Ann. Zool. Fennici 44: 115–140 ISSN 0003-455X
Helsinki 25 April 2007

Indexing long-term regional bird population dynamics with nestling ringing data

Jukka Rintala[1,2] & Juha Tiainen[1]

[1)] *The Finnish Game and Fisheries Research Institute, P.O. Box 2, FI-00791 Helsinki, Finland (e-mail: first name.surname@rktl.fi)*
[2)] *Finnish Museum of Natural History, P.O. Box 26, FI-00014 University of Helsinki, Finland*

Received 24 Oct. 2006, revised version received 16 Nov. 2006, accepted 16 Nov. 2006

Rintala, J. & Tiainen, J. 2007: Indexing long-term regional bird population dynamics with nestling ringing data. — *Ann. Zool. Fennici* 44: 115–140.

Finnish nestling ringing data were used to index regional starling *Sturnus vulgaris* population trends from 1951 to 2001 using log-linear models. A population model with a similar pattern of decline to the actual one was initialised using a resource selection function, which related presence–absence observations of ringed broods to environmental covariates. A data correction was necessary because uncorrected missing counts (indistinguishable in the source data from zero counts) seriously underestimated the population decline. On the basis of the corrected estimate, starlings declined by 80% between the early 1970s and mid-1980s. The decline was greatest in northern Finland. Extinctions were common among local populations during the decline; their frequency increased towards the north, resulting in overall range contraction.

Introduction

European farmland birds have declined over more than three decades, as shown in an analysis based on eighteen national bird census schemes (Gregory *et al.* 2005). Long-term population decreases have often coincided with changes in farmland habitats, these being caused by a general intensification of agriculture (e.g. Newton 1998). The starling *Sturnus vulgaris* is one of the species that has suffered greatly from these changes. It is distributed in the Palaearctic between 40°N and 70°N, and the European breeding population reaches the arctic zone in Finland (Tiainen & Pakkala 1997, Väisänen *et al.* 1998). Finnish starlings overwinter mainly in western Europe, from England to northern France (Fliege 1984). Starlings used to be very common in farmland habitats, but during recent decades there have been substantial declines in local and national populations, first in Finland (Orell & Ojanen 1980, Solonen *et al.* 1991, Rintala *et al.* 2003) and later in other northern, central and north-west European populations (Møller 1983, Robinson *et al.* 2002, BirdLife International 2004, Svensson 2004b).

As a consequence of structural changes in Finnish agriculture, the use of field areas has changed profoundly over the last 20–40 years (Tiainen 2001, 2004). In order to investigate the impact of changes in habitat availability, Tiainen *et al.* (1989) studied the breeding success of starlings in typical agricultural areas. They found that the nestling mortality of southern Finnish starling populations was clearly lower in traditional mixed farming areas (including dairy cattle) than in areas with only cereal and root crop cultivation; they suggested that the large-scale disappearance of pastures and sown grass fields from farmlands during the 1970s and 1980s had had a wide-ranging negative impact on the breeding habitats of starlings.

According to Tiainen *et al.* (1989), the increased nestling mortality in the poorest habitats was most probably due to the reduced availability and quality of nestling food. Nestlings are likely to starve if the nests are situated far from the pasture habitats that starlings prefer in seeking food for their young (Dunnet 1955, Tinbergen 1981, Tiainen *et al.* 1989, Smith & Bruun 2002, Olsson *et al.* 2002). Tiainen *et al.* (1989) hypothesised that due to the decrease in the average nestling survival of the population as a whole, the production of young did not balance adult mortality. This would have caused the population decline. Solonen *et al.* (1991) showed that the declines among twenty local populations from southern to northern Finland coincided with the cessation of cattle farming. In northern Finland there were declines in both highly productive and poorly productive populations (Solonen *et al.* 1991), a phenomenon explicable by the harsh northern climate that may limit the persistence of populations (Järvinen & Väisänen 1984, Svensson 2004a). Solonen *et al.* (1991) suggested that in order to persist, populations in the north needed immigrants from the south.

In order to understand regional starling population dynamics, an analysis based on data with good geographical coverage is needed, not only for the period of the decline, but also for the 1950s and 1960s, i.e. the period before the steep decline that set in towards the start of the 1970s (Rintala *et al.* 2003). Relevant annual census data are not available from before 1979, i.e. the first year of the continuous national census programme in Finland (Väisänen & Järvinen 1981, Väisänen *et al.* 1998). So far, there have been no estimations of long-term population trends for Finnish starlings, with regional differences analysed using up-to-date statistical methods. Nestling ringing data provide a potential basis for such an analysis, since they date back a very long time and cover the entire country. The starling has long been a popular target species for bird ringers: it readily accepts nest-boxes for breeding in the vicinity of houses, and it tends to breed colonially, making it possible for ringers to access several nests at a time.

Volunteer ringers have ringed large numbers of nestlings since the early 1950s. The availability of data from this source led Rintala *et al.* (2003) to use annual species-specific totals to index starling population changes (cf. Ginn 1969, Hjort & Lindholm 1978, Österlöf & Stolt 1982, Bairlein *et al.* 1994, Haapala & Saurola 1995, Peach *et al.* 1998, Berthold *et al.* 1999, Karlsson *et al.* 2002).

Usually, when the objective is to estimate population trends for areas of comparable size, indices of abundance change are calculated on the basis of sample censuses. The censuses are performed by carrying out constant routines along transect routes, or within sampling plots scattered randomly over the total area (Bibby *et al.* 1992, Gilbert *et al.* 1998). A wide variety of statistical methods have been developed in order to control the uncertainty of the estimated population indices; biases in these indices are often due to missing observations within the series of counts from the sampling areas (ter Braak *et al.* 1994, Thomas 1996).

In the present study, we use nestling ringing data from 1951–2001 in order to index regional population trends for starlings in Finland. The data were structured according to sampling area (2-km grid squares) and year, in a manner resembling the structure of the ordinary census data collected in large-scale bird monitoring schemes (e.g. Bibby *et al.* 1992, Väisänen *et al.* 1998, van Strien *et al.* 2001). Population trends were estimated and tested using log-linear models (Pannekoek & van Strien 2003). Finnish starlings almost exclusively lay only one clutch per season. This improves the usefulness of the data in the trend analysis, as each brood represents a single pair.

The study seeks to test the relevance of ringing data for estimating long-term population trends within regions (i.e. southern, central, and northern Finland). In particular, we focus on what is to be done regarding missing observations (i.e. zero broods ringed) in a sampling unit. Note that these can be missing due to either (1) absence of ringers or (2) extinctions of local populations — or to both. Unfortunately these causal factors cannot be proved on the basis of the source data. If this problem is ignored in trend analyses, assuming no extinctions among local populations, the degree of population decline will be underestimated if extinctions have indeed occurred. Given these missing data points, and the probable extinctions of local populations (Orell & Ojanen 1980, Solonen *et al*. 1991, Rintala *et al*. 2003), how is it possible to achieve realistic indices of the population change?

The analytical procedures can be outlined as follows:

1. We detail a simulation procedure in which random samples are taken from an artificial population in order to explore biases in the index estimates (relative to true population indices).
2. Based on the estimated frequencies of locally extinct populations within simulation samples, we propose and apply a correction procedure that has been tested on the simulations. The correction procedure suggests a location and timing for the extinctions of local populations (i.e. no breeders present). The corrections are applied to minimise the expected bias.
3. We carry out statistical testing on the starling data to determine whether the starling population trends differ from the null hypotheses, i.e. “no differences in trends between regions” and “no temporal changes in trends within a region”.
4. In order to approximate the spatial distribution of starlings, we estimate a resource selection function (RSF) by quantifying the effect of environment covariates (the coverage of fields and the number of houses within and around breeding areas) on the site-selection of starlings.
5. Finally, we analyse whether the average locations of nests have changed regionally over recent decades.

In this study, which presents an approach to using nestling ringing data for monitoring purposes, we shall show that these data, using a brood as the basic unit of observation (rather than a nestling, in order to avoid biases emerging from brood size varying in time; *see* Solonen *et al*. 1991, Rintala *et al*. 2003), can be useful in the analysis of long-term regionally sub-divided nationwide data. We shall discuss the possibility that source–sink dynamics, involving surplus individuals emigrating from well-producing local populations (source) to poor-producing ones (sink), could have regulated the persistence of local and regional starling populations in Finland.

Material and methods

The ringing data

The ringing data come from the database and archives of the Ringing Centre of the Finnish Museum of Natural History. From the early years of ringing, including the 1950s, passerine birds have been commonly ringed as nestlings. During the 1950s and 1960s ringing activities increased rapidly, stabilising at around 50 000 ringed nestlings per year until the late 1960s (Rintala *et al.* 2003). All the original ringing reports by the ringers are stored in archives, and those from 1973 to the present have been digitised. We ourselves digitised all the annual nestling records of starlings from 1951–1972 and processed the data to a unit database, covering the years 1951–2001 (Fig. 1, *see* also Table 1 for a summary of observations). In 1951–1972, ringers registered the spatial information on the nests mainly by the names of communes and villages, and occasionally by farm names or street addresses. These we used to define the geographical coordinates (degrees and minutes) of each ringing site, referring to a collection of detailed maps. If we did not have more precise information than the name of the commune we used the coordinates of the centre of the commune; however, the proportion of those cases out of all nests was very low (only a few per mill).

In the data (1973–2001) delivered as a database by the Ringing Centre, the ringers had been told to mark the coordinates of the ringing locations. Initially, the degrees and minutes of geographical coordinates were used, but ringers were later advised to use the Finnish uniform coordinate system (100 m precision). Since the end of the 1970s there has been a rapid

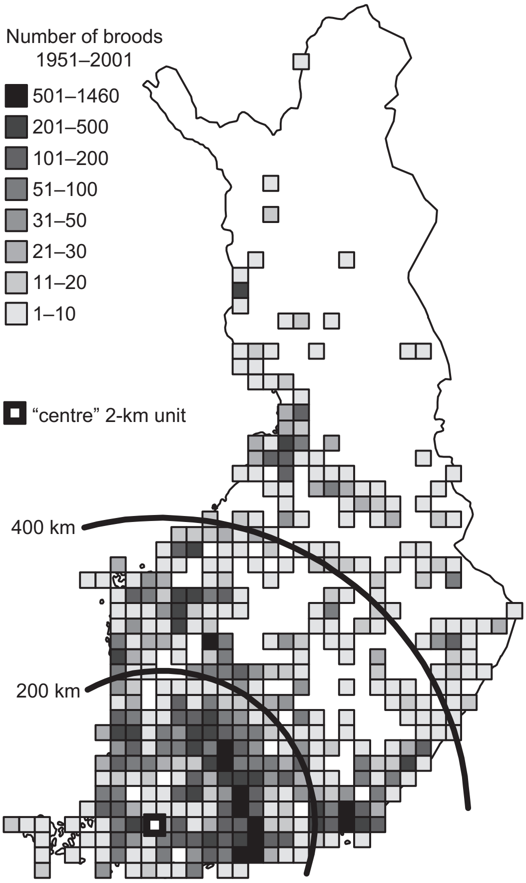

Fig. 1. Number of broods ringed in Finland within 20-km grid squares in 1951–2001. Regions were determined by distances from the "centre unit": south (0–200 km), central (200–400 km), and north (> 400 km). The total number of broods was 27 875. The southwest weighted location of the centre unit is relevant in terms of the general climate-based biogeographical zonation of Finland.

increase in the use of the high-precision recording system.

We projected the coordinates of the locations of all the nests according to the Finnish uniform coordinate system and rounded the locations to the centres of 1-km grid squares. For reasons given below, we calculated the total number of broods by 2-km squares and by year. The annual number of broods within the squares (the "count") was used as the basic unit of measurement of population changes.

We chose a 2-km square for the basic unit on the basis of the following assumptions: (1) within the chosen unit, one active ringer working alone is basically capable of ringing a large number of broods from the population available for ringing; this minimises the bias due to, for instance, a strong increase in the ringing effort on a regional scale (Fig. 2, *see* also Rintala *et al*. 2003); (2) the spatial unit is large enough to represent one or more local populations; (3) the spatial unit is large enough (with certain restrictions: *see* following paragraph) in relation to the precision used in locating the nests.

The indices of abundance change were derived using data from the two separate data sets, i.e. from 1951–1973 and 1973–2001. In both data sets, the indices for the year 1973 were set to unity, enabling inferences to be made on the population changes over the total period 1951–2001. We used the separate data sets because we assumed that not every series of counts calculated for 2-km squares for the total period 1951–2001 would always have related to the same breeding area: we had to take into

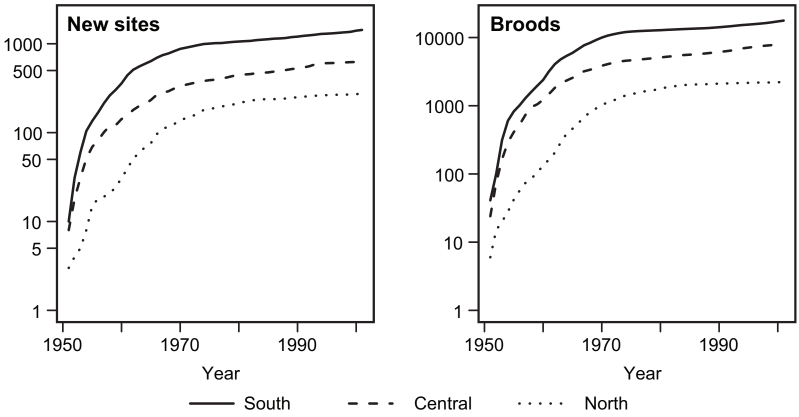

Fig. 2. Cumulative numbers of sites (2-km squares) and broods ringed in 1951–2001 from the southern, central, and northern regions (cf. Fig 1). Only the first occurrence of the ringing sites was summed annually. The total numbers of sites and broods were respectively: 1431 and 17 729 (South), 629 and 7920 (Central), and 274 and 2226 (North).

