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Population trends of the Finnish starling *Sturnus vulgaris,* 1952–1998, as inferred from annual ringing totals

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Finnish starling populations have declined, a phenomenon first noted towards the end of the 1970s. Here we use national ringing totals to estimate changes in the starling population. However, the numbers ringed depend not only on the population size but also on yearly variations in ringing activities. Thus, it was necessary to correct these totals based on the records of other ringed passerines. In this study, we used a Monte Carlo simulation based on time series regressions for the estimation of confidence of indices. The results suggest that the population size from the early 1970s to the 1990s was significantly smaller than in the 1950s and 1960s. It was concluded that (*i*) the population was fairly stable in the period 1952–1970, (*ii*) the population started a consistent decline around 1970, and (*iii*) the population declined by approximately 90% in the period 1970–1985.

Introduction

Until the mid-1900s, the starling, *Sturnus vulgaris*, was one of the most common bird species in farmed Finland. Its breeding range covers most of Europe, with Finland being situated in the northern margin of the distribution area (Feare 1984). The population in Finland increased rapidly from the late 1800s until the early 1990s (Tiainen & Pakkala 1997). However, by the end of the 1970s it was found that several local populations had decreased drastically (Ojanen *et al*. 1978, Orell & Ojanen 1980, Solonen *et al*. 1991). The collapse of the Finnish populations was at first suggested to be due to increased adult mortality in the wintering areas, mainly resulting from mass culling in Belgium and France (Orell & Ojanen 1980).

Tiainen *et al*. (1989) were the first to point out that the population decrease in Finland could not be due to mass destruction of flocks in Belgium, since these measures were carried out before Finnish starlings arrived in the wintering areas. In France, on the other hand, the destruction was started as late as the early 1980s, at a time when the Finnish breeding population had already decreased. Tiainen *et al*. (1989, *see* also Korpimäki 1978) suggested that the quality of the breeding habitats had declined due to changes in the agroecosystems of southern Finland during recent decades, i.e. replacement of pastures and leys with cereal and root crop fields (cf. Robinson *et al.* 2002, Smith & Bruun 2002). They also showed that nestling survival was much higher (70%–90%) in traditional mixed farming areas where dairy cattle were grazing than in areas with only cereal and root crop cultivation (20%–40%). The differences in nestling mortality were most probably due to differences in the quality and amount of nestling food, since starlings prefer short-grass areas, such as pastures and leys, as foraging sites (Dunnet 1955, Tinbergen 1981, Varjonen 1991, Olsson *et al.* 2002). This conclusion was supported by the finding that the nestlings thrived better within mixed farming areas, even in large broods, than within areas of monoculture cultivation in small broods (Varjonen 1991). Hence, Tiainen *et al.* (1989) suggested that it was increased nestling mortality that was causing the decline of the Finnish starling populations.

To test the hypothesis of Tiainen *et al.* (1989), Solonen *et al.* (1991) studied the long-term dynamics of twenty local starling populations in various parts of Finland. They found differences in the onset of decline both regionally and locally. These differences coincided with changes in farming practices in the areas in question; thus, supporting the hypothesis. The dynamics of local populations suggested that the decline had already started at the turn of the 1960s, i.e. more than half a decade earlier than had been thought.

To evaluate the hypothesis that large scale deterioration of breeding habitats was the reason for the decline of starlings (Tiainen *et al.* 1989, Solonen *et al.* 1991), it would be interesting to know the changes in the abundance and reproduction of the Finnish population before, during and after the decline. The starling was a very successful species in Europe in the last century, increasing hugely in its numbers and expanding its range (Feare 1984). It has generally been assumed that the population increase continued in Finland until the 1950s and 1960s (von Haartman *et al.* 1963–1972, Cramp & Perrins 1994, Väisänen *et al.* 1998), but these suggestions are not based on comprehensive data since it was not until 1978 that the Finnish breeding bird monitoring programme was organised (e.g. Väisänen & Järvinen 1981, Väisänen *et al.* 1998). Ringing data provide the only annual long-term information covering several decades, but the value of the data for the monitoring and reconstruction of population history is lessened as a result of several uncontrolled sources of variation in ringing activity (e.g. Ginn 1969, Saurola 1978, Bibby *et al.* 1992). If the variations in the ringing activity could be taken into account, however, the data could be used to estimate population changes, the aim being to standardise the recorded annual numbers of the ringed species under study with a variable derived from the changes in the ringing activity (Österlöf & Stolt 1982, O'Connor & Mead 1984).

The present paper reports a study on changes in the size of the annual starling population in Finland during the period 1952–1998. In this study, our first objective was to standardise the annual numbers of ringed starlings on the basis of the ringing numbers of various passerine bird groups. The population estimates thus obtained make it possible to suggest answers to the following questions: (*i*) what was the trend of the starling population size before the decline, (*ii*) when did the decline start and, if the decline has ended, when did this happen, and (*iii*) how much of the population diminished during the decline?

The methodological aspects of using ringing data to monitor bird populations are of paramount importance in a study of this nature. The current data cannot be analysed appropriately with standard statistical methods. Hence, we also report on a Monte Carlo simulation model based on time series regression analyses that we constructed for the estimation of the confidence limits of indices.

