springtime vegetation cover that has been shown to be an important aspect for many farmland bird species, c.f. Piha *et al*. 2003).
7) Area of non-managed or extensively managed fields in the square (set-asides and other minor habitats in this class can be expected to have more diverse vegetation than managed fields, and may thus provide more seed and insect food for birds, c.f. Pitkänen & Tiainen 2001).
8) Area of bush and forest patches in the square (this variable describes small-scale biological and structural diversity in the landscape, because bush and forest patches can be expected to serve as potential sources of food and shelter in an otherwise relatively open environment).
9) Area of settlements in the square (this variable is related to variable 4, but includes also yards and farmyards, not just buildings. Thus, the variable describes the amount of possible food resources. The Sparrow species are known to be associated with humans and to feed in yards (Väisänen *et al*. 1998, Tiainen & Pakkala 2001). As with the number of buildings, this variable may be expected to describe the amount of nest-boxes and nest sites in buildings).
10) Length of open ditches in the square (ditches usually have ditch banks, often with vegetation. This variable is included for the same reasons as variable 8).
11) Length of roads in the square (roads usually have road banks, often with vegetation. This variable is included for the same reasons as variables 8 and 10).
12) Time period (the colonization patterns may depend on time, especially in a rapidly increasing population).

The first two variables, and the time period, were defined as categorical (effect) variables, the remainder being continuous variables. Since the areas of land-use types in the study area are not independent of each other, we used composite transformations (ln(proportion of land use type/proportion of managed tilled fields)) that related land-use types to the dominant potential Tree Sparrow habitat in the study area, namely the managed tilled fields (Table 1). Zero proportions were replaced by 0.00003, which was an order of magnitude smaller than the smallest proportion observed. Composite transformations were used for the following land use types: 1) settlement and farm yards, 2) managed rotational grasslands, 3) forest and bush patches, and 4) non-managed or extensively managed fields. The lengths of linear land use types (i.e. roads and open ditches) were log-transformed.

Along with the usual 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 models. The SAS statistical software package (version 8) was used for the analysis.

2.5. The possibility of inter-specific competition

To study whether or not the probability of the disappearance of the House Sparrow was associated with the Tree Sparrow, we checked whether the disappearance of the House Sparrow from a grid cell between time t and $t + 1$ was accompanied by i) a synchronous colonization of a grid cell by the Tree Sparrow, ii) a synchronous disappearance of the Tree Sparrow from a grid cell, iii) the continuous presence of the Tree Sparrow in a grid cell, or iv) the continuous absence of the Tree Sparrow from a grid cell. The same four possibilities for Tree Sparrow occurrence were also counted for the situations where a grid cell was colonized by a House Sparrow between time t and $t + 1$, and for

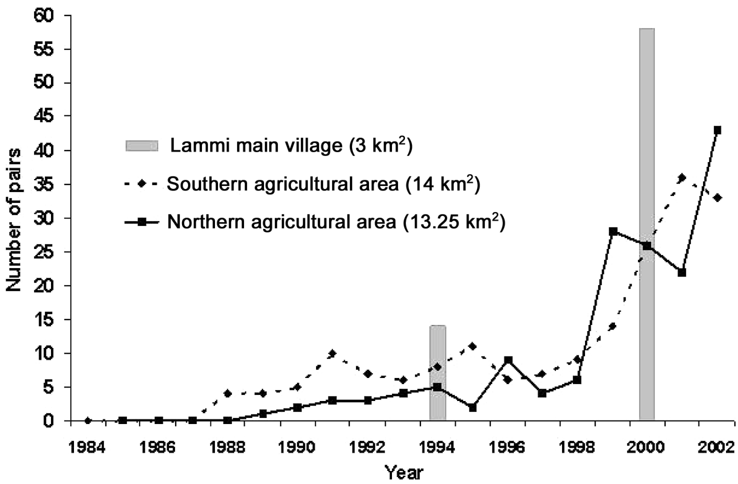

Fig. 3. Population changes of the Tree Sparrow in different parts of the study area. The Tree Sparrow arrived in the area in the winter of 1979/1980, when it settled in the area of Lammi main village.

the situations where the House Sparrow remained present in a grid cell between time t and $t + 1$. The risk for the disappearance of the House Sparrow was calculated as a proportion (%) of the number of House Sparrows relative to the number of all cases, in each of the four different situations of Tree Sparrow occurrence mentioned above.