Table 1. Number of ringed starling broods in Finland within three regions (South, Central, North, as well as Total) in 1951–2001. Observations within the base units (2-km grid squares i.e. sites) are expressed as the annual averages (Mean) and standard deviations (SD). The numbers of sites (*N*) and the percentage of the sites containing ringed broods out of all sites (%) also shown. The numbers of sites for 1951–1973 (Set 1) were 963 (South), 372 (Central), 163 (North), 1498 (Total); the numbers for 1973–2001 (Set 2) were 719 (South), 336 (Central), 144 (North), 1199 (Total).

		South				Central				North				Total			
Set	Year	Mean	SD	*N*	%	Mean	SD	*N*	%	Mean	SD	*N*	%	Mean	SD	*N*	%
1	1951	4.1	3.4	10	1.0	3.0	1.8	8	2.2	2.0	1.0	3	1.8	3.4	2.7	21	1.4
1	1952	2.5	2.1	24	2.5	4.2	4.4	12	3.2	3.0	3.5	3	1.8	3.0	3.1	39	2.6
1	1953	5.5	6.9	39	4.0	5.0	8.4	18	4.8	2.5	2.1	2	1.2	5.2	7.2	59	3.9
1	1954	4.7	5.8	62	6.4	4.2	6.0	30	8.1	2.0	0.8	4	2.5	4.4	5.7	96	6.4
1	1955	3.7	3.7	61	6.3	4.0	4.9	30	8.1	2.0	1.0	7	4.3	3.6	4.0	98	6.5
1	1956	3.2	3.3	60	6.2	4.0	6.3	30	8.1	3.0	2.3	5	3.1	3.4	4.4	95	6.3
1	1957	3.3	3.5	84	8.7	5.0	6.8	41	11.0	4.3	4.7	4	2.5	3.9	4.9	129	8.6
1	1958	3.5	2.9	88	9.1	5.3	6.9	42	11.3	3.3	3.9	4	2.5	4.0	4.6	134	8.9
1	1959	4.1	4.8	89	9.2	4.2	3.0	22	5.9	3.0	2.9	5	3.1	4.0	4.4	116	7.7
1	1960	3.6	4.2	119	12.4	4.7	7.6	37	9.9	2.8	3.5	12	7.4	3.8	5.1	168	11.2
1	1961	4.5	5.7	177	18.4	6.1	7.7	43	11.6	2.5	2.3	10	6.1	4.7	6.1	230	15.4
1	1962	5.1	6.4	171	17.8	6.4	9.6	54	14.5	2.3	2.3	19	11.7	5.2	7.1	244	16.3
1	1963	4.7	6.0	152	15.8	5.0	7.4	57	15.3	3.7	3.2	23	14.1	4.7	6.2	232	15.5
1	1964	4.6	6.6	130	13.5	5.1	6.7	45	12.1	4.2	3.7	24	14.7	4.6	6.3	199	13.3
1	1965	4.1	5.1	138	14.3	4.4	7.3	50	13.4	3.7	3.2	19	11.7	4.1	5.6	207	13.8
1	1966	4.7	6.0	175	18.2	5.0	6.3	74	19.9	3.0	2.8	31	19.0	4.6	5.8	280	18.7
1	1967	4.9	6.5	190	19.7	4.7	4.5	57	15.3	4.2	4.0	33	20.2	4.8	5.9	280	18.7
1	1968	4.7	6.4	139	14.4	4.0	6.1	42	11.3	4.1	5.0	26	16.0	4.5	6.2	207	13.8
1	1969	4.7	6.0	177	18.4	4.0	6.2	59	15.9	3.7	3.5	31	19.0	4.4	5.8	267	17.8
1	1970	4.4	6.0	178	18.5	4.9	5.2	52	14.0	3.9	7.1	33	20.2	4.4	6.0	263	17.6
1	1971	4.7	5.3	147	15.3	4.1	5.0	52	14.0	3.7	3.5	18	11.0	4.5	5.1	217	14.5
1	1972	3.6	4.4	138	14.3	4.3	4.6	48	12.9	4.1	4.6	22	13.5	3.8	4.5	208	13.9
1	1973	4.1	3.9	114	11.8	4.1	4.3	40	10.8	4.5	5.7	22	13.5	4.1	4.2	176	11.7
2	1973	4.1	3.9	114	15.9	4.1	4.3	40	11.9	4.5	5.7	22	15.3	4.1	4.2	176	14.7
2	1974	3.9	4.0	98	13.6	3.8	4.0	32	9.5	3.6	3.6	31	21.5	3.8	3.9	161	13.4
2	1975	3.1	3.1	69	9.6	3.0	2.9	25	7.4	4.3	4.0	16	11.1	3.2	3.2	110	9.2
2	1976	2.5	2.0	65	9.0	3.0	3.2	27	8.0	2.8	2.1	21	14.6	2.7	2.4	113	9.4
2	1977	2.5	2.5	46	6.4	3.1	3.7	30	8.9	3.2	2.5	24	16.7	2.8	2.9	100	8.3
2	1978	2.0	1.9	55	7.6	2.8	2.6	35	10.4	2.0	1.5	23	16.0	2.2	2.1	113	9.4
2	1979	2.4	2.2	44	6.1	2.4	1.6	34	10.1	2.4	1.6	19	13.2	2.4	1.9	97	8.1
2	1980	2.3	2.0	42	5.8	3.0	2.3	37	11.0	3.0	3.7	26	18.1	2.7	2.6	105	8.8
2	1981	2.2	2.1	60	8.3	3.5	3.1	35	10.4	3.2	3.8	23	16.0	2.8	2.9	118	9.8
2	1982	2.4	2.1	53	7.4	2.8	2.1	35	10.4	2.6	4.4	22	15.3	2.5	2.7	110	9.2
2	1983	2.0	1.6	58	8.1	3.7	2.9	30	8.9	2.3	2.7	21	14.6	2.5	2.4	109	9.1
2	1984	2.3	2.2	53	7.4	4.3	4.2	26	7.7	2.5	3.8	19	13.2	2.9	3.2	98	8.2
2	1985	2.2	2.3	48	6.7	3.6	5.8	18	5.4	2.1	1.8	13	9.0	2.5	3.4	79	6.6
2	1986	2.6	2.5	42	5.8	3.4	4.3	27	8.0	1.4	0.7	10	6.9	2.7	3.1	79	6.6
2	1987	2.8	2.6	37	5.1	2.4	2.3	33	9.8	1.3	0.8	6	4.2	2.5	2.4	76	6.3
2	1988	2.5	2.3	46	6.4	4.2	6.1	26	7.7	1.8	1.0	4	2.8	3.1	4.0	76	6.3
2	1989	2.9	3.1	70	9.7	3.8	6.4	35	10.4	2.5	1.8	8	5.6	3.1	4.3	113	9.4
2	1990	3.4	3.4	63	8.8	4.6	8.0	31	9.2	2.0	1.6	10	6.9	3.6	5.1	104	8.7
2	1991	3.1	3.6	78	10.8	3.5	5.2	33	9.8	1.2	0.4	6	4.2	3.1	4.0	117	9.8
2	1992	3.0	2.9	81	11.3	3.3	4.6	51	15.2	2.3	2.1	6	4.2	3.1	3.6	138	11.5
2	1993	3.2	3.0	99	13.8	3.2	4.2	66	19.6	1.9	1.1	8	5.6	3.1	3.4	173	14.4
2	1994	2.9	3.0	99	13.8	3.7	4.8	79	23.5	1.2	0.4	5	3.5	3.2	3.9	183	15.3
2	1995	3.3	3.3	67	9.3	3.3	4.7	53	15.8	2.2	2.4	6	4.2	3.2	3.9	126	10.5
2	1996	3.3	3.8	77	10.7	4.6	5.4	40	11.9	3.0	1.6	4	2.8	3.7	4.3	121	10.1
2	1997	3.3	3.0	86	12.0	3.9	4.6	43	12.8	2.8	1.5	4	2.8	3.5	3.6	133	11.1
2	1998	3.0	2.5	101	14.0	3.9	4.9	37	11.0	1.0	–	1	0.7	3.2	3.3	139	11.6
2	1999	3.5	3.0	121	16.8	3.9	4.7	33	9.8	1.7	1.2	3	2.1	3.6	3.4	157	13.1
2	2000	3.0	3.0	165	22.9	3.3	4.5	27	8.0	2.5	3.2	6	4.2	3.0	3.2	198	16.5
2	2001	3.1	3.0	158	22.0	2.7	3.6	32	9.5	2.3	1.5	7	4.9	3.0	3.1	197	16.4

account changes in the registering practices for nest site locations starting from 1973 (*see* the beginning of this section). Moreover, five decades (about two human generations) is quite a long time to assume that voluntary ringing activities remained more or less unchanged — or to assume that such activities as a whole existed consistently at most of the sites; cf. assumption (1) above, *see* also Rintala *et al.* (2003). After all, it is possible that increased ringing activities especially during the 1950s might have underestimated population estimates for the first years of the study period (Fig. 2; *see* also Rintala *et al.* 2003).

Some of the ringers who were active in 1951–1973 did not document the number of broods they had ringed, but only the total number of nestlings. For those locations with missing brood numbers, the annual numbers of broods were estimated by dividing the total number of nestlings by the average brood size during 1951–1973 (about four nestlings per nest) and by rounding the quotient to the nearest integer. The annual estimated brood numbers diminished steadily during 1951–1973, from 27% to 1% of the annual total numbers of broods (the average annual percentage being 9%). There was some variation in the annual average brood size, but this caused at most a bias of less than one percent in the annual total number of broods.

The number of ringed broods can be assumed to express the number of breeding pairs within a unit because starlings only exceptionally lay second clutches (von Haartman 1969). The laying of second clutches could theoretically start in the second week of June. Nestlings from such nests would be at a ringing age after about 25 June. It was found that 1.6% of broods had been ringed after that date.

The spatial information in the ringing data was processed using MapInfo version 5.5. (MapInfo 1999a, 1999b).

Log-linear model for the estimation of annual indices

Indices of change in annual abundance and trend parameters (i.e. slopes) were estimated using the program TRIM (TRends and Indices for Monitoring data, version 3.30; Pannekoek & van Strien 2003). With TRIM, a variety of log-linear models (i.e. Poisson regression; also a class of generalised linear models, GLMs) can be applied to the analyses of the series of counts. The data in question usually consist of counts from several census routes or plots, and they may contain a substantial number of incomplete series (ter Braak *et al.* 1994, Thomas 1996, Gilbert *et al.* 1998, van Strien *et al.* 2001). The index series estimated may consist of one linear trend affected by a constant slope, or several sequential trends, which change at certain years. The particular years when changes in the estimated sequential trends occur are called *change points* (Pannekoek & van Strien 2003).

The trend parameters that control possible changes in index trends were tested, and those that were not significant were rejected by a stepwise elimination procedure. One covariate was included within the models in order to compare population trends in the southern, central, and northern regions (*see* Fig. 1 for the regional division). The null hypothesis assumes a zero effect for all slope and covariate parameters. A Wald test was used to test the significance of (groups of) parameters. Over-dispersion and a serial correlation of counts were estimated, and their effect on the standard errors of slopes and indices was taken into account (Pannekoek & Strien 2003).

Comparisons of all the annual indices over the three geographical regions were performed using the *t*-test. Both data sets (periods 1951–1973 and 1973–2001) were analysed separately with unchanged modelling options, but with repeatedly changed base-years, making it possible to test the deviation of annual indices from every possible base-year index (set to unity). The significance of a covariate at each change-point was tested by means of the *t*-statistics. The value of *t* was calculated as the difference between two slopes divided by their common standard error.

Dealing with the missing data problem

Nestling ringing data have not primarily been collected for the purpose of monitoring changes in population size. Thus, caution is needed in interpreting indices of change based on such data. An important source of bias is confusion between local extinctions (zero counts), and an absence of local ringing activities. Both of these are indicated similarly in the source data (missing counts), since measurements of ringing activities are not available for the huge number of local populations (Rintala *et al*. 2003). A great many populations went extinct during the study period, especially in northern Finland (Ojanen *et al*. 1978, Orell & Ojanen 1980, Solonen *et al*. 1991). These populations are included in our data, but probably a good many other populations disappeared as well. Estimates for the magnitude of population changes will be underestimated if zero counts are not considered in estimations.

Our aim was to arrive at a site/time-specific correction method for the missing counts. A log-linear structure was estimated for the missing counts, and for the cases with very small estimates (smaller than unity) a zero count was adopted using certain criteria (*see* section "Missing *vs*. zero counts" below). A quantitative simulation approach was constructed to imitate a ringing process over a 24-year period. Within the model population, local populations diminished and became extinct with increasing intensity towards northern Finland (*see* overall decline and range contraction, Thomas 1996). Using a Monte Carlo simulation (Manly 1997), 200 independent ringing data sets were generated. Each replicate data set was explored consecutively in order to structure and test the method for the positioning of local extinctions in the model population.