Material and methods

Ringing data

We used the ringing data recorded in the database and the archives of the Ringing Centre of the Finnish Museum of Natural History. All the original ringing reports by ringers are stored in archives, and those from 1973 to the present are digitised in a database. We digitised the nestling ringing data of starlings from the original ringing reports for the period 1952–1972. In addition, we used the annual ringing totals of starlings and other passerines published in annual ringing reports and summaries from 1952 to 1972. It is only since 1968 that the ringing numbers of

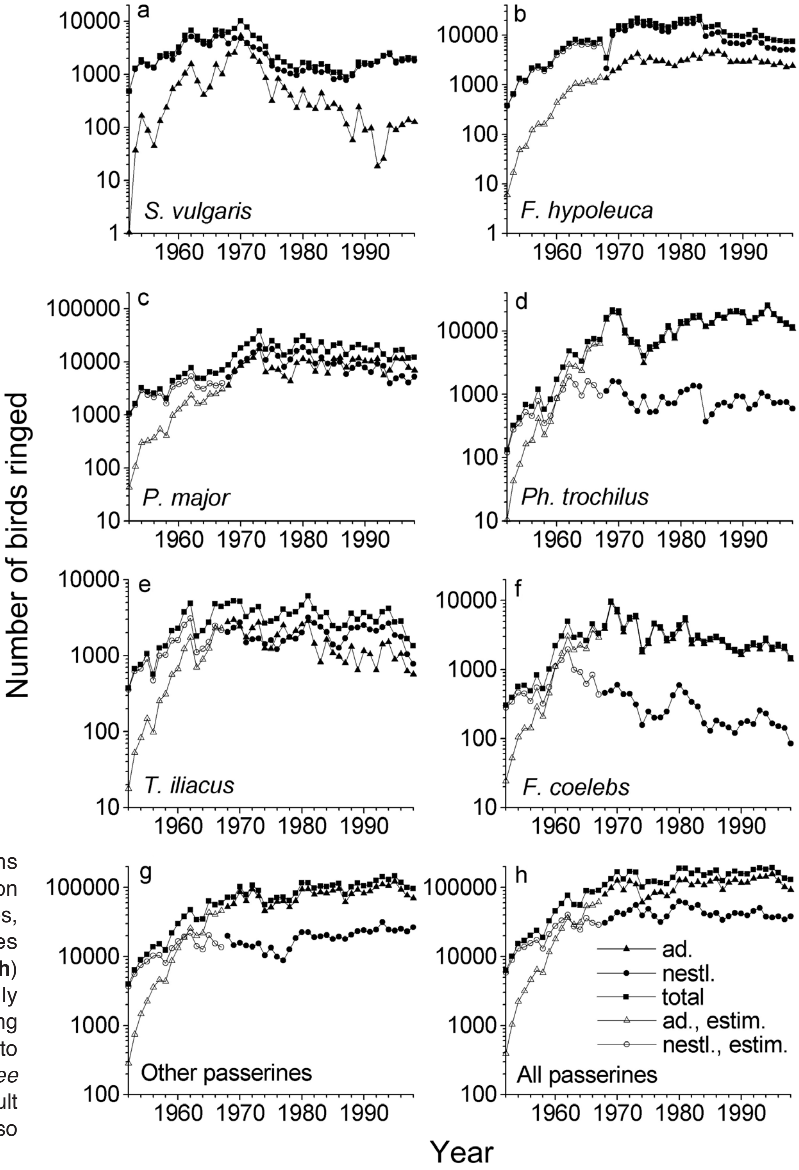

Fig. 1. Annual ringing sums of (**a**) starlings, (**b**–**f**) common hole and open-nesting species, (**g**) other passerine species excluding species **a**–**f**, and (**h**) all passerines excluding only starlings. In cases **b**–**h**, nestling and adult bird numbers had to be estimated until 1967 (*see* Methods). In the graphs, "adult birds" include birds ringed also as fledglings and juveniles.

nestlings and adults have been separated in the reports and summaries (e.g. Stén 1968, 1974). The annual number of adult starlings during 1952–1967 was calculated by subtracting the number of nestlings from the total number of ringed birds (Fig. 1 and Appendix 1).

Standardisation

It is not advisable to use the annual ringing numbers of a given species to estimate its population trends unless annual changes in ringing activity can be accounted for (Ginn 1969, Saurola 1978, Österlöf & Stolt 1982, O'Connor & Mead 1984, Bibby *et al.* 1992). In fact, in order to get reliable estimates of any variation in ringing effort, one should know (*i*) the annual total number of hours ringers spend on ringing, (*ii*) the total length of the mist-nets used for catching the birds, (*iii*) the time of year, and (*iv*) the weather conditions during ringing (e.g. Bibby *et al.* 1992). This kind of information is very difficult to collect, especially if data from several decades are required.

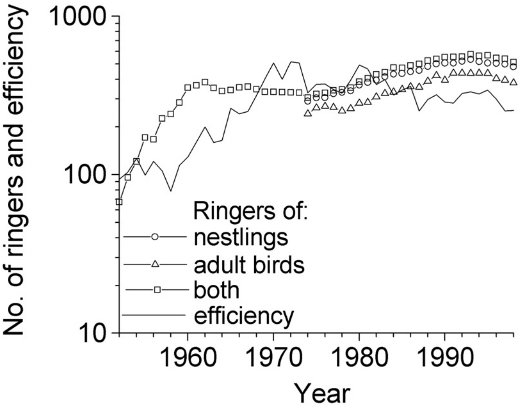

Fig. 2. Number of active ringers in Finland during 1952–1998. The numbers of ringers who had ringed nestlings or adult birds could be listed separately only since 1974. Total number means the sum of ringers who had ringed whatever species, nestlings or adult birds. The efficiency refers to the total number of passerine birds ringed per ringer.