The diversity of nest site choice was assessed by calculating the Shannon-Wiener diversity index $H' = -\Sigma p_i \ln p_i$, where p_i is the proportion in each nest site class i. These associations between the two Sparrow species were studied using the total pooled data.

Table 2. Forward stepwise logistic regression analysis of the colonization characteristics of the Tree Sparrow. Variables entered the model if $P < 0.05$. For variables that did not enter the model, the direction (positive + or negative –) of the effect is given, as well as the residual chi-square score and its significance. Composite transformations were calculated as ln(proportion of land use type/proportion of intensively managed field). The total amount of variation of colonisation characteristics explained by the model was 43.1 % ($R^2 = 0.431$); value of maximum rescaled R^2 was 0.578.

Variable in the model	Coefficient	P	% of variation explained
Constant	–2.512		
Presence of the House Sparrow in the square	1.881	< 0.001	28.7
Presence of the Tree Sparrow in some of the adjacent squares	2.782	< 0.001	11.0
Number of buildings in the square	0.060	0.032	3.4
Variable not in the model	**Effect**	**χ^2 Score**	**P**
Composition of area of non-managed or extens. managed fields in the square	–	3.559	0.060
Time period	–	2.384	0.123
Composition of area of managed rotational grasslands in the square	–	1.957	0.162
Number of livestock farms in the square	+	1.006	0.316
Length of roads in the square	+	0.489	0.484
Composition of area of settlement in the square	–	0.133	0.715
Composition of area of bush and forest patches in the square	+	0.279	0.597
Length of open ditches in the square	–	0.036	0.850

3. Results

3.1. Tree Sparrow population changes

In 1984–2002 the population changes of the Tree Sparrow in Lammi were similar in the two parts of the agricultural study area: after a slow initial phase of increase the populations increased five-fold during the last four years of the study; the population growth was significant also in the area of Lammi main village (Fig. 3), where no Tree Sparrows had been found in 1979 (Tiainen *et al*. 1982).

3.2. The characteristics of Tree Sparrow colonization

The presence of the House Sparrow in the 500 × 500 m square had a significant positive effect on the probability of colonization by Tree Sparrows, and also explained most of the variation in the stepwise logistic regression model (Table 2). In practice, this result means that the two sparrow species were found in a similar type of environment. Moreover, the presence of Tree Sparrows in adjacent squares, and also the number of buildings present, had a positive effect on colonization probability. Other environmental variables related to the agricultural area, or to the time period, showed no statistically significant effect on colonization (Table 2). However, the rather small p-value (0.06) of the composition of the area of non-managed or extensively managed fields in the square suggests that this (negative) effect might have some ecological significance.

3.3. Inter-specific interactions

The occurrences of the two sparrow species are not independent of each other, and the species are found in the same local environments. This general coexistence between the Tree Sparrow and the House Sparrow in 500 × 500 m squares was significant in every study period (goodness-of-fit test; 1986–1989: $\chi^2 = 8.71$, $P < 0.003$; 1990–1993: $\chi^2 = 10.7$, $P < 0.001$; 1994–1997: $\chi^2 = 14.1$, $P < 0.001$; 1998–2001: $\chi^2 = 45.9$, $P < 0.001$; d.f. = 1 in all cases). Moreover, the risk of the disappearance of the House Sparrow was not independent of the occurrence of the Tree Sparrow (goodness of fit test; $\chi^2 = 17.1$, d.f. = 6, $P = 0.009$, see Table 3). In fact, the risk was higher when the Tree Sparrow also disappeared, and was small in grids occupied and colonized by the Tree Sparrow.

3.4. Nest sites of the Tree Sparrow and the House Sparrow

The distribution of the various nest sites of the Tree Sparrow differed significantly from that of

Table 3. Patterns of House Sparrow and Tree Sparrow presence – absence between time t and t + 1 in the 500 × 500 m grid cells, expressed as the number of cases. Different types of changes in the species' occurrence between two sequential time periods are expressed as follows: A → P = species colonizes into a grid cell; P → A = species disappears from a grid cell; P → P = species remains in a grid cell; A → A = species remains absent from a grid cell. Changes between all sequential time periods (i.e. 1986–89 to 1990–93, 1990–93 to 1994–97, and 1994–97 to 1998–2001) were pooled.