Model population

A resource selection function (RSF) based on the logistic regression (Manly *et al*. 2002, Keating & Cherry 2004) was estimated in order to index the probability that starlings would breed in a particular habitat unit (2-km square). Primarily, the analysis was carried out to initiate a model population structure. The secondary objective was to explore the site-selection preferences of starlings — "secondary" because we did not have sufficient environmental data for a thorough analysis.

Ideally, RSFs are proportional to the probability that an area will be used by a particular species (Boyce & McDonald 1999). Assuming that ringers were not able to explore every possible unit within their ringing area, an unknown number of "hidden" used units (unrecorded nesting of starlings) may have been included in the unused sample (cf. Keating & Cherry 2004). This may have detracted from the usefulness of an RSF in respect of its proportionality to the true probability of habitat use (Manly *et al*. 2002, Keating & Cherry 2004). A spatial autocorrelation in the occurrences of broods between neighbouring spatial units (due for instance to ringers' behaviour or to the spatial dependencies of local starling populations) was not considered in the estimation of the RSF. For our purposes, an ordinary logistic regression provided an adequate method for the estimation of the large-scale characteristics of distribution (*see* Augustin *et al*. 1996).

The breeding of starlings within 2-km squares was recorded on the basis of the ringing of nestlings in 1951–1975, covering the years when the population was relatively abundant (Rintala *et al*. 2003). Thus, we assumed that starlings consistently accepted those sites for breeding in which nestlings were ringed at least once (up to 1975, during the sample period 1951–1975). The availability of habitat units was restricted to 20-km grid squares containing one or more ringing records. In the sampling design (Fig. 3), breeding units that were first chosen by starlings and then by ringers were labelled as "used" units; the remaining available units were labelled as "unused" units. Environmental variables were extracted from existing databases for each available unit over the entire country.

Habitat units were given a value according to the coverage of fields and to the number of houses. A map of arable fields (Anonymous 1982) was scanned and processed to a raster image corresponding to the Finnish uniform coordinate system. The correspondence of the raster image (a map picture that consists of equally sized squared units or "pixels" labelled according to land characteristics) to the original map was optimised by a resample routine based on several control points of known coordinates within the raster image. Every pixel (0.2-km square) was regarded as a patch of field or as "other" habitat. The proportions of field area were finally calculated for 2-km squares (cor-

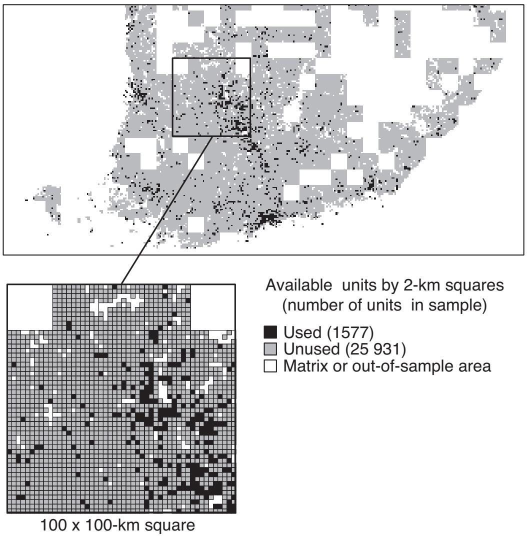

Fig. 3. Sampling design for the RSF, exemplified with data from the southern part of Finland. Available units were sampled on the basis of 20-km grid squares containing ringed broods (used units).

responding to habitat units) in which a 0.2-km pixel of the patch of the field was regarded as a unit percentage of arable land. The computer program Idrisi version 4.0 (Idrisi 1992a, 1992b) was used in the processing of the raster image.

The number of houses (database from Statistics Finland) was pooled for the 2-km squares, based on an age classification as follows: (1) old (built before 1941), (2) middle-aged (built during 1941–1960), and (3) new (built during 1961–1970). The classification was made to allow for the possibility that the age of houses could have an effect on the site selection of starlings, for instance, via differences in the management of farmlands and via varying numbers of nest-boxes set in the vicinity of houses of different ages.

To measure the average habitat structure surrounding breeding localities, the above environmental measures were averaged on the basis of all the squares (including also matrix squares lacking fields and houses) within 1–3, 3–10, and 10–50-km buffer zones around a core unit containing fields and/or housing. As regards those areas outside the Finnish land area, only sea areas were included within the matrix. In the 3–10 and 10–50-km buffer zones, the age of the houses was not considered within the analysis. The inner buffer zone consisted of eight 2-km squares, around the core-square. All the environmental variables were used as continuous variables in the logistic regression. The changes in the probability that a habitat unit would be used $P(y = 1)$ or not used $P(y = 0)$ in respect of changes in a particular variable x was measured with odds ratios (e.g. Keating & Cherry 2004), as follows:

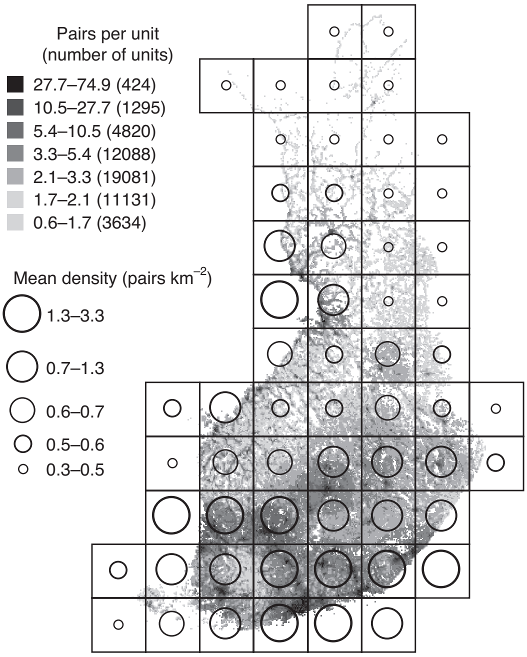

Fig. 4. Numbers of breeding starlings in Finland, as estimated with the RSF. The base habitat-unit is a 2-km grid square. Mean densities (pairs km^{-2}) are given for the habitat units (matrix excluded) within 100-km grid squares.

$$\exp(b) = \left[\frac{P(y=1 \mid x+1)}{P(y=0 \mid x+1)}\right] \Bigg/ \left[\frac{P(y=1 \mid x)}{P(y=0 \mid x)}\right],$$

where b is the coefficient for the variable x. When continuous x variables are scaled to a mean of zero and unit variance, their odds ratios measure a (multiplicative) effect size produced by a variable within an RSF. The spatial structuring and statistical analyses of the RSF data were performed with MapInfo (MapInfo 1999a, 1999b) and statistical package R (R Development Core Team 2005).

The spatial distribution of the initial model population (Fig. 4) was extrapolated with an RSF of the form:

$$w(\mathbf{x}) = \frac{\exp\left(\mathbf{x}\hat{\boldsymbol{B}}\right)}{1+\exp\left(\mathbf{x}\hat{\boldsymbol{B}}\right)} b, \qquad (1)$$

where the matrix $\mathbf{x}$ $[x_{i1}, x_{i2}, \ldots, x_{ip}]$ contains p environment variables and their values for all available breeding units i in Finland. The vector $\hat{\boldsymbol{B}}$ $\left(\hat{\beta}_1, \hat{\beta}_2, \ldots, \hat{\beta}_p\right)$ contains parameter estimates from the logistic regression. The scaling factor b was adjusted so that $\sum_i w_i = 200\,000$ (the maximum record for breeding pairs; Väisänen *et al.* 1998).

The "decline factor" (Y) of the initial population (Eq. 1) was based on the logistic equation:

$$Y_i = \frac{Y_{\max} - Y_{\min}}{1+\left(d_i / d_0\right)^p} + Y_{\min}, \qquad (2)$$

where d_i = the distance (km) of a unit i from the "centre unit" in southern Finland (Fig. 1), d_0 = 320 (the midpoint of the range in Y), $Y_{\max}$ = 0.96 (the maximum in Y), $Y_{\min}$ = 0.8 (the minimum in Y), and p = 6 (the steepness of the change in Y). The number of pairs in each site i over the entire country and all years j (w_{ij}) was calculated with the equation:

$$w_{ij} = w_{i,j=0} Y_i^j, \qquad (3)$$

giving the annual (j = 0 … 24) size of local populations by the site-specific multiplicative trend factor Y_i (Eq. 2). Note that $w_{i,j=0}$ is defined by the RSF (Eq. 1).

Site/time-specific counts for breeding pairs in the total model population ($M_{(\mathrm{TOT})ij}$) were randomised according to the Poisson distribution, expecting the values of w_{ij} for the average of counts:

$$M_{(\mathrm{TOT})ij} = \mathrm{Poisson}(w_{ij}). \qquad (4)$$

In the "total model population" constructed (Eqs. 1–4), the declines in the local populations were deeper and more rapid the farther apart (towards the north) the breeding sites were located from the southern "centre area". A major proportion of this artificial population was located in the southern breeding sites, with annually increasing proportions. Thus, in the initial population, 90% of pairs were within about 500 km from the centre area, whereas after a 24-year simulation run, 90% of the population was distributed no further than about 250 km from the centre. Over the same period, the total number of breeding pairs declined by about 80% from the initial level (Fig. 5). As we were not able to base the estimation of the parameters in Eq. 2 on proper data, they were assumed on the basis of what is known from a few local populations and from national patterns (Ojanen *et al.* 1978, Orell & Ojanen 1980, Solonen *et al.* 1991, Väisänen *et al.* 1998, Rintala *et al.* 2003).

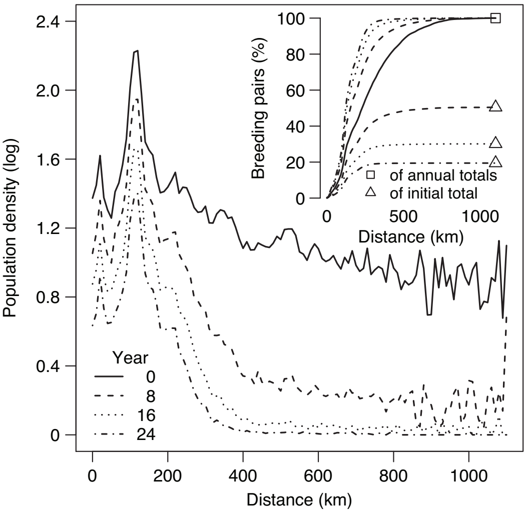

Fig. 5. Average densities (log[pairs + 1] per 2-km grid square) of the model population calculated according to 10-km wide buffer zones around the "centre unit" located in southern Finland. The densities take into account only those areas (i.e. squares) containing possible breeding environments, fields and/or settled areas. Lines correspond to four different years sampled from the total data. In the insert graph, the spatial distribution of breeding pairs is plotted as a cumulative percentage against the increasing distance from the south. Percentages for the population in years 0, 8, 16, and 24 are the proportions of the total initial population (in year 0) and of the corresponding annual totals.

Procedures constructed on the basis of the model population data

In order to test the reliability of the estimated indices, we constructed a simulation set-up imitating starling population dynamics (Eqs. 1–3) and the ringing of broods. The simulation was for the period 1973–1997, which included the decline of starlings. The concept "actual population of starlings" $A_{i,j = 0 \ldots 24}$ is assumed to cover approximately 2000 sites that we know to be a representative sample for measuring total population change (*see* Table 2 for the summary and explanation of the terms used in this section). These sites represent the potential breeding areas (for starlings) in which bird ringers, more or less actively, have been ringing starlings and/or other birds (*see* also Fig. 2). Due to a lack of ringing activities *vis a vis* starlings and/or to rapid disappearances of local starling populations at some of the sites, not all of the potential sites have ended up among the final "actual ringing data" a_{ij} tested here. Thus, the number of ringing sites consisted of "only" those 1050 sites that were sampled at least once during the period 1973–1997.

Random (ringing) samples of broods were taken from a representative population fraction M_{ij} ("Model population", Table 2), consisting of 2000 randomly chosen sites from the total model population (Eq. 4 and Fig. 4). In order to see how representative M_{ij} is of the total population $M_{(\mathrm{TOT})ij}$, the confidence limits of the model population change-index I_M were estimated on the basis of 1000 random samples (random combinations of sites) $M_{ij(\mathrm{SAMPLE} = 1 \ldots 1000)}$ from $M_{(\mathrm{TOT})ij}$. The number of sites in each random sample was 1184 (the number of particular sites, within $M_{(\mathrm{TOT})ij}$, in which starlings actually had been ringed from 1973 onwards).

Random data files were automatically arranged and written out, using a macro language for a spreadsheet (Visual Basic 6.0©, 1987–1999 Microsoft Corp.), in a format acceptable for the TRIM program. R (R Development Core Team 2005) and @Risk (1997) were used for random sampling and organisation of the data. TRIM command files (Pannekoek & Strien 2003) were used in order to automate the successive analyses of randomised data sets.

Random sampling

Two hundred randomised samples m_{ij} were generated from M_{ij} to estimate the precision with which output indices I_m (Table 2) are estimated. Each replicate of m_{ij} was derived with the equation:

$$m_{ij} = \mathrm{PRESENT}_{ij} \times \text{binomial}\ (n = 1, p = 0.5)_{ij} \times \text{binomial}\ (n_{ij} = M_{ij}, p = 0.39)_{ij}, \qquad (5)$$

where the binomial $(n,p)_{ij}$ calls a binomial random

Table 2. Explanations and relationships of symbols referred to in the estimation of indices for the model population and the actual starling population. REP denotes the ordinal (1 … 200) of replicated data sets in a simulation procedure. Note that the model population M_{ij} is a random sample of 2000 sites out of the total model population $M_{(\mathrm{TOT})ij}$ (cf. Fig. 4). Indices are estimated for three regions out of the total area, which is not considered in the notation.