Because exact data on changes in ringing efforts were not available, we used the annual ringing numbers of other species as indicators of ringing effort (*see* Ginn 1969, Österlöf & Stolt 1982, O'Connor & Mead 1984). We standardised the annual ringing numbers of starlings according to the ringing numbers of (*i*) two other abundant hole-nesting species (pied flycatcher *Ficedula hypoleuca*, great tit *Parus major*), (*ii*) three common open-nesting species (willow warbler *Phylloscopus trochilus*, redwing *Turdus iliacus*, chaffinch *Fringilla coelebs*), (*iii*) all other passerine species, excluding the two groups mentioned above and the starling, and (*iv*) all passerine species except the starling (Fig. 1).

In each group *i*–*iv* the annual ringing numbers of nestlings and of all birds (totals) were used as standards. The number of active ringers was not used. This is because ringing practices have been changing during the study period; for instance, the number of passerines ringed per individual ringer has increased during the 1950s and 1960s (Fig. 2). We assume that the ringing numbers of the standard species have been independent of abundance changes in the starling population: i.e. the changing availability of starlings for ringing has not affected ringing activities related to the other species.

Numbers of ringed starlings

In addition to the effects of variation in ringing effort and population density, the number of nestlings ringed is also affected by annual variations in brood size. The average brood size of starlings based on nestling ringing data has varied annually between 3.5 and 4.7 from the 1950s onwards, being at its lowest at the end of the 1960s (J. Rintala & J. Tiainen unpubl.). Solonen *et al.* (1991) found an increase in the average brood size from ca. 3.7 to 4.5 during the period 1968–1989. Assuming that ringers always ring all the nestlings from a brood, the original numbers of nestlings are a biased estimate of population change if the average brood size fluctuates. Hence, the effect of brood size on the number of ringed starling nestlings was corrected by the equation:

$$n'_t = n_t \frac{\bar{b}}{b_t}, \tag{1}$$

where n'_t = the corrected number of nestlings in year t, n_t = the number of nestlings ringed in year t, $\bar{b}$ = average brood size for 1952–1998, and b_t = average brood size in year t.

The brood size in a given year also has an effect on the number of birds other than nestlings that are ringed that year, mainly due to juvenile birds ringed in the autumn. Thus, the number of adult birds, including also full-grown juveniles, was corrected as:

$$a'_t = a_t \left(\frac{\bar{b}}{b_t} \right)^{0.5}, \tag{2}$$

where a'_t and a_t refer to corrected and real annual sums of adult starlings ringed, respectively. We then get the corrected total number of starlings (tot'_t) in year t as:

$$\text{tot}'_t = n'_t + a'_t. \tag{3}$$

Changes in brood size directly affect the number of nestlings ringed, but the number of adult birds ringed in a given year is not affected to the same extent as the nestlings, since a proportion of the ringed full-grown birds have been born in previous years. Furthermore, if juvenile mortality between fledging and ringing events is density dependent, year-to-year differences in the ringing numbers of adults due to variation in brood size will be even smaller. Thus, the realistic value of the exponential term in Eq. 2 would be somewhere between 0 (annual average brood size has no effect on adult numbers) and 1 (annual average brood size affects equally adult and nestling numbers). The real value for the exponent is not known, so we have used a midpoint value of 0.5. With an exponent of 0.5 and the same annual numbers of adult birds (a_t) and nestlings (n_t) ringed in years *t* and *t* + 1, a'_t and n'_t would increase by about 16% and 34%, respectively, if the average brood size simultaneously decreased from 4.7 to 3.5 nestlings per brood. However, the annual abundance indices of the starling are not very sensitive to the possible bias in the exponent, since nestlings constitute the majority of starling ringing data (Appendix 1). In the indices based on totals (*see* Fig. 4), the effect of the exponent on the maximum percentage of decrease in each series (mean ± SD, 95.58% ± 0.57% with exponent value of 0.5) varied by 0.03% ± 0.02% (mean ± SD), with exponent values of 0 and 1, respectively.

We do not have evidence at the national level for any long-term change in the average brood size of the other species (Fig. 1b–h). If such species-specific changes have occurred, we assume that they average out when ringing numbers of several species are pooled. The annual changes in age-structure (e.g. due to changes in annual survival) of populations of starlings and the remaining passerines (on average) might bias indices via changes in availability of nestling and adult birds for ringing. These effects are not considered here due to lack of data, and it may be that they are of only minor concern when estimating the confidence of the indices (*see* below).