House Sparrow	Tree Sparrow			
	A → P	P → A	P → P	A → A
P → A	2	3	2	29
P → P	36	9	37	94
A → P	3	0	3	22
Total	41	12	42	145
Probability of House Sparrow disappearance:	2/41 = 0.049	3/12 = 0.25	2/42 = 0.048	29/145 = 0.20

the House Sparrow (goodness-of-fit test: $\chi^2 = 155.0$, d.f. = 2, $P < 0.001$; Fig. 4). Tree Sparrows were more diverse and flexible than House Sparrows in their use of different kinds of nest sites: the Shannon-Wiener diversity index *H'* was, for the Tree Sparrow nest sites, 0.90, but for the House Sparrow *H'* was 0.31. Tree Sparrows were often observed to breed in nest-boxes and in the metal tubes of electricity poles whereas House Sparrows clearly preferred buildings.

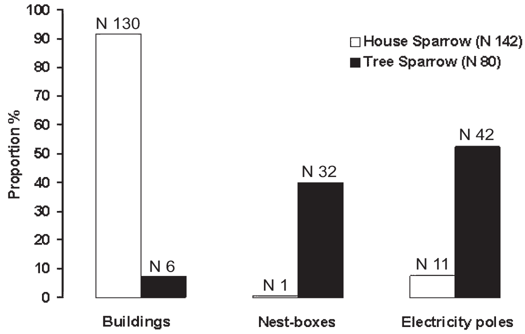

Fig. 4. Nest sites of the Tree Sparrow and the House Sparrow, based on the data for 2002.

4. Discussion

4.1. Colonisation and range expansion of the Tree Sparrow

This study demonstrates the good colonization capacity of the Tree Sparrow, and we expect that the population growth and expansion of the species in Finland will continue in the near future. In our study area, the impressive and rapid population growth of the Tree Sparrow clearly reflects the exponential population growth of the species in Southern Finland. The first reported Tree Sparrow in the study area appeared in the main village of Lammi in the winter of 1979/1980 (Vickholm 1981), and the first breeding there was confirmed in 1983 (T. Pakkala unpubl.). During the 1980s, the species started to colonize agricultural areas near the main village, in small settlement centres a few kilometres south and north of the main village. It was probably from these secondary centres that the species colonized new areas in the agricultural landscape, as colonizations were common in areas where there were already Tree Sparrows in the surroundings. However, most of the early expansion took place within the area of the main village, which partly explains the positive effect of the number of buildings on colonization. The colonization proceeded rapidly thereafter, demonstrating the efficiency of the species in colonizing new breeding areas, both in rural and in more densely inhabited environments.

We suggest that the number of buildings may correlate positively with the amount of nest-boxes and winter-feeding sites, i.e. two aspects for which we do not have annual data. As known previously (e.g. Scherner 1972), and as shown by our results, nest-boxes are important nest sites for the Tree Sparrow. Winter-feeding of birds has become increasingly common in Finland ever since the 1950s, and it has increased the survival of many over-wintering bird species (Hildén 1985, Väisänen & Solonen 1997). The population growth of the Tree Sparrow is comparable to the strong population increase of the Blue Tit *Parus caeruleus* and the Greenfinch *Carduelis chloris* in Finland – phenomena that have been explained, at least partly, by the increase in winter-feeding (Väisänen & Solonen 1997). Although we do not have exact data about the amount and changes in winter-feeding over the study period, it can be supposed that the trend within our study area has been similar to the trend elsewhere in Finland, and that the increase in winter-feeding may well be one factor contributing to the changes in the Tree Sparrow observed in our study area.

The history of the Tree Sparrow in Finland is interesting because the species has expanded its distribution from two separate areas: mainly from south-eastern Finland (areas near the Russian border), but (possibly) also from the Åland Islands (situated between continental Finland and Sweden) (c.f. Lehikoinen *et al.* 2003). The expansion of the range from the south-east has been relatively rapid during recent decades, but the expansion from the west has proceeded rather slowly. Although the species has been abundant in the Åland Islands for over 30 years, in the late 1990s it was still breeding only in small numbers on the west coast of continental Finland (Väisänen *et al.* 1998, Lehikoinen *et al.* 2003). However, according to the wintertime census data of the Ornithological Society of Turku, the first years of the 21st century have seen a remarkable increase in Tree Sparrow numbers in country villages and suburban areas in south-western Finland, around the city of Turku (E. Gustafsson unpubl).