Population		Sample (ringing data)
Model population $M_{i,j = 0 \ldots 24}$ ↓ True index series for time points j $I_{M(j = 0 \ldots 24)}$	→	Broods "ringed" from model population: $m_{ij\mathrm{REP}}$ ↓ Estimated primary (uncorrected) index series I_m — biased estimate of I_M ↓ Correction: $m_{\mathrm{REP}} \rightarrow m'_{\mathrm{REP}} \rightarrow I_{m'\mathrm{REP}}$ ↓ Mean $(I_{m'\mathrm{REP}}) = \bar{I}_{m'} = \hat{I}_M$ — estimate of I_M
Actual population of starlings $A_{i,j = 0 \ldots 24}$ ↓ True index series I_A to be estimated	→	Broods ringed from actual population: a_{ij} ↓ Estimated primary (uncorrected) index series I_a — biased estimate of I_A ↓ Correction: $a_{ij} \rightarrow a'_{ij} \rightarrow I_{a'}$ — better estimate of I_A

number such that the average of the generated values (0 … n) converges to $n \times p$. PRESENT$_{ij}$ (*see* Table 3 for the key to the parameter) denotes a period (a collection of successive years) for the possibility of the ringing of starlings (PRESENT$_{ij}$ = 1) or not (PRESENT$_{ij}$ = 0) at site i. The first binomial function (with $n = 1$) realises the probability of whether a ringer present at site i will ring starlings (function value = 1) or not (function value = 0). According to the model, in half of the cases ringers seek out starling nests for ringing. The second binomial function (with $n_{ij} = M_{ij}$) determines how many broods out of all available broods are ringed at site i and year j, in the case when there are ringing efforts in respect of starlings. The expected proportion of ringed broods ($p = 0.39$) was calculated as follows:

$$p = \Sigma_{i \in \text{ringing sites}} \mu_{i,j = 1973} / \Sigma_{i \in \text{ringing sites}} w_i,$$

i.e. the sums of estimates for the unit year (i.e. 1973) based on a log-linear model ($\mu_{ij = 1973}$) and the RSF (w_i, Eq. 1), respectively, summed over the sites (number of sites = 1184) containing ringed starlings in any year during the period 1973–2001. As an explanation, p approximates the average fraction of ringed broods from the total number of broods in the case of the ringing of starlings at any site-by-time combination within the data. In the first binomial function (Eq. 5), $p = 0.5$ was set to a midway value as we did not have data for the estimation basis.

In the real world, on the basis of the ringing data for starlings, the time span from the first year to the last year of the ringing of starlings at site i must, on average, be shorter than the duration from the first to the last year of ringing activity within a site, since "no starlings ringed" at a given site does not exclude the aim of ringing birds — but starling nestlings just were not found or sought for ringing. For this reason, the frequency distribution of period-length values (PERIOD$_i$; Table 3 and Fig. 6) was assumed on the basis of an arbitrary exponential function generating lesser right-skewed distribution than was measured directly from the actual ringing data (Fig. 6). When random ringing data m_{ij} were generated (with Eq. 5) and period lengths were calculated from the data sets, it appeared that, on average, the measures matched quite well with those in the actual ringing data (Fig. 6).

Missing *vs.* zero counts

The database does not distinguish between the cases of *no count made* and *no starlings ringed*. In the ringing data, zero counts (i.e. the non-existence of a breeding population at a particular location and year) were not verifiable, due to a lack of knowledge of the variations in local ringing efforts. Therefore, "no starlings ringed" was primarily registered as a missing count.

The correction procedure for indices I_a was

Table 3. Explanations of parameters used in the context of Eq. 5.

Parameter and equation	Explanation
PRESENT$_{ij}$ = 1 | if $j \geq j_{(\text{start})i}$ and $j < (j_{(\text{start})i}$ + PERIOD$_i$) else PRESENT$_{ij}$ = 0	A parameter denoting the succesive years (one period per site) when the bird ringer/ringers is/are present (unity) or not (zero) at site i; $j = 0 \dots 24$.
PERIOD$_i$ = discrete {1 … 25}{$p_1 \dots p_{25}$}	An integer, of a range 1 ... 25, denoting the period length (number of years) of the possibility for ringing at site i; p_{PERIOD} denotes the expected probability (by discrete random distribution) of choosing a certain PERIOD (*see* Fig. 6).
$j_{(\text{start})i}$ = discrete uniform {0 … (25 – PERIOD$_i$)}	An integer of range 0 … 24, denoting the year when ringing could start at site i; the value of the randomly chosen (by discrete uniform distribution) integer depends on the variable PERIOD$_i$ (for instance: if PERIOD = 1, all $j = 0 \dots 24$ would be possible; if PERIOD = 25, only $j = 0$ would be possible).

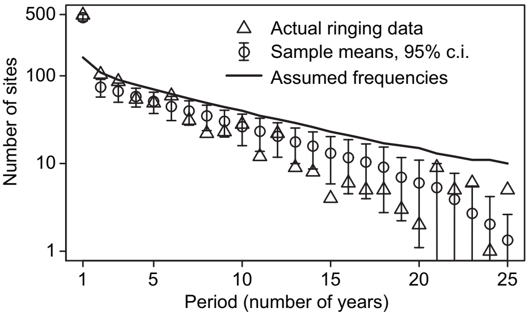

Fig. 6. Number of sites plotted against Period from the first to the last year of ringing within sites. Means of samples (± 2 SD, c.i. minima below 1 not shown) were calculated on 200 simulated ringing data sets $m_{ij\mathrm{REP}=1\ldots200}$ (Table 2). Corresponding frequencies were calculated for the Actual ringing data a_{ij} from 1973–1997. The values for the Assumed frequencies form the basis for the expected proportions p_{PERIOD} of PERIOD_i values (Table 3).

calibrated on the basis of replicate samples $m_{ij\mathrm{REP}=1\ldots200}$ (Eq. 5 and Table 2). Log-linear estimates μ_{ij} for each sample m_{ij} were used as the probability estimators for zero counts. The probabilities of a ringing effort (directed at starlings), were approximated with the function:

$$P_{(\mathrm{EFFORT})ij} = \frac{\sum_i m_{ij}}{\sum_i \mathrm{IMPUTED}_{ij} \,\Big|\, \text{if } \mathrm{IMPUTED}_{ij} \geq 1, \text{ else not summed}}. \quad (6)$$

Imputed counts (Pannekoek & van Strien 2003) $\mathrm{IMPUTED}_{ij}$ consist of observed counts and estimated counts μ_{ij} (with a log-linear model) that replace missing counts. Summations in the numerator denote the annual totals from the population available for ringing. In the denominator, annual imputed counts are summed only if they are greater than or equal to a unity. This ought to eliminate cases where "no starlings ringed" would be due to non-existent or very sparse local populations, and it should better focus on the effect of ringing activities on the probability of ringing effort $P_{(\mathrm{EFFORT})ij}$. For a unit data set, the estimated probabilities change only by years j; i.e. within year j, the probabilities are the same for each site i.

Poisson-distributed random counts averaging close to zero (expected mean $\lambda = 0.01$) were inserted into corrected ringing data m'_{ij} (Table 2) if (1) a count was missing (in m_{ij}), (2) the estimated count μ_{ij} was smaller than one, and (3) a uniform random number between 0 and 1 was smaller than or equal to the probability of ringing effort $P_{(\mathrm{EFFORT})ij}$ (Eq. 6) — otherwise, original values of m_{ij} were retained in m'_{ij}. It was assumed that the correction of indices based on simulations could be generalised to attain better estimates for the true starling population as well (Table 2). The procedure was not sensitive to the expected average (λ) of the Poisson counts. On the basis of starling data, indices were almost identical with $\lambda = 0.001$ and $\lambda = 0.01$; but $\lambda = 0.1$ resulted in smaller declines. Our idea was that the inserted count should most often be zero, acknowledging the Poisson-distributed nature of the data.

The variation in the change indices calculated on the simulation data sets increased with the decrease in the statistical significance of change-points within the log-linear model. In order to avoid the far from significant changes in index trends estimated for both m_{ij} and m'_{ij}, only those change-points were retained that had a significance level of $P \leq 0.15$ (Wald test).

For each random data set, changes in a covariate (region effect) and in the change-points of trends (time effects) were allowed for every fourth year in the initial models. We kept the covariate in the models even if it was not significant (as was the case in most of the data sets). Removal of the covariate would have diminished the error variation of the indices, especially in the northernmost region.

The effects of dispersion and serial correlation (Pannekoek & van Strien 2003) were not considered in the analyses of randomised data sets, since the model population dynamics consisted of only trend and Poisson-distributed random effects (Eqs. 3 and 4).

Total change in the starling population

Regionally varying ringing efforts and (presumably) geographically divergent population trends could cause a bias in the total population estimate. The possible bias was compensated by region-specific weight factors (cf. the offset in GLM, Pannekoek & van Strien 2003). Assuming that the RSF would give a relevant estimate of the abundance distribution of breeding starlings, estimates for the site-specific numbers of broods in 1973 $\mu_{ij=1973}$ from the log-linear model were multiplied, such that their regional mean corresponded to the average of RSF estimates ($M_{(\mathrm{TOT})i,j=0}$, Eqs. 3 and 4) in the respective regions; then further multiplied such that the effect of regionally divergent sampling ratios (numbers of sites sampled out of all available sites) was compensated by weight factors. Thus, we had six different weights (2 data sets × 3 regions).

Consider as an example the southern region and the data set 1973–2001: the weight was derived as 13972/719 × 5.939/3.933 = 29.34, where the first division corresponds to the total number of sites within the region, divided by the number of sites in the corresponding sample, and the second division to the average of the initial counts within the total region divided by the average of initial estimated counts in the corresponding sample. In the data set for 1951–1973 the weights relative to the southern region were 2.81-fold for the central region and 2.29-fold for the northern region. In the data set for 1973–2001 the corresponding weights were 0.78-fold and 0.77-fold.

Changes in the geographical gravity of ringing locations

The centres of gravity (Perdeck 1977) of the annual positions of ringing locations (average of mid-points of 2-km squares) were measured to explore if there had been a consistent regional drift in localities in 1951–2001. Clearly, most of the variation in the annual centres of gravity was due to variation in the south–north dimension, which allowed us to inspect the shifts based on north coordinates alone. Randomisation tests, i.e. bootstrap samples (Manly 1997, R Development Core Team 2005), were used in the statistical testing of the changes observed in the gravity centres.

Results

Model population

Indices based on randomly chosen sites from the total model population $M_{(\mathrm{TOT})ij}$ did not show any apparent variation with respect to the true indices, as calculated for all possible sites within each region (Fig. 7, analogous to regions in Fig. 1). Ninety-five percent of the annual change indices based on random samples showed no inaccuracy exceeding about ± 5% (i.e. ± 0.05 index units, *see* confidence limits in Fig. 7) of the initial population size in the regions in question. Indices that were calculated on the basis of a sample corresponding to the actual ringing sites remained within the 95% confidence intervals, except for a small excess in the central region in the latter half of the simulation period (Fig. 7). Indices based on a single random sample, i.e. the base population (M_{ij}, Table 2) for ringing simulations, did not exceed the confidence limits at all (Fig. 7).

On average, index series based on log-linear models on corrected data replicates were upward-biased (approximately 0.05–0.25 index units) until they converged with the total population indices, at the same time as regional populations declined to about one tenth of the initial levels (Fig. 7). Indices based on uncorrected data replicates were roughly upward-biased, in such a way that the bias increased towards the north and towards the end of the simulation period. Surprisingly, the uncorrected series, on average, declined even less in the northern region than in the other regions (Fig. 7).

The annual confidence bars calculated on 200 corrected series covered approximately 0.02–0.6 index units (lower index subtracted from the upper one, Fig. 7), being at their narrowest in the northern region during the latest years of the simulation realisation and at their widest (± 0.3 index units) in the same region in the fourth year (Fig. 7). Otherwise, the 95% confidence intervals usually converged less than ± 0.2 index units (i.e. ± 20% of the initial population size). The tapering of confidence intervals towards the north and towards the end of the period was due to a similar pattern of correction frequency, i.e. the changing of missing counts (or true zeros) to zeros (*see* Fig. 5 for the model population structure). The corrected series indicated relatively good precision for the low indices, especially in the northern region. In the corresponding uncorrected series, the confidence limits for the northern region consistently widened as a function of time (Fig. 7).