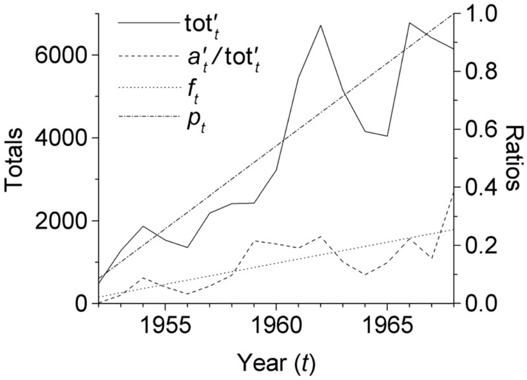

Fig. 3. Estimation of nestling numbers of standard species during 1952–1967 (Fig. 1b–h). Values are based on ringed starlings in 1952–1968 (Fig. 1a). On the left *y*-axis, tot'_t = corrected totals of starlings defined by Eq. 3, a'_t = corrected number of full-grown starlings by Eq. 2, and on the right *y*-axis, $f_t = 0.015t - 0.736$ (linear regression fitted for a'_t/tot'_t during 1952–1968), $p_t = f_t/f_{t=68}$.

Numbers of ringed standard species

The numbers of starlings ringed as adults increased faster than those of nestlings during the period 1952–1967 (Figs. 1a and 3). This tendency was mostly due to the rapid increase in the use of mist-nets during the 1950s and 1960s, especially at bird observatories (Nordström 1963, Saurola 1985, 1990). Until 1967, only the annual pooled sums of nestling and adult numbers of other species ringed were available. Thus, the proportions of nestling and adult birds were estimated for the period 1952–1967, assuming that during those years the trend for other passerine species did not differ from that for the starling. This trend was estimated by fitting a linear regression model (Fig. 3) of adult-to-total ratio a'_t/tot'_t for starlings during 1952–1968. The annual prediction of the linear model f_t was then scaled to proportions, $p_t = f_t/f_{t=68}$ (Fig. 3); these were used as annual estimators of the numbers of adult birds $\tilde{a}_t$ of each standard species group in the period 1952–1967 as follows:

$$\tilde{a}_t = \left(\sum_{t=68}^{72} a_t \Big/ \sum_{t=68}^{72} \mathrm{tot}_t \right) \mathrm{tot}_t p_t, \qquad (4)$$

where the summations are the numbers of adult and all individuals of standard species ringed during 1968–1972, and tot_t = total number of individuals of standard species ringed in year *t*. In the summations, a five-year period (1968–1972) was selected instead of a single year, to avoid the influence of annual variations in ringing practices.

The estimated annual number of nestlings $\tilde{n}_t$ of each standard species group was then calculated as:

$$\tilde{n}_t = \mathrm{tot}_t - \tilde{a}_t. \qquad (5)$$

For each standard group, the calculated nestling numbers $\tilde{n}_t$ for 1952–1967 and thereafter the nestling numbers actually recorded for 1968–1998 were used as standards. When standardising with totals, the original ringing numbers of 1952–1998 specific to each standard group were used (Appendix 1).

Indices denoting changes in abundance

The indices denoting changes in the annual abundance of the starling population i_t were calculated as follows:

$$i_t = x_{t,\text{starling}}/x_{t,\text{standard}}, \qquad (6)$$

where $x_{t,\text{starling}}$ is the annual number of starling nestlings or totals from Eq. 1 or 3, and $x_{t,\text{standard}}$ is the corresponding standard group value (*see* above).

We evaluated the consistency of results from various calculated abundance indices using principal component analysis (PCA) that gives a general view of the similarities between different time series. The synchrony of different index series and their ability to detect and time possible major changes in the size of the starling population were estimated by fitting a running five-year linear regression model on each series. The regression coefficients were calculated and tested to estimate the strength of the trend.

The simulation model

In order to define confidence limits for the change indices, a Monte Carlo simulation (e.g. Manly 1997) based on time series regression analyses of the ringing totals of both starlings and a standard group (all passerines) was constructed. In the simulation, randomised indices were generated, based on a "null model" (*see* Appendix 2) with the expectation of "no short or long-term trends in the indices" (i.e. with the trends for ringed starlings and the standard species group being the same).

The annual ringing totals involved in the analyses were first log-transformed and differenced ($y_t = x_t - x_{t-1}$), allowing interpretation of the values as relative changes in abundance between successive years (Chatfield 1989, Hendry & Doornik 1996). The principal components of the transformed total numbers of the three passerine bird groups (hole-nesting, open-nesting, and the remaining species) were derived, and the first principal component (PC1) was used as the explanatory variable in the regressions. In spite of the difference transformations, slight long-term trends still remained in the time series (and in PC1). Because of this, the time series were thoroughly detrended by regressing the variables against polynomials for the year t (linear, quadratic, and cubic forms). Finally, the resulting residuals were used as variables in the regression analyses (Chatfield 1989). If the long-term trends had not been removed, the specification of the null-model parameters would not have been exact.

The "real" ringing activity variable X (*see* Appendix 2) is more or less arbitrary. Ideally, X should correlate well with the applied standard group (all passerines). On this basis, it was convenient to choose PC1 to represent X (*see* Table 1). Because principal components are not affected by the sample size of the variables, we assumed PC1, *a priori*, to be equally affected by the standards (hole-nesting, open-nesting, and other passerines). It should be borne in mind that quantitatively speaking, PC1, if transformed to counts in a multiplicative scale, would not have much to do with the theoretical "ringing activity potential"; however, above all, the variation in PC1 should explain most of the variation in the numbers of both starlings and all passerines.