Since the Tree Sparrow is expanding its range, it is likely that its increase is connected to environmental factors that are operating on a much larger spatial scale than the one used in this study. In order to study the range expansion of the Tree Sparrow at larger geographical scales, reliable information would be needed on the population development of the Tree Sparrow in Russian Carelia, the area adjacent to Finland's south-eastern border. However, no comprehensive census data can presently be obtained from there.

4.2. Land use and the Tree Sparrow population

It has been suggested that agricultural intensification and other changes in agricultural practices and land use are the main reason behind the decline of many farmland bird species in Western and Central Europe during recent decades (e.g. Tucker & Heath 1994, Fuller *et al.* 1995, Siriwardena *et al.* 1998, Chamberlain *et al.* 2000, Tiainen & Pakkala 2001, Piha *et al*. 2003, Rintala *et al*. 2003, Vepsäläinen *et al*. 2005). As elsewhere in Western Europe, the agricultural environment in Finland has changed radically since the 1950s, when the process of agricultural intensification began (Raatikainen 1986, Hanski & Tiainen 1988, Tiainen 2001). The main changes involved are: a shift from mainly dairy farming to farming dominated by spring cereals, increases in the average size of farms and in the specialization of farms, an increase in subsurface drainage, an increase in the use of artificial fertilizers, and an increase in the use of herbicides lasting up to the mid-1970s (Tiainen 2001). While many bird species have declined due to the intensification of agriculture, the Tree Sparrow's situation in Finland seems to be different, as shown by this study. However, the population size and densities of Tree Sparrows in Finland are still smaller than in other European countries, and the general trend elsewhere in Western Europe is for the Tree Sparrow populations to be either decreasing or relatively stable (BirdLife International 2004).

In this study, the presence of managed tilled fields may have had some positive effect on Tree Sparrow colonization, as revealed through the rather strong negative effect of composition of non-managed fields and the weaker negative effects of composites of other land use types. Nevertheless, our results suggest that – at the spatial scale we used – the successful colonization of the Tree Sparrow over the agricultural and semi-urban area under study was not greatly dependent on the habitat types of the farmland or their diversity, and probably had more to do with the availability of suitable nest sites.

In a British study, Tree Sparrows showed a strong colonization capacity and a preference for nest sites adjacent to wetland habitats, and an avoidance of nest sites in intensively managed farmland, in a situation in which the availability of nest sites (nest-boxes) and food resources (seed alimentation) was manipulated (Field & Anderson 2004). In our study, however, the Tree Sparrow frequently colonized areas of open, intensively managed farmland, as long as suitable nest sites were available. It should be noted that the population trend of the Tree Sparrow in Britain is totally different from that in Finland: in the UK the Tree Sparrow population crashed by 94% between 1970 and the 1990s (Gregory *et al*. 2004). Thereafter, the species appears to have increased by about 55%, starting from the mid-1990s (Gregory *et al*. 2004).

4.3. Inter-specific relations between Tree Sparrows and House Sparrows

The habitat requirements of the Tree Sparrow and the House Sparrow at local landscape scale seem to be rather similar, since these two species are found syntopically. We do not find evidence of negative interactions between the species, and the areas that the Tree Sparrow successfully colonized were regularly occupied also by the House Sparrow. In fact, House Sparrows have a higher probability to disappear from those areas where Tree Sparrows have disappeared or were absent, compared to areas that have been colonized or were occupied by Tree Sparrows. The lack of notable competition between the two Sparrow species is also suggested by Väisänen *et al.* (1998). On the other hand, Cordero & Senar (1990) report interspecific competition between the two sparrow species for nest-boxes in nest-box colonies, and, along with Summers-Smith (1963), suggest that the House Sparrow is more aggressive, and dominant over the Tree Sparrow. We did not observe, and there are no published reports, of interspecific competition for nest sites between the Tree Sparrow and the House Sparrow in Finland. In a Spanish study, the number of available natural cavities was the most important factor affecting the number of breeding House Sparrows, whereas the number of breeding Tree Sparrows was positively related to the number of available nest-boxes (Cordero 1993). However, our results reveal only consequences at the 25 ha scale used in this study. The situation may by different at a smaller scale, in the proximity of nest sites, outside the breeding season, or for resources not measured in this study.