The estimated confidence limits (from log-

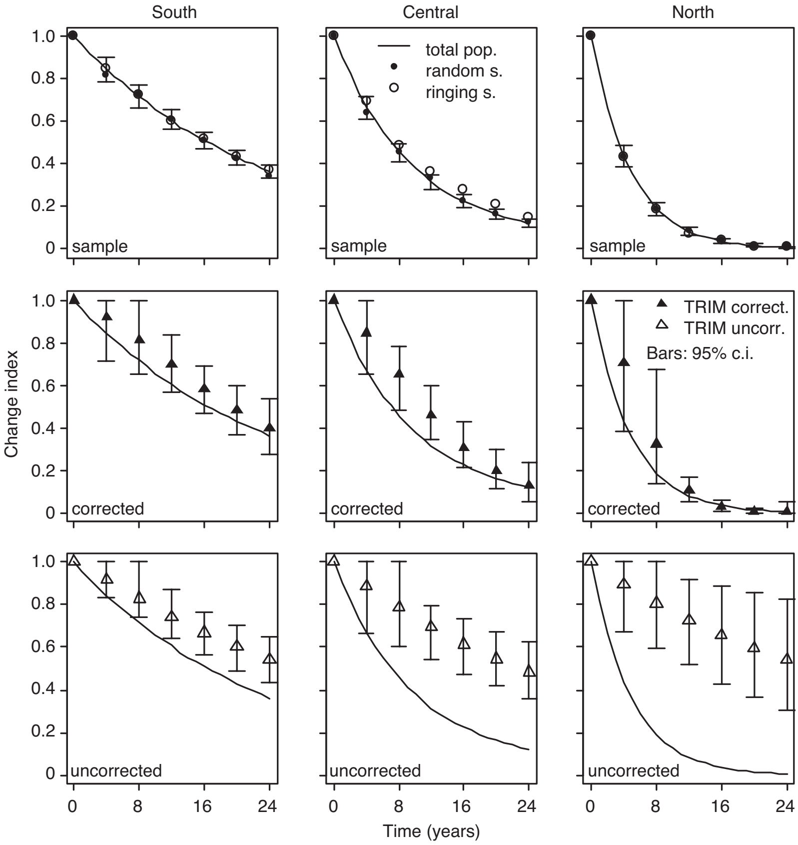

Fig. 7. Indices of regional population decline (South, Central and North; cf. Fig. 1) simulated over 24 years. Estimates of the total population change are shown for every fourth year. 95% confidence intervals were derived from 1000 random samples (the number of sites, *N* = 1184 in each sample) out of the total population (*N* = 52 473). Index series were also calculated for a single random sample (*N* = 2000; M_{ij}, *see* Table 2) and for a sample based on actual ringing sites (*N* = 1184) out of the total model population. The average corrected and uncorrected indices with 95% confidence intervals are based on 200 randomly realised data sets (*see* methods); these were indexed on the basis of log-linear models (TRIM, Pannekoek & van Strien 2003). Ideally, annual change indices vary exactly in proportion to the total population size for that year, as is the case in the total model-population indices.

linear models) of indices were more relevant when based on corrected data replicates than when calculated on the basis of the corresponding uncorrected ones (Fig. 8). This emerged from relatively consistent estimates based on the corrected series, especially at the end of the simulation period (small variation between replicate data sets). On average, the corrected confidence estimates (Fig. 8) were also good approximations for the simulation-based confidence limits (Fig. 7).

Starling population

Population trends were analysed on the basis of all the nestling ringing data from 1951–2001 totalling 27 875 broods. The total number of sites (2-km squares) was 1468 for 1951–1973, and 1199 for 1973–2001 (cf. Table 1, Figs. 1 and 2).

Corrected *vs.* uncorrected indices

The annual proportions of inserted zero counts were maximally 7%, 11% and 17% of all sites within the southern, central, and northern regions, respectively, in the data set 1973–2001 (Fig. 9).

The correction of ringing data by manipulating missing counts had a greater effect on

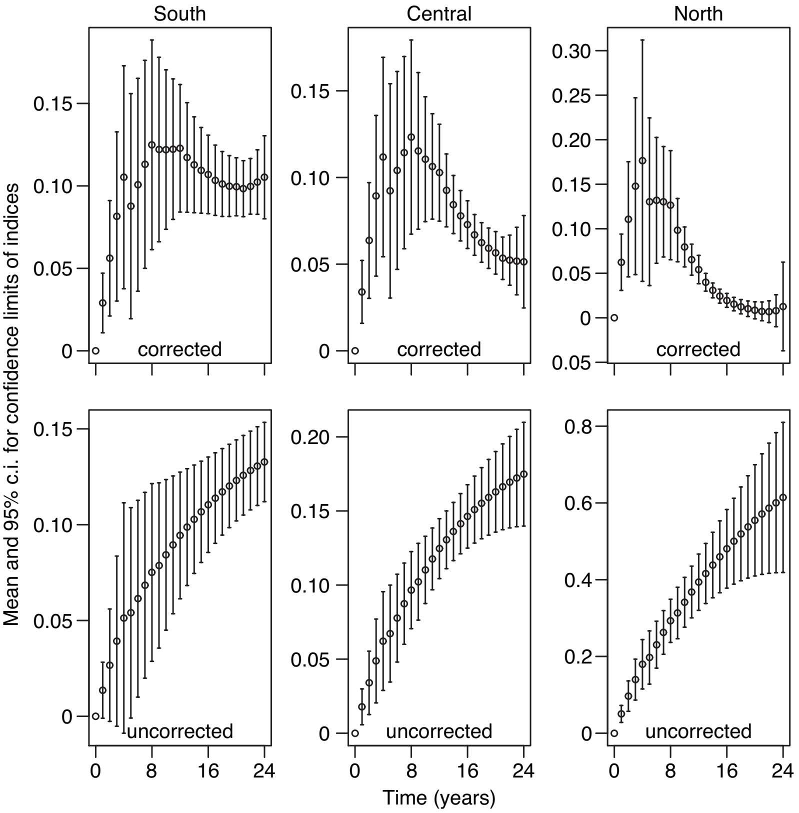

Fig. 8. Mean and 95% confidence intervals (by *t* distribution) calculated for confidence limits of indices (1.96 times SE of annual index, i.e. 95% limit) on the basis of 200 random data sets from three regions (South, Central and North) analysed with log-linear models. Estimates refer to deviations (± index-units) from the annual average-indices in Fig. 7. Results are shown for corrected and uncorrected data sets.

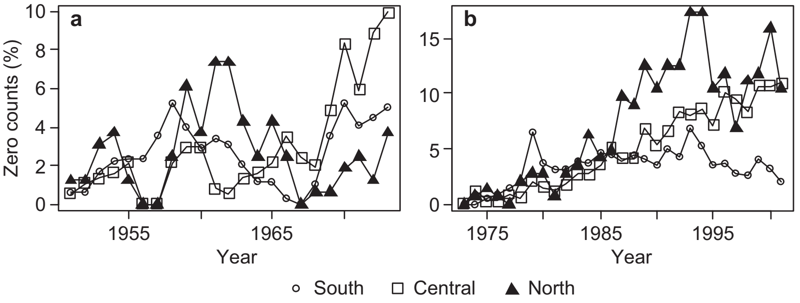

Fig. 9. Annual proportions (%) of sites whose missing value was replaced with a zero count out of all sites within a region. (**a**) The total numbers of sites were 963 (South), 372 (Central), and 163 (North) in the data set for the period 1951–1973, and (**b**) 719 (South), 336 (Central), and 144 (North) in the data set for 1973–2001.

the 1973–2001 data set than on the 1951–1973 one. It mainly affected indices in the central and northern regions, with a northwardly increasing correction power (Fig. 10). For instance, the correction of the indices for year 2001 was 0.17 index units downwards in the central region and 0.19 index units downwards in the northern region. In the northern region, the confidence belts were much narrower in the corrected data than in the uncorrected data from the mid-1990s onwards. Most of the unreasonably low confidence limits (below zero in the north) found from the uncorrected data were improved to a level above zero by the correction procedure.

Main trends

Up until 1987, the estimated total population (Fig. 11) declined by 78% in comparison with

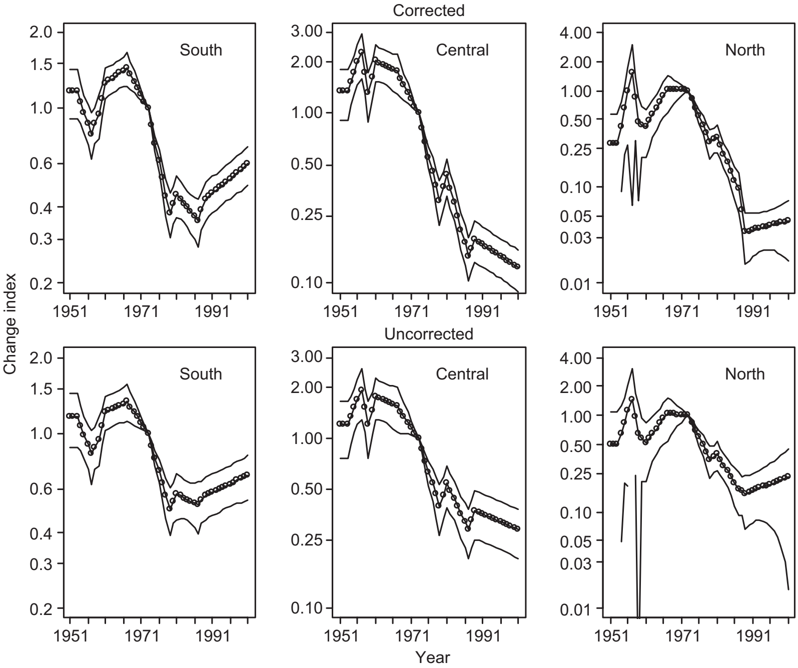

Fig. 10. Index series with 95% confidence belts estimated on the basis of log-linear models for regional starling populations (South, Central, and North; cf. Table 5) for 1951–2001. Each time-series consists of two data sets (1951–1973 and 1973–2001, the base-year is 1973; *see* methods). Calculations were based on corrected and uncorrected data sets (cf. Fig. 7). Unreasonable negative lower confidence limits of indices (a consequence of insufficient data for certain years) were not drawn because of the logarithmic scale.

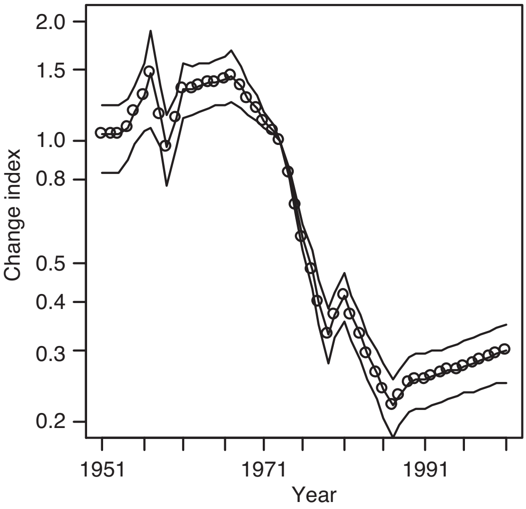

Fig. 11. Index series with 95% confidence belt estimated for the total starling population on the basis of log-linear models on two data sets (1951–1973 and 1973–2001, the base-year is 1973). Indices were derived from the corrected data (cf. Fig. 10) using regional weight factors in the calculus (*see* methods).

1973, and by 82% in comparison with the average index for 1951–1972. Up until 2001, the indices increased by 37% from 1987, converging to 30% of the index for 1973, and 24% of the average level for 1951–1972. The total population indices (Fig. 11) mostly resemble, or are weighted by, the southern population indices (Fig. 10, corrected), because most of the breeders come from the south.

During 1973–2001, the estimated change indices declined maximally by 64% (southern region), 88% (central region) and 97% (northern region). When the lowest indices in 1973–2001 were compared with the average indices for 1951–1972, the declines in the respective regions were 69%, 93%, and 95%. However, a substantial increase (67%) was estimated for the southern region for 1987–2001; in this region the indices ended up at 59% of the index in 1973, and 51% of the average index for 1951–1972 (cf. Fig. 10).

Table 4. Estimated dispersion parameter (σ), serial correlation (ϱ), and goodness-of-fit statistics from the log-linear models used for the estimation of indices (LR = likelihood ratio, df = degrees of freedom, *P* = statistical significance of uncorrected and corrected starling data sets from two time periods.

Data set	σ	ϱ	χ^2	LR	$P(\chi^2)$	P(LR)	df
$1951–1973_{\text{UNCORRECTED}}$	2.89	0.16	7092	7208	< 0.001	< 0.001	2452
$1951–1973_{\text{CORRECTED}}$	2.33	0.17	7888	8066	< 0.001	< 0.001	3383
$1973–2001_{\text{UNCORRECTED}}$	1.03	0.18	2488	2678	0.117	< 0.001	2405
$1973–2001_{\text{CORRECTED}}$	0.91	0.22	3566	3894	1.000	0.553	3906

Statistical comparisons of index trends

The correction improved the precision of the index estimates by reducing standard errors (cf. explanation above for Fig. 8), and for this reason, the corrected data were used as the basis for statistical tests. The model for 1973–2001 explained variations in the observed data better than the model for 1951–1973, owing to the relatively high probabilities of goodness-of-fit tests (notably by the χ^2 statistics, Table 4). However, goodness-of-fit tests would not have provided an exact means for testing the parameters in the models, due to the probable dependency of sequential counts ($\varrho > 0$ for both periods) and to a larger error variation than expected by the Poisson distribution (over-dispersion, $\sigma > 1$ for the earlier period). Thus, the Wald test (that allow for σ and ϱ) was used (Table 5).

The covariate effect was significant for both data sets, suggesting divergent population trends between regions (Table 5). Basically, the significant covariate effect may be due to regionally divergent changes in trends at one or more change-points within the data. According to the *t*-test, the covariate had significant impacts in 1953, 1957, 1961, 1967, 1981, 1987, and 1989 (Table 5, cf. Fig. 10). A significant covariate effect at change points 1981 and 1989 caused a steeper decline in the central than in the southern region. The indices for the northern region declined significantly more than those for the other two regions from 1981 until 1989; this was the result of a significant covariate effect at change points 1981 and 1987 (Table 5, cf. Fig. 10).