The time series regression models fitted on the observed data take the form:

Table 1. Factor loadings of principal components calculated on detrended (log-transformed and differenced) ringing totals of three standard groups (+ variables, cf. Fig. 7). Pearson correlation coefficients are shown also for the corresponding time series of all passerines and the starling (Fig. 8).

Variable	PC1	PC2	PC3
+ Hole-nesting	0.792	0.557	0.250
+ Open-nesting	0.788	–0.567	0.241
+ Other passerines	0.903	0.006	–0.429
All passerines	0.982	0.035	–0.174
Starling	0.474	–0.226	0.148

$$Y_t = \beta_0 X_t + \ldots + \beta_p X_{t-p} + \rho_1 Y_{t-1} + \ldots + \rho_p Y_{t-p} + \varepsilon_t, \quad (7)$$

where β_is are regression slopes for the annual ringing activity estimate X (= $X_{t=0} \ldots X_n$) and for its time lagged values of order p years (X_{t-p}). Notice that the ρ_i terms characterise the autoregressive process (of order p, Y_{t-p}) in Y (= $Y_{t=0} \ldots Y_n$), and that ε (= $\varepsilon_{t=0} \ldots \varepsilon_n$) contains annual residual errors. Separate regression models were estimated on the detrended totals of starlings and passerines (Y).

In simulations, the randomised ringing effort and the random residuals of the starling and passerine models ($\hat{X}$, $\hat{e}_{\mathrm{ST}}$, and $\hat{e}_{\mathrm{ALL}}$, respectively; *see* Appendix 2) had zero means and standard deviations of X (i.e. PC1), e_{ST}, and e_{ALL}, respectively, as expectation values (Appendix 2); all calculations from Eq. 7.

The randomised (logarithmic) counts of starling and passerine totals were derived as follows:

$$\begin{aligned} \log \hat{N}_{1953} &= \log N_{1952} + \hat{Y}_{1953} \quad (8) \\ \log \hat{N}_{1954} &= \log \hat{N}_{1953} + \hat{Y}_{1954} \\ &\vdots \\ \log \hat{N}_{1998} &= \log \hat{N}_{1997} + \hat{Y}_{1998}, \end{aligned}$$

where $N_{t=1952}$ is the initial number ringed in 1952, $\hat{N}_t$ is the randomised annual number of ringed starlings or passerines, and $\hat{Y}_t$ is the corresponding randomised Y_t (cf. Appendix 2). Finally, indices in the multiplicative scale were obtained by calculating $10^{\log \hat{N}_{t,\mathrm{starlings}} - \log \hat{N}_{t,\mathrm{passerines}}}$.

A procedure was set up to generate 5000 independent random index series. Each of these was finally scaled by the index value of every possible base year (i.e. indices of base years were fixed to one), thus allowing year-by-year comparisons of the simulation results. The expectations (H_0) for the model based numbers and indices are straight lines with no short or long-term trends. By comparing the output distribution of randomised indices to the observed index series, it was possible to make statistical inferences about the observed population trends. Regression analyses were carried out with PcGive version 9.10 (Hendry & Doornik 1996) and randomisations with @Risk (1997).

Stationarity is a crucial property of variables in time series models. Stationarity means that relatively long time series do not exhibit any systematic changes in mean and variance and the autocorrelation becomes small when the time lag increases. If stationarity is violated, the results of statistical models will be inaccurate and biased. Therefore, all the time series of regression models that we used were tested for the existence of unit roots (Dickey-Fuller test, Hendry & Doornik 1996). If non-stationarity is the case, time series are said to have a unit root, and differencing of the series is needed. According to the test, non-stationarity was characteristic of the time series of the log-transformed numbers of ringed starlings and the other species groups involved in the analyses. One time differencing of the respective numbers resulted in significant unit root test statistics, indicating stationarity of each detrended time series. In addition, the first principal component used in the regression analyses was stationary.

A variety of diagnostic tests were performed on the structure of the error terms and on the validity of regression models; the tests comprised serial correlation, heteroscedasticity, autoregressive conditional heteroscedasticity (ARCH), normality, and a regression specification test (RESET). For more detailed information on these diagnostics for the validation of models *see* Hendry and Doornik (1996). The diagnostic tests did not indicate misspecifications in the models.

The confidence intervals of indices were also estimated using generalised linear models, experimenting with Poisson errors and acknowledging serial correlation and overdispersion of counts (e.g. McCullagh & Nelder 1989). These were estimated using the TRIM package designed specifically for the analyses of census data (Pannekoek & van Strien 2001). The ringing totals of starlings were set as the explanatory variable and the standard (totals of all passerines) was used as a weight factor in a log-linear model (Pannekoek & van Strien 2001).