Based on our observations in the study area, the Tree Sparrow is rather more mobile than the House Sparrow, and is thus probably more effective in finding feeding and breeding places. The Tree Sparrow's tendency to breed in nest-boxes and in the horizontal metal tubes of electricity poles, and also in buildings, demonstrates its adaptive flexibility in heterogeneous and changing environments. Electricity poles with suitable open tubes have been used in Southern Finland since the late 1970s (*pers. comm.* by Jukka Lehtonen, a representative of Vattenfall Electricity Company), and according to our own field data, they have been common since the late 1980s in the Lammi study area. As for nest-boxes, it is common knowledge among Finnish birdwatchers and ornithologists that their number has increased since the 1950s–1960s. This increase may be one aspect explaining the population growth of the Tree Sparrow. The tendency of the species to breed in nest-boxes has been shown also by e.g. Scherner (1972). Lastly, the role of climatic change cannot be ruled out. On average, winters have become warmer by several degrees Celsius in Finland over the past decade, as compared to the winter temperatures of 1960–1980 (Drebs *et al.* 2002). Together with increased food availability, this may have improved the winter survival of Tree Sparrows.

4.4. Conclusions

We studied the population increase and colonization of Finnish Tree Sparrows in detail for the first time. Our study shows that the Tree Sparrow is an exceptional species among the birds found in Finnish agricultural environments, since it is undergoing a strong increase and does not seem to be suffering from the prevailing intensification of agriculture. This study emphasizes also the exceptionality of the population trend of the species in Finland, as compared to most other European countries. However, in order to arrive at more detailed explanations for the recent successful population development of the Tree Sparrow in Finland, we need further studies on habitat selection, population biology, and local population dynamics, and on the relationship of the species with the House Sparrow.

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Pikkuvarpusen kannankasvu ja kolonisaation piirteet sekä lajin suhde varpuseen eteläsuomalaisessa maatalousympäristössä

Suomen pikkuvarpuspopulaatio on runsastunut huomattavasti viimeisten vuosikymmenien aikana. Suomen tilanne on poikkeuksellinen – muualla Euroopassa pikkuvarpusen kannat joko vähenevät tai ovat vakaita. Tutkimme pikkuvarpusen kannanmuutoksia, uusien alueiden kolonisaatiota sekä erilaisten pesäpaikkojen käyttöä eteläsuomalaisessa maatalousympäristössä vuosina 1984–2002. Selvitimme kolonisaation etenemistä ja erityispiirteitä paikallisella maisematasolla 25 hehtaarin ruuduissa laajalla tutkimusalueellamme Lammilla, ja otimme huomioon seuraavien tekijöiden vaikutuksen kolonisaatioon: pikkuvarpusen läsnäolo ympäröivissä ruuduissa, resurssien määrä (karjatilat), varpusen (mahdollinen kilpailija) läsnäolo,

maatalousalueen maankäyttö, sekä ihmisen vaikutus (asutetun alueen koko ja talojen määrä).

Pikkuvarpuskanta kasvoi huomattavasti tutkimusjakson aikana ja voimakkain kasvu alkoi 1990-luvun puolivälin jälkeen. Pikkuvarpusen havaittiin kolonisoivan paikkoja, jossa varpunen oli läsnä, eikä kilpailua lajien välillä havaittu. Ihmisen vaikutuksella oli positiivinen vaikutus kolonisaatioon, mikä luultavasti epäsuorasti heijastaa talviruokinnan ja pönttöjen määrän positiivista vaikutusta. Viljellyn peltoalan erilaisilla maankäyttötavoilla ei ollut merkittävää vaikutusta kolonisaatioon.

Tutkimus osoittaa lajin kolonisaatiokyvyn olevan erittäin hyvä sekä maatalousympäristöissä että edellistä tiheämmin asutetussa kyläympäristöissä. Pesäpaikkojen käytössä pikkuvarpunen oli varpusta monipuolisempi – laji pesi usein pöntöissä sekä sähköpylväiden ontoissa vaakaputkissa, ja vain harvoin varpusen tapaan rakennusten koloissa. Tutkimus osoittaa pikkuvarpusen olevan poikkeuksellinen maatalousympäristön lintulaji sillä se ei, monien muiden lintulajien tapaan, näytä kärsivän maatalouden tehostumisesta. Pikkuvarpusen kanta on Suomessa kuitenkin yhä varsin pieni, ja idästä alkanut kannan levittäytyminen jatkuu monilla alueilla maassamme.

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