Indices and their standard errors were estimated for every possible base-year (1973–2000, set at one, SE = 0) and the *t*-test was used to test the deviation of all forthcoming indices from one. In the southern region, all the indices were significantly ($P < 0.001$ or $P < 0.01$) smaller than those in the preceding base-years 1973–1975. By contrast, all the indices were significantly greater than the indices for the preceding base-years 1987–2000 ($P < 0.001$, $P < 0.01$, or $P < 0.05$). Subsequent indices were always significantly smaller (in all, $P < 0.001$) in relation to the previous base-years 1973–1978. The statistics suggest a general reduced status for the southern popula-

Table 5. Significance of index trends, as estimated with log-linear models on the basis of the original uncorrected starling data (*see* Material and methods, Fig. 10). The Wald statistics (Pannekoek & van Strien 2003), degrees of freedom (df) and statistical significance (*P*) for the covariate (REG; southern, central, and northern regions) and time effects (change points) were estimated for two data sets (1951–1973 and 1973–2001). Models were constructed following a backward stepwise elimination of parameters, a procedure which retained change-points having a significance level of $P \leq 0.1$. In the initial models, parameter effects were allowed for every second year. The estimates for dispersion and serial correlation (Table 4) of counts were taken into account in the estimation of parameters.

Covariate and change-point	Wald	df	*P*
$\text{REG}_{(1951–1973)}$	32.53	10	< 0.001
1953	11.91	3	0.008
1957	11.55	3	0.009
1959	6.96	3	0.073
1961	8.84	3	0.032
1967	11.62	3	0.009
$\text{REG}_{(1973–2001)}$	50.03	10	< 0.001
1973	99.67	3	< 0.001
1979	27.98	3	< 0.001
1981	17.21	3	< 0.001
1987	12.73	3	0.005
1989	7.37	3	0.061

tion during 1973–2001, with a recovery since the late 1980s (cf. Fig. 10).

Significantly declining trends dominated in the central and northern regions: 92% (Central) and 79% (North) of comparisons yielded statistically significant declines (in the majority of them $P < 0.001$). In the north, the decline stabilised from 1989 onwards (cf. Fig. 10). In the total area, all the indices were significantly smaller than those for the previous base-years 1973–1977 and 1981–1982 (in all, $P < 0.001$). During 1989–2001, the indices grew significantly every year ($P < 0.001$, $P < 0.01$, or $P < 0.05$) from the corresponding previous base-years (cf. Fig. 11).

On the basis of the data set 1951–1973, in the southern, central, and total areas, all the indices were significantly smaller (in all, $P < 0.001$) than the indices for the previous base-years 1967–1972, suggesting a constant population decline during 1968–1973. In the northern region, the starting-point for the decline of starlings cannot be detected within 1951–1973 (cf. Fig. 10).

Table 6. Logistic regression coefficients (*b*) and their standard errors (SE), test statistics (*z*), statistical significances (*P*), and odds ratios based on available sites (2-km squares) used (i.e. broods ringed) or not used (i.e. no broods ringed). Variables, denoting site specific habitat structure, are proportion of fields (FIELD), number of different aged houses (OLD: built before 1941, MID: 1941–1960, NEW: 1961–1970), and all houses built until 1970 (ALL) within available squares, and averagely in the squares surrounding the available squares (RAD1, RAD2, and RAD3: 1–3 km, 3–10 km, and 10–50 km buffer zones, respectively). Squares of the variables (^2) were used to allow for parabolic responses. For the analysis, explanatory habitat variables were scaled to a mean of zero and unit variance. In the backward elimination of coefficients, $\text{FIELD}^{\wedge 2}$, $\text{FIELD}_{[\text{RAD1}]}$, $\text{FIELD}_{[\text{RAD1}]}{}^{\wedge 2}$, $\text{FIELD}_{[\text{RAD2}]}{}^{\wedge 2}$, $\text{FIELD}_{[\text{RAD3}]}{}^{\wedge 2}$, MID, $\text{MID}^{\wedge 2}$, $\text{MID}_{[\text{RAD1}]}{}^{\wedge 2}$, $\text{OLD}_{[\text{RAD1}]}$, $\text{OLD}_{[\text{RAD1}]}{}^{\wedge 2}$ were rejected.

Variable	*b*	SE	*z*	*P*	Odds ratio
Intercept	–3.07	0.03	–98.38	< 0.001	
FIELD	0.21	0.03	6.61	< 0.001	1.24
$\text{FIELD}_{[\text{RAD2}]}$	–0.34	0.05	–6.62	< 0.001	0.72
$\text{FIELD}_{[\text{RAD3}]}$	–0.36	0.06	–6.20	< 0.001	0.69
NEW	0.30	0.05	6.43	< 0.001	1.35
$\text{NEW}^{\wedge 2}$	–0.19	0.04	–4.67	< 0.001	0.83
$\text{NEW}_{[\text{RAD1}]}$	0.16	0.07	2.35	0.019	1.17
$\text{NEW}_{[\text{RAD1}]}{}^{\wedge 2}$	–0.18	0.04	–4.33	< 0.001	0.83
$\text{MID}_{[\text{RAD1}]}$	0.13	0.04	3.07	0.002	1.14
OLD	0.25	0.04	6.34	< 0.001	1.28
$\text{OLD}^{\wedge 2}$	–0.14	0.03	–4.48	< 0.001	0.87
$\text{ALL}_{[\text{RAD2}]}$	0.35	0.05	6.82	< 0.001	1.42
$\text{ALL}_{[\text{RAD2}]}{}^{\wedge 2}$	–0.17	0.04	–4.30	< 0.001	0.84
$\text{ALL}_{[\text{RAD3}]}$	1.26	0.11	11.25	< 0.001	3.52
$\text{ALL}_{[\text{RAD3}]}{}^{\wedge 2}$	–0.74	0.09	–8.15	< 0.001	0.48

Spatial distribution of starlings

Site selection

An RSF for modelling the spatial distribution of starlings was performed using the data from the period 1951–1975, when starlings were relatively abundant. The total number of broods was 18 341 and the total number of sites 1577. By the logistic regression (Tables 6 and 7), both the coverage of fields and the number of houses gave a statistically significant explanation of the distribution of ringed broods among the spatial units sampled. The number of houses within and around core units (2-km square) explained most of the variation in the probability for habitat use. The maximal effect was due to the numbers of houses within 10–50 km of breeding sites (Table 6): an increase by one standard error from the mean value (i.e. zero) would have caused an increase of almost 10% in the response probability if the remaining variables had stayed at zero. The corresponding quadratic variable functioned as an inhibitory effect on the growth of probabilities towards high house densities. The main pattern of the effect due to settlements did not vary according to the age of the houses or the spatial scale of the measurements (Table 6).

When the variables chosen for inclusion in the final model (Tables 6 and 7) were inspected separately in single-variable models, each variable had a positive effect. Their odds ratios varied from 1.07 ($z = 2.69$) to 1.18 (6.91) for variables related to fields, and from 1.26 (8.80) to 1.52 (26.31) for variables related to human settlement. The coefficients were significantly different from zero ($P < 0.001$ or $P < 0.01$).

Centres of gravity

During 1991–2001, the centres of gravity of ringing sites shifted consistently southwards (by approximately 25–50 km) from the overall centre of gravity (for the total period 1951–2001). The annual positions clearly exceeded (in nine cases) or stayed on the boundary (in one case) of the 95% confidence area (Fig. 12). From the 1960s up to 1990, the annual gravity centres moved both southwards and northwards from the average locations, often staying within or close to the 95% confidence belts (Fig. 12). It is possible that the relative instability of the centres of gravity before the 1990s was due to rapid variations in the annual breeding distribution of starlings, but more probably it was due mainly to inconsistent regional ringing activities, since these activities underwent rapid expansion during the study period (Fig. 2). When centres of gravities were calculated on the basis of the numbers of ringed broods (location weighted by the annual numbers of broods), the shift pattern turned out to be basically similar to the one presented (Fig. 12), with the exception of narrower confidence limits (due to increased sample size) and shifts that extended even further southwards in 1991–2001, all of these being clearly outside the 95% confidence range.

Discussion

We have shown in this study that long-term nestling ringing data can be used for studies in regional population patterns for the periods preceding the establishment of national monitoring schemes, and for species that are not well covered in general monitoring censuses. However, such data are far from ideal, since they are not collected for monitoring purposes, and since nest searching and ringing effort are not measured — factors that raise many questions as to the quality of the data. The main problem addressed here is how to deal with missing counts, which may represent either a lack of ringing activity or local extinctions. Elaborated modelling and testing are needed to explore and secure the applicability of the data.

When sufficient in volume, nestling ringing data can function as a tool in population monitoring. Not only can national indices be constructed via standardisation of the ringing totals (Rintala *et al.* 2003); the data also provide useful “real” census data that enable the use of standard statistical methodology (van Strien *et al.* 2001). Our novel approach has allowed new inferences to be made concerning the past population dynamics of the Finnish starling.

The populations declined most in northern Finland. The decline was partly due to local extinctions, which became more widespread towards the north, indicating a contraction of the range in the north. Along with local extinctions in northern and central Finland, the centres of gravity of the local breeding populations have been moving more and more towards the south.

Local and regional dynamics of starlings

The substantial decline in Finnish starling populations, which began at the turn of the 1960s (this study, also Rintala *et al.* 2003), can be expressed

Table 7. Deviance table of a logistic regression applied for an RSF (cf. Table 6). Deviances (DEV), degrees of freedom (df) and statistical significance (*P*, χ^2-test) are given for the effect of different variables and for the comparison of different models (FINAL = final model, FULL = initial model). Residual degrees of freedom (R.DF) and residual deviances (R.DEV) are shown for models. NULL is a model with intercept only. For explanations of variables, *see* Table 6.

Variable or model	df	DEV	R.DF	R.DEV	*P*
NULL	–	–	27507	12079	–
FIELD	1	45.8	27506	12033	< 0.001
$\text{FIELD}_{[\text{RAD2}]}$	1	2.8	27505	12030	0.100
$\text{FIELD}_{[\text{RAD3}]}$	1	9	27504	12021	0.003
NEW	1	590.7	27503	11431	< 0.001
$\text{NEW}^{\wedge 2}$	1	187.2	27502	11243	< 0.001
$\text{NEW}_{[\text{RAD1}]}$	1	96.2	27501	11147	< 0.001
$\text{NEW}_{[\text{RAD1}]}^{\wedge 2}$	1	50.1	27500	11097	< 0.001
$\text{MID}_{[\text{RAD1}]}$	1	19	27499	11078	< 0.001
OLD	1	25.1	27498	11053	< 0.001
$\text{OLD}^{\wedge 2}$	1	21.9	27497	11031	< 0.001
$\text{ALL}_{[\text{RAD2}]}$	1	109.6	27496	10922	< 0.001
$\text{ALL}_{[\text{RAD2}]}^{\wedge 2}$	1	28.8	27495	10893	< 0.001
$\text{ALL}_{[\text{RAD3}]}$	1	106.9	27494	10786	< 0.001
$\text{ALL}_{[\text{RAD3}]}^{\wedge 2}$	1	71.8	27493	10714	< 0.001
Comparison of models (the effect of removed variables)					
FINAL			27493	10714	
FULL	10	9.9	27483	10704	0.400

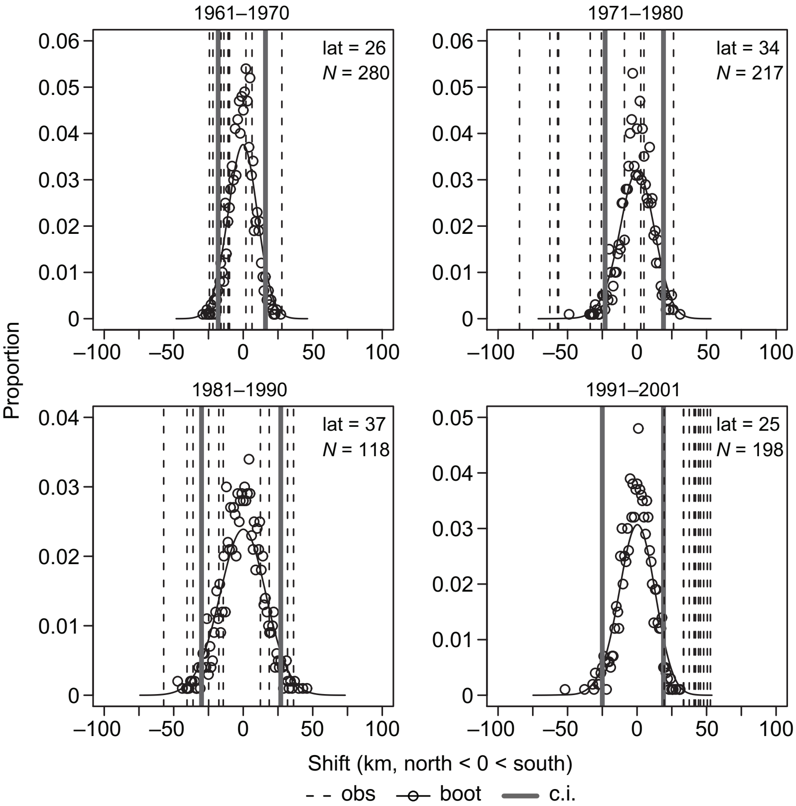

Fig. 12. Shifts in the centres of gravity of ringing locations (kilometres northwards/southwards) grouped in four periods within 1961–2001. The annual observed shifts (obs) were calculated by subtracting the annual centre of gravity from the overall centre of gravity (lat[itude], in kilometres according to the Finnish uniform grid). For each period (e.g. 1961–1970) the overall centre of gravity was calculated on the basis of the data from 1951 up until the end of the corresponding period (e.g. up to 1970). 95% confidence intervals of shifts (c.i.) were calculated on the basis of 1000 bootsrap (boot) samples (taken from the data from 1951 up to the end of the corresponding period). Frequency distribution (Proportion) of bootstrapped shifts and their density functions are shown for each period. The maximum annual number of sites (*N*) within the periods was chosen as representative of the number of sites in each bootstrap sample.

by "range contraction" and also by declines in the "centre" areas (Thomas 1996). As was shown via the simulations, it was crucial to take into account the extinction and occasional disappearance of local populations in order to gain realistic estimates of regional decline (Fig. 7). Following on studies of local starling populations in Finnish farmland (Tiainen *et al.* 1989, Solonen *et al.* 1991) and also research in Sweden (Svensson 2004b), we were able to formulate an *a priori* hypothesis concerning the high extinction rates of local populations.