Results

Abundance change indices

The annual numbers of ringed adult starlings increased much faster than the numbers of

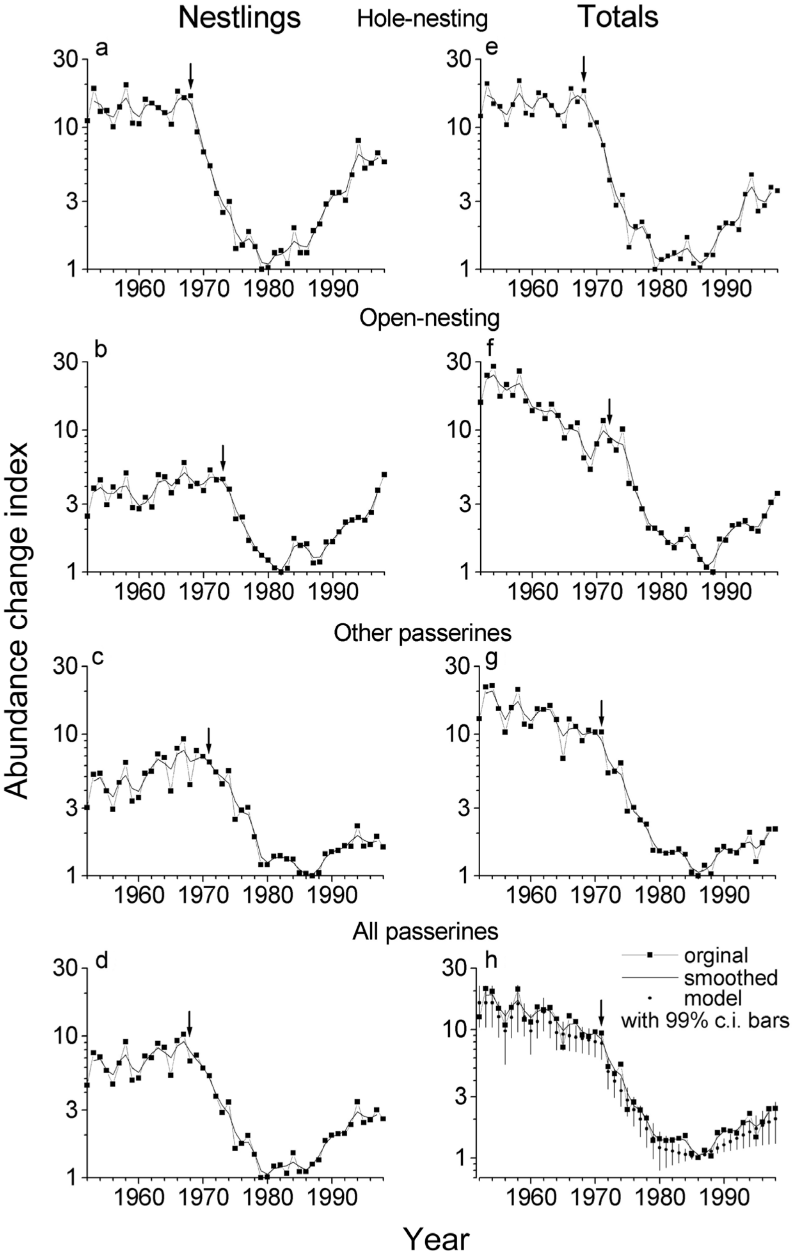

Fig. 4. Abundance change indices of the starling population based on eight different standardisation methods. Indices by Eq. 6 were scaled such that the smallest value is unity for every index series. Lines show smoothed index series according to a three-year weighted running mean, $(i_{t-1} + 2i_t + i_{t+1})/4$ (cf. Österlöf & Stolt 1982). On the left side of a panel (**a**–**d**) standardisation is based on numbers of nestlings and on the right side (**e**–**h**) total number of birds ringed. Different standard species groups are arranged by rows of the panel. Hole-nesting species consist of the pied flycatcher *Ficedula hypoleuca* and great tit *Parus major* (**a**, **e**); open-nesting species of the willow warbler *Phylloscopus trochilus*, redwing *Turdus iliacus*, and chaffinch *Fringilla coelebs* (**b**, **f**); other passerine species excluding the two previous groups and the starling (**c**, **g**); and all passerine species excluding the starling (**d**, **h**). The estimated start of the collapse is denoted by an arrow on each graph. The arrows were positioned by the start of the continuous decline according to the smoothed index series. Model based indices and their 99% confidence intervals (**h**) were estimated with generalised linear models (*see* text). The base year of the model indices were set at 1986.