The results suggest that the extinctions of local populations took place at higher rates in the north than in the south, since the correction of missing counts to zeros applied increasingly to the north as the overall population declined (Figs. 9 and 10). We hypothesise that the overall deterioration of farmland habitats in Finland (Tiainen *et al.* 1989) could have reached and exceeded a certain threshold level such that, due to purely random factors, emigration from remaining source populations would not have been sufficient to maintain the most isolated and smallest sink populations (e.g. Gilpin & Hanski 1991, Newton 1998, Chamberlain & Fuller 2000, 2001, Foppen *et al.* 2000, *see* also Svensson 2004b). This would cause an increasing risk of local extinctions and an overall decline in the population, most drastically expressed in northern Finland (cf. Solonen *et al.* 1991). The decline was most probably caused by a rapid and consistent deterioration in the breeding habitats of starlings within farmland areas, which in turn would bring about a deficiency in reproductive output (Tiainen *et al.* 1989, Rintala *et al.* 2003).

Solonen *et al.* (1991) studied the dynamics of local starling populations that were breeding in nest-box colonies in five geographical regions, from southern to northern Finland. They suggested that both local and regional processes had affected the declines of these populations. It has been shown that the availability of good-quality breeding habitat — i.e. the pastures and short-cut grasslands that form the most important foraging areas of breeding starlings (Feare 1984, Tiainen *et al.* 1989, Smith & Bruun 2002, Olsson *et al.* 2002, Källander 2004) — forms the basis for the successful reproduction and thus the longevity of local populations in Finnish farmland areas (Tiainen *et al.* 1989, Solonen *et al.* 1991, Rintala *et al.* 2003). Such a causal connection between the cessation of cattle farming and the declines in starling populations has been suggested for several other northern and western European starling populations (Møller 1983, Solonen *et al.* 1991, Smith & Bruun 2002, Robinson *et al.* 2002, Källander 2004, Svensson 2004b). The timing and degree of the decline has varied between different populations in Finland (Solonen *et al.* 1991). The same is true for Sweden (Svensson 2004b) and Britain (Robinson *et al.* 2002). In Finland, the declines were recorded more immediately in those areas where pastures were converted into arable fields than in those cases where pastures, after abandonment, were left to develop naturally (Solonen *et al.* 1991).

These findings support the idea that local factors would explain the declines rather than more general reasons such as mortality in wintering areas (Tiainen *et al.* 1989). Tiainen *et al.* (1989) hypothesised that as a result of decreased availability of good breeding habitats (a consequence of the abandonment of pastures and sown grass field along with structural changes and specialisation in agriculture), the entire southern Finnish population became less productive and that, consequently, the overall population started to decline.

According to the hypothesis put forward by Solonen *et al.* (1991), there were no longer enough southern emigrants to replenish the northern populations, i.e. populations in which reproduction was insufficient to balance mortality (there is a declining trend from the south to the north in reproductive output). Finnish ring recovery data (from 1974 onwards, Ringing Centre of the Museum of Natural History of University of Helsinki) support the idea of a capacity of starlings to disperse from southern to northern Finland. Adults ringed from April–June were recovered at a distance of 7.2 ± 27.6 km (mean ± SD, $N = 22$, range 0–129 km), whereas nestlings were recovered at 39.5 ± 97.6 km ($N = 121$, range = 0–802 km). Five percent of adults dispersed more than 23 km, but the corresponding fraction for nestlings was more than 162 km. In a study based on ringing recoveries in Britain, where starlings are resident, dispersal distances were found to be 3.4 ± 19.1 km (mean ± SD, $N = 1672$) for individuals ringed at breeding age, and 9.5 ± 28.1 km ($N = 401$) for fledglings (Paradis *et al.* 1998).

On the basis of the above considerations, we suggest that source–sink dynamics (Pulliam 1988) could have regulated starling populations in Finland. The rapid deterioration of breeding habitats (Tiainen *et al.* 1989, Solonen *et al.* 1991, Tiainen 2001, 2004) could have directed the source–sink balance of local populations more towards the sink in most farmland areas. Such a phenomenon would be expressed as expanding declines and extinctions among local populations, and also as an overall population collapse, especially in northern Finland. The dispersal ability of starlings, assuming that there had been a large enough source-oriented population structure before the collapse, could have ensured the former persistence of sinks (Brawn & Robinson 1996) — including also the most remote ones, such as the populations in northern Finland (*see* Figs. 1 and 10, Solonen *et al.* 1991).

According to our estimate, the decline started earlier in the southern and central regions (1968) than in the northern region (1974, Fig. 10). This is surprising, if one assumes that the northern populations function mainly as a sink. However, it is possible that the most isolated sink populations in the north were under-represented in the ringing data. This could be due to the ringing of broods predominantly from those southwestern parts of the northern region (actually the city of Oulu and its neighbouring localities, plus the village of Pello; cf. Fig. 1) in which the number of farms and cattle was still high in 1969 (Anonymous 1962, 1971). It could also be that these breeding habitats had not deteriorated as drastically and as quickly as habitats overall (Solonen *et al*. 1991, Tiainen 2001, 2004).

The analysis yielded a more precise estimate (lower standard errors) of the total population decline (approximately 80% from the late 1960s until the mid-1980s) than our previous study (approximately 90%, Rintala *et al*. 2003). The trends over the period 1951–1972 showed statistically significant variation in time and between regions. These fluctuations, which in fact were not large in comparison with the collapse, may reflect short-term population regulation driven, for instance, by annual variations in survival of birds (e.g. Kaitala *et al*. 1996, Thomson *et al*. 1997, Rintala *et al*. 2003). The significant and consistent recovery of starlings since the end of the 1980s in southern Finland (Fig. 10, cf. Rintala *et al*. 2003) is still not adequately explained. It may be that recent changes in the use of arable lands — involving the set-aside agreements that increased in Finland in the late 1980s (Tiainen 2001, 2004) — could have improved the feeding opportunities for breeding starlings.

It is known that nest predation can be an important factor inhibiting the fecundity of passerines (e.g. Martin 1995). In Finland, the effect of nest predation on the life history traits of starlings is probably small in relation to other causes of unsuccessful breeding such as a shortage of food and harsh weather conditions (Tenovuo & Lemmetyinen 1970, Korpimäki 1978, Tiainen *et al*. 1989). We still do not know if factors other than the quality of breeding habitats have affected populations (in one direction or another) during the last few decades. A sensitivity analysis that would account for the effect of variations in demographic parameters — births, deaths, immigration, and emigration — should be performed in order to gain a better understanding of starling population dynamics.

Inferences from the resource selection function

Implications for the starling population

The inclusion of habitat variables was based on general knowledge of the habitat preferences of starlings (e.g. Feare 1984, Gregory & Baillie 1998) and on a realistic assessment of what was feasible. According to the RSF, increasing numbers of houses had a notable positive effect on the probability of habitat use. This can be easily understood from the fact of starlings having been largely associated with human habitation — farms, rural villages, suburbs, and cities (Feare 1984, Tiainen *et al*. 1993, Gregory & Baillie 1998). In the 1950s, 1960s, and even in the early 1970s, the Finnish countryside contained a large number of small farms with mixed farming: 75%–90% of all farms had dairy cattle (Tiainen 2001, 2004). Livestock and rotational pastures were distributed in farmland patches that were usually adjacent to houses; also adjacent to barns and sheds for animals and vehicles (Tiainen 2001, 2004). These kinds of environments provided an abundance of artificial nest-boxes attached to trees and farm buildings, and also ensured good-quality habitats for the successful breeding of starlings (*see* above). Starlings often breed semi-colonially, feeding in flocks in grassland even during breeding (Feare 1984, Källander 2004). This may mean that in most farmland habitats it has not been the low coverage of fields that has been the limiting factor on the breeding of starlings (cf. Table 6), but rather the presence of good-quality foraging habitats (such as pastures and other short-cut grassland) in the vicinity of farming estates. In any case, there is no straightforward explanation as to why the increasing coverage of fields surrounding the core units (2-km squares) should have decreased the probability of habitat use (Table 6). The answer may lie in unmeasured interactions between habitat variables that would have popped up as seemingly illogical parameter effects. Such interactions were not incorporated into the models because it was hard to come up with an objective classification basis, and it would have been questionable to rely on results from variables that had been classified subjectively.

Overall, the effects of the variables on the probabilities of habitat use were quite low, except for the number of houses in the vicinity of habitat plots (Table 6). For this reason, in the extrapolation of the population based on the RSF, local and regional "hot spots" of breeder-numbers emerged within and around towns up to a distance of 50 km (as determined by the environment variables; *see* Fig. 4 and Table 6).

Information on long-term changes in farming activity within restricted areas like towns is of interest in exemplifying local habitat changes near human settlements. The agricultural censuses of 1959, 1969, and 1990 (Anonymous 1962, 1971; data for 1990: The Information Centre of the Ministry of Agriculture and Forestry in Finland) allowed us to inspect the changes in agriculture in a sample of communes, i.e. Helsinki (the capital of Finland) plus 14 smaller towns whose administrative borders had not changed during 1959–1990. The communes, with their regional position in Finland in parentheses, were: Hamina, Helsinki, Kauniainen, Lahti, Lohja, Porvoo (south Finland), Kaarina, Raisio (south-west), Kouvola, Loviisa (south-east), Imatra, Joensuu, Mikkeli (east), Jyväskylä (central), and Rovaniemi (north). As compared with more recent times, during the period covering the RSF data (1951–1975), the urban areas were actually fairly pastoral. In 1959 and 1969 (pooled data), the average number of farms in these locations was 136 (± 143 SD, $N = 30$) and the average number of cattle was 378 (± 458). In 1990, the corresponding numbers were 43 (± 52, $N = 15$) and 76 (± 129). Thus, up until the 1990s, farms and cattle declined on average by 68% and 80%, respectively. To illustrate this further, consider the city of Helsinki in the years 1959, 1969, and 1990. Here, the numbers of farms declined over the corresponding years from 162 to 61 to 7, and the numbers of cattle declined from 300 to 251 to 55. To sum up, urban and suburban areas (at their best) probably provided both nest sites and plenty of good foraging habitats for breeding starlings, manifested as high densities of breeding pairs within and around towns and other densely populated areas. The abandonment of cattle farming — as exemplified by the above commune data — is part of the overall deterioration of farmland habitats that has taken place during recent decades, and this is probably the primary reason for the major collapse of Finnish starlings (e.g. Tiainen *et al*. 1989, Solonen *et al*. 1991).

Methodological constraints

In the RSF, one problem was how to define the available units (i.e. the potential sampling area). The spatial scale applied for the outlining of the available units alters the proportional availability of different habitat types. This was a problem, since the ringing of starlings could not be considered a random sample over all the available units. As an example, let us consider a large area with a certain number of good and poor habitats; let us further assume that starlings would have access to both habitat types and would favour the better one, but that ringers would reach the poor habitats proportionally more often than would be expected by the proportional coverage of the good and poor habitats within the sampling area. Under these circumstances, an RSF would overestimate the use of the poor breeding areas at the expense of the better areas. For this reason, we restricted the sampling so that it was close to the sites where starlings were ringed. We used 20-km squares containing breeding starlings as the basis for the selection. We took the view that this was the area that a bird ringer could have covered without too much effort during the sampling period (1951–1975), and thus that ringers would have been able to sample different types of habitat in the proportions as they were available.

One may ask why we did not use buffer zones around units with ringed broods. This was necessary for the aim of incorporating a regional interaction term within the model. To avoid biases due to regional variation in sampling frequencies, we set the ratio of used and unused units at a constant value (Johnson *et al*. 2004) within the 20-km squares across Finland (the adjustment carried out most easily for constant-sized grid squares). Unfortunately, this "regional" RSF turned out to be unrealistic, most probably due to the constraint that the ringing of broods had not been a random sample over every possible available unit in our design. Thus the results were not convincing. Accordingly, we rejected the regional effect, but accepted the current sampling routine without laborious rearrangements for a new analysis. However, we are fairly sure that a buffering technique, on average, would not have changed the function essentially. Overall, we accepted a general RSF, assuming equal effects in spite of varying locations of samples (Boyce & McDonald 1999, Manly *et al*. 2002). It is possible that due (for example) to productivity decreasing northwards (Solonen *et al*. 1991), this assumption could have led to an overestimation of the value of certain habitats in the north as compared to similar habitats in the south.