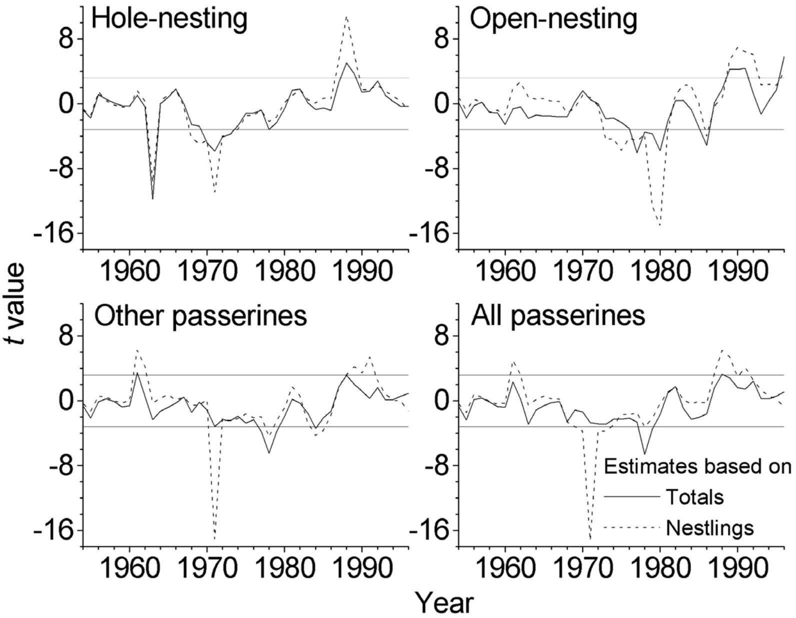

Fig. 5. Values of the *t* distribution for slopes of regression equations fitted for each index series (cf. Fig. 4). Regression coefficients are based on annually shifting five-year periods during 1952–1998 (median year of each period on *x*-axis). Critical values of the *t* distribution ($P = 0.05$, df = 3) are shown with horizontal lines on the graphs. The main purpose is to give an overall view of the general patterns. This is more or less descriptive, since serial correlations are not considered in the analyses. Thus, inferences from the statistics should be made cautiously.

nestlings during 1952–1967 (Figs. 1 and 3). Abundance change indices based on nestlings as the standard showed more or less increasing or steady trends from 1952 to 1970. However, over the same period, indices based on totals merely showed declining trends (Fig. 4). According to the indices using totals as the standard, the percentage decline was 90% ± 2.6% (mean ± SD) during 1967–1986 and 51% ± 18.7% during 1976–1988. The different standardising methods showed a large (two to six-fold) increase from the mid-1980s until 1998. Overall, the increasing trends diminished when large species groups were used as the standard instead of smaller species groups. The increase was at its smallest when the ringing totals of passerines were used as the standard (Fig. 4g and h). Several index series showed a relatively deep drop followed by a sudden recovery during 1984–1989, but even prior to that time, the population seems to have stabilised after the main collapse (e.g. Fig. 4h).

The annual statistical significances of the five-year running regression coefficients (Figs. 5 and 6) on the eight index series (Fig. 4) suggested (*i*) no increasing nor decreasing trends, (*ii*) increasing or no trend, (*iii*) decreasing or no trend. As regards the occurrence of significant declines, the population turned quite sharply towards a decline, from a more or less steady state, in the late 1960s and early 1970s (Fig. 6). According to the smoothed indices, the decline started at the earliest in 1968 or at the latest in 1973 (Fig. 4). During 1974–1986 significant declining trends were common among the index series; in 1978 in particular most of the regressions suggest significant declines (Fig. 6). Significant increasing trends occurred during five-year periods denoted by the median years 1961, 1962, 1987–1992, and 1996. In 1989 most of the series showed increasing trends.

According to the principal component analysis (PCA) on all the eight index series for 1952–1998 (Fig. 4), the first principal component (PC1) alone explained 84.7 and the second (PC2) 8.6 percent of total variance. The correlations of PC1 with indices based on the ringed nestlings of hole-nesters, open-nesters, other species, and all species were 0.94, 0.80, 0.86, and 0.97,

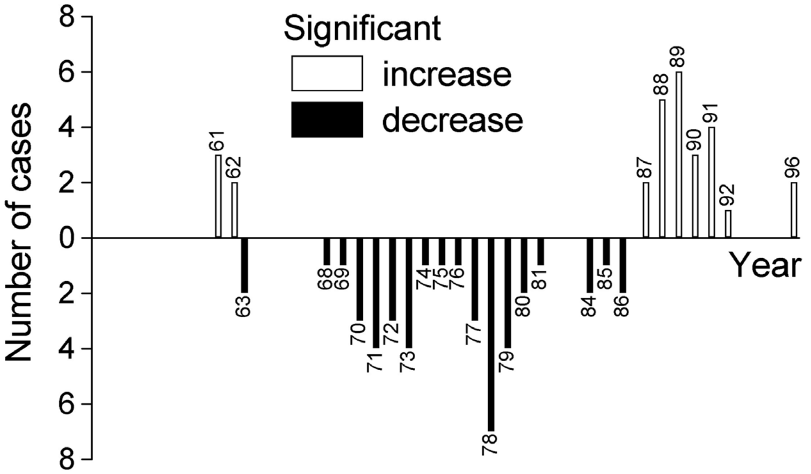

Fig. 6. The annual number of significantly increasing or decreasing five-year index trends among the eight index series (Fig. 4) based on running regression coefficients during 1954–1996 (cf. Fig. 5).

respectively. The correlations with indices based on the total numbers of the respective groups were 0.96, 0.89, 0.96, and 0.97, respectively.

Model based indices (4h) were estimated stepwise (backward) using Wald statistics as selection criteria for the parameters of the generalised linear model. To avoid a (practically) saturated model being selected, and hence meaninglessly narrow confidence intervals for the indices, the stepwise selection was started from a reduced model, with turning points allowed for every second year starting from 1952, with the exception of the period 1968–1972 for which annual changes were allowed. Changes in the index trends were statistically significant in years 1954, 1956, 1958, 1960, 1962, 1964, 1971, 1972, 1980, and 1986 (Fig. 4h; Wald statistics ≥ 6.02, $P < 0.05$, df = 1).