Acknowledgements

We are grateful to the hundreds of Finnish starling ringers who worked over the five decades we deal with. We thank the Ringing Centre of the Museum of Natural History of the University of Helsinki, which provided the data for this study, and Jukka Haapala and Seppo Niiranen for assistance. We also wish to thank Jyrki Holopainen and Arco van Strien who were very helpful in many technical discussions, and Ilpo K. Hanski and Heikki Lokki who provided instructive comments and suggestions. Our sincere thanks go to two anonymous referees for their in-depth revision and numerous useful suggestions for the improvement of the manuscript. Donald Adamson kindly revised the English. This study was part of the Finnish Biodiversity Research Programme of the Academy of Finland. It was financed by the Ministry of Agriculture and Forestry within the framework of the projects for Monitoring the Biodiversity Impact of the National Agri-environmental Scheme (MYTVAS) and the Programme of Biodiversity Research (LUMOTTU/MOSSE).

References

@Risk 1997: *Risk analysis and simulation add-in for Microsoft Excel or Lotus 1-2-3*. — Palisade Corporation, New York.

Anonymous 1962: Agriculture, vol. II. Census of agriculture. Data per commune, 1959. — *Official Statistics of Finland* III: 54.

Anonymous 1971: Agriculture, vol. II. Census of agriculture. Data per commune, 1969. — *Official Statistics of Finland* III: 67.

Anonymous 1982: *Atlas of Finland. Folio 231. Farming*. — National board of survey/Geographical society of Finland, Helsinki.

Augustin, N. H., Mugglestone, M. A. & Buckland, S. T. 1996: An autologistic model for the spatial distribution of wildlife. — *J. Appl. Ecol*. 33: 339–347.

Bairlein, F., Berthold, P., Dhondt, A., Jenni, L., Peach, W., Spina, F. & Wassenaar, R. 1994: *Bird ringing in science and environmental management*. — The European Union for Bird Ringing, Bologna.

Berthold, P., Fiedler, W., Schlenker, R. & Querner, U. 1999: Population development of central European songbirds: final report of the MRI-program. — *Vogelwarte* 40: 1–10.

Bibby, C. J., Burgess, N. J. & Hill, D. A. 1992: *Bird census techniques*. — Academic Press, London.

BirdLife International 2004: *Birds in Europe: population estimates, trends and conservation status*. — BirdLife International, Cambridge.

Boyce, M. S. & McDonald, L. L. 1999: Relating populations to habitats using resource selection functions. — *Trends Ecol. Evol*. 14: 268–272.

Brawn, J. D. & Robinson, S. K. 1996: Source–sink population dynamics may complicate the interpretation of long-term census data. — *Ecology* 77: 3–12.

Chamberlain, D. E. & Fuller, R. J. 2000: Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. — *Agric. Ecosyst. Environ*. 78: 1–17.

Chamberlain, D. E. & Fuller, R. J. 2001: Contrasting patterns of change in the distribution and abundance of farmland birds in relation to farming system in lowland Britain. — *Global Ecology & Biogeography* 10: 399–409.

Dunnet, G. M. 1955: The breeding of the starling *Sturnus vulgaris* in relation to its food supply. — *Ibis* 97: 619–662.

Feare, C. J. 1984: *The starling*. — Oxford University Press, Oxford.

Fliege, G. 1984: Das Zugverhalten des Stars (*Sturnus vulgaris*) in Europa: Eine Analyse der Ringfunde. — *J. Ornithol*. 125: 393–446.

Foppen, R. P. B., Chardon, J. P. & Liefveld, W. 2000: Understanding the role of sink patches in source–sink metapopulations: reed warbler in an agricultural landscape. — *Conserv. Biol*. 14: 1881–1892.

Gilbert, G., Gibbons, D. W. & Evans, J. 1998: *Bird monitoring methods*. — The Royal Society for the Protection of Birds, The Lodge.

Gilpin, M. & Hanski, I. 1991: *Metapopulation dynamics: empirical and theoretical investigations*. — Academic Press, London.

Ginn, H. B. 1969: The use of annual ringing and nest record card totals as indicators of bird population levels. — *Bird Study* 16: 210–248.

Gregory, R. D. & Baillie, S. R. 1998: Large-scale habitat use of some declining British birds. — *J. Appl. Ecol*. 35: 785–799.

Gregory, R. D., van Strien, A., Vorisek, P., Gmelig Meyling, A. W., Noble, D. G., Foppen, R. P. B. & Gibbons, D. W. 2005: Developing indicators for European birds. — *Phil. Trans. R. Soc. B* 360: 269–288.

Haapala, J. & Saurola, P. 1995: Constant effort sites scheme in Finland 1992–1994. — *Linnut* 30: 32–33. [In Finnish with English summary].

Hjort, C. & Lindholm, C. G. 1978: Annual bird ringing totals and population fluctuations. — *Oikos* 30: 387–392.

Idrisi 1992a: *Idrisi: Technical reference*. — Worcester, Massachusetts.

Idrisi 1992b: *Idrisi: User's guide*. — Worcester, Massachusetts.

Järvinen, A. & Väisänen, R. A. 1984: Reproduction of pied flycatchers (*Ficedula hypoleuca*) in good and bad breeding seasons in a northern marginal area. — *Auk* 101: 439–450.

Johnson, C. J., Seip, D. R. & Boyce, M. S. 2004: A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. — *J. Appl. Ecol.* 41: 238–251.

Kaitala, V., Ranta, E. & Lindström, J. 1996: External perturbations and cyclic dynamics. — *Ann. Zool. Fennici* 33: 275–282.

Källander, H. 2004: Starlings *Sturnus vulgaris* and cattle — a widespread feeding association. — *Ornis Svecica* 14: 11–20.

Karlsson, L., Ehnbom, S., Persson, K. & Walinder, G. 2002: Changes in numbers of migrating birds at Falsterbo, South Sweden, during 1980–1999, as reflected by ringing totals. — *Ornis Svecica* 12: 113–137.

Keating, K. A. & Cherry, S. 2004: Use and interpretation of logistic regression in habitat-selection studies. — *J. Wildl. Manage.* 68: 774–789.

Korpimäki, E. 1978: Breeding biology of the starling *Sturnus vulgaris* in western Finland. — *Ornis Fennica* 55: 93–104.

Manly, B. F. J. 1997: *Randomization, bootstrap and Monte Carlo methods in biology*. — Chapman & Hall/CRC, London.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L. & Erickson, W. 2002: *Resource selection by animals: Statistical design and analysis for field studies*. — Kluwer Academic Publishers, Dordrecht.

Martin, T. E. 1995: Avian life history evolution in relation to nest sites, nest predation, and food. — *Ecological Monographs* 65: 101–127.

MapInfo 1999a: *MapInfo: Reference*. — MapInfo Corporation, New York.

MapInfo 1999b: *MapInfo: User's guide*. — MapInfo Corporation, New York.

Møller, A. P. 1983: Changes in Danish farmland habitats and their populations of breeding birds. — *Holarct. Ecol.* 6: 95–100.

Newton, I. 1998: *Population limitation in birds*. — Academic Press, San Diego.

Ojanen, M., Orell, M. & Merilä, E. 1978: Population decrease of Starlings in northern Finland. — *Ornis Fennica* 55: 38–39.

Olsson, O., Bruun, M. & Smith, H. G. 2002: Starling foraging success in relation to agricultural land-use. — *Ecography* 25: 363–371.

Orell, M. & Ojanen, M. 1980: Numbers of starlings *Sturnus vulgaris* breeding in northern Finland still low in 1978–79. — *Ornis Fennica* 57: 133–134.

Österlöf, S. & Stolt, B. O. 1982: Population trends indicated by birds ringed in Sweden. — *Ornis Scand.* 13: 135–140.

Pannekoek, J. & van Strien, A. J. 2003: *TRIM 3 manual* (*TRends and Indices for Monitoring data*). — Statistics Netherlands, Voorburg.

Paradis, E., Baillie, S. R., Sutherland, W. J. & Gregory, R. D. 1998: Patterns of natal and breeding dispersal in birds. — *J. Anim. Ecol.* 67: 518–536.

Peach, W. J., Baillie, S. R. & Balmer, D. E. 1998: Long-term changes in the abundance of passerines in Britain and Ireland as measured by constant effort mist-netting. — *Bird Study* 45: 257–275.

Perdeck, A. C. 1977: The analysis of ringing data: pitfalls and prospects. — *Die Vogelwarte* 29 (Sonderheft): 33–44.

Pulliam, H. R. 1988: Sources, sinks, and population regulation. — *Am. Nat.* 132: 652–661.

R Development Core Team 2005: *R: A language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna. Available at http://www.R-project.org.

Rintala, J., Tiainen, J. & Pakkala, T. 2003: Population trends of the Finnish starling *Sturnus vulgaris*, 1952–1998, as inferred from annual ringing totals. — *Ann. Zool. Fennici* 40: 365–385.

Robinson, R. A., Siriwardena, G. M. & Crick, H. Q. P. 2002: Status and population trends of the starling *Sturnus vulgaris* in Great Britain. — In: Crick, H. Q. P., Robinson, R. A., Appleton, G. F., Clark N. A. & Rickard, A. D. (eds.), *Investigation into the causes of the decline of starlings and house sparrows in Great Britain*: 11–31. BTO Research Report No. 290. DEFRA, Bristol.

Smith, H. G. & Bruun, M. 2002: The effect of pasture on starling (*Sturnus vulgaris*) breeding success and population density in a heterogeneous agricultural landscape in southern Sweden. — *Agric. Ecosyst. Environ.* 92: 107–114.

Solonen, T., Tiainen, J., Korpimäki, E. & Saurola, P. 1991: Dynamics of Finnish starling *Sturnus vulgaris* populations in recent decades. — *Ornis Fennica* 68: 158–169.

Svensson, S. 2004a: Onset of breeding among Swedish starlings *Sturnus vulgaris* in relation to spring temperature in 1981–2003. — *Ornis Svecica* 14: 117–128.

Svensson, S. 2004b: The recent decline of the starling *Sturnus vulgaris* population in Sweden: a 22-year nest-box study. — *Ornis Svecica* 14: 28–46.

Tenovuo, R. & Lemmetyinen, R. 1970: On breeding ecology of the Starling *Sturnus vulgaris* in the archipelago of south-western Finland. — *Ornis Fennica* 47: 159–166.

ter Braak, C. J. F., van Strien, A. J., Meijer, R. & Verstrael, T. J. 1994: Analysis of monitoring data with many missing values: which method? — In: Hagemeijer, W. & Verstrael, T. (eds.), *Bird numbers 1992: Distribution, monitoring and ecological aspects, Proceedings of the 12th International Conference of IBCC & EOAC. 1992*: 663–673. SOVON, Beek-Uppergen.

Thomas, L. 1996: Monitoring long-term population change: why are there so many monitoring methods? — *Ecology* 77: 49–58.

Thomson, D. L., Baillie, S. R. & Peach, W. J. 1997: The demography and age-specific annual survival of song thrushes during population stability and decline. — *J. Anim. Ecol.* 66: 414–424.

Tiainen, J. 2001: The Finnish agricultural environments. — In: Tiainen, J. & Pitkänen, M. (eds.), *Biodiversity of agricultural landscapes in Finland*: 9–12. Birdlife Finland, Helsinki.

Tiainen, J. 2004: Maatalousympäristön historia. — In: Tiainen, J., Kuussaari, M., Laurila, I. P. & Toivonen, T. (eds.), *Elämää pellossa: Suomen maatalousympäristön monimuotoisuus*: 26–42. Edita Publishing Oy, Helsinki.

Tiainen, J. & Pakkala, T. 1997: Starling. — In: Hagemeijer, W. & Blair, M. (eds.), *The EBCC atlas of breeding birds in Europe*: 688–689. T & AD Poysen, London.

Tiainen, J., Hanski, I. K., Pakkala, T., Piiroinen, J. & Yrjölä, R. 1989: Clutch size, nestling growth and nestling mortality of the starling *Sturnus vulgaris* in south Finnish agroenvironments. — *Ornis Fennica* 66: 41–48.

Tiainen, J., Vuorisalo, T., Multala, V., Pyyhtiä, T., Komulainen, M., Landa, K., Normaja, J. & Veistola, S. 1993: Turun linnuston runsausuhteet. — In: Vuorisalo, T. & Tiainen, J. (eds.), *Kaupungin linnut*: 36–91. Turun biologinen museo, Turku.

Tinbergen, J. M. 1981: Foraging decisions in starlings *Sturnus vulgaris* L. — *Ardea* 69: 1–67.

Väisänen, R. A. & Järvinen, O. 1981: Population monitoring of Finnish land bird species in 1978–80. — *Lintumies* 16: 111–117. [In Finnish with English summary].

Väisänen, R. A., Lammi, E. & Koskimies, P. 1998: *Distribution, numbers and population changes of Finnish breeding birds*. — Otava, Helsinki. [In Finnish with English summary].

van Strien, A. J., Pannekoek, J. & Gibbons, D. W. 2001: Indexing European bird population trends using results of national monitoring schemes: a trial of a new method. — *Bird Study* 48: 200–213.

von Haartman, L. 1969: The nesting habits of Finnish birds. I. Passeriformes. — *Commentationes Biologicae Soc. Scient. Fenn.* 32: 1–187.