Simulation results

The first principal component of the transformed time series for ringing totals of the three passerine bird groups correlated especially strongly with the detrended totals of passerines, and also relatively well with the corresponding numbers of starlings (Table 1 and Fig. 7). The explanatory variables of stepwise (backward) multiple regression models constructed on starling and passerine

Table 2. Regression models for the relative changes of ringed starlings (SV) and passerine totals (ALL). The explanatory variables are two-year lagged starling series (SV_2), one-year lagged passerine totals (ALL_1), the first principal component of the standard species groups (PC1), and PC1 with lags of one year (PC1_1). All the variables are thoroughly detrended by polynomials on the differenced logarithmic series. Parameter estimates (β) with standard errors (SE), *t* statistics, significances (*P*), and coefficients of multiple determination (R^2) are given for each variable. Sample periods are shortened due to differencing and time lags of variables.

Model	Variable	β	SE	*t*	*P*	R^2	Sample period
SV	SV_2	–0.284	0.099	–2.864	0.0066	0.17	1955–1998
	PC1	0.043	0.009	4.777	< 0.001	0.36	
	PC1_1	0.047	0.009	5.198	< 0.001	0.40	
$F_{(3,41)} = 18.193$, $P < 0.001$, $R^2 = 0.57$							
ALL	ALL_1	–0.427	0.141	–3.032	0.0042	0.18	1954–1998
	PC1	0.067	0.002	32.602	< 0.001	0.96	
	PC1_1	0.025	0.010	2.628	0.0119	0.14	
$F_{(3,42)} = 384.670$, $P < 0.001$, $R^2 = 0.96$							

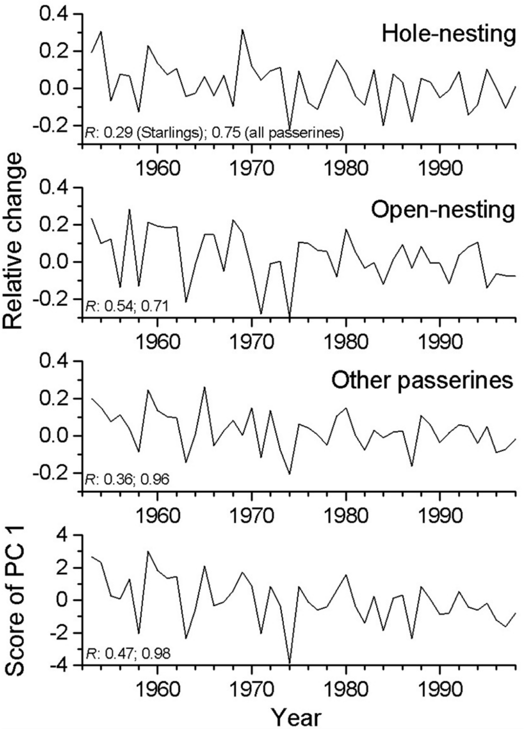

Fig. 7. Log-transformed and differenced time series of ringing totals of three passerine bird groups. Values denote the relative increases or decreases of ringing numbers. The scores for the first principal component of the above variables are shown in the bottom graph. Pearson correlation coefficients (*R*) with relative changes of ringing totals of starlings and all passerines are shown for each time series.

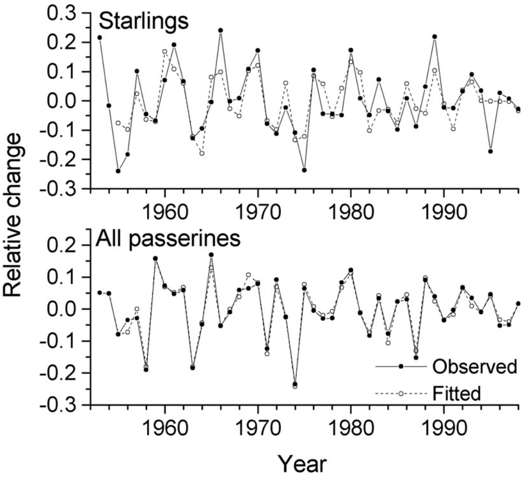

Fig. 8. Fitted values of the time series regression models (Table 2) on the observed log-transformed and detrended ringing totals of starlings and all passerines in Finland, 1953–1998.

data, respectively (Table 2 and Fig. 8), comprised the first principal component and its lagged values up to four years, as well as autoregressive variables up to order four. Specification of the passerine model was straightforward. The starling model was somewhat more complicated, since the autoregressive mutually exclusive parameters with lags two and four produced ostensibly quite similar model fits: the coefficients of determination were 0.57 and 0.56 for lags two (coefficient = –0.284 ± 0.099 SE) and four (coefficient = 0.198 ± 0.098 SE), respectively. A strict stepwise path led to the choice of lag two. Furthermore, partial autocorrelation functions (PACF) on (*i*) the detrended starling series itself, and on (*ii*) the residuals of three models without autoregressive elements reduced from the final model (explanatory variables PC1 + PC1_1, PC1, and PC1_1; Table 2) supported the chosen specification of the model. PACF coefficients were always negative at lag two and positive at lag four. Significant correlations were detected at lag two on the detrended starling series (PACF: coefficient = –0.37, $P < 0.05$) and on the residual series of the model, with only PC1 as the explaining variable (PACF: coefficient = –0.36, $P < 0.05$).

Simulation results suggested statistically significant short and long-term changes in the observed indices (Figs. 9 and 10). In the long term, all the indices starting from 1972 were significantly smaller than the index for 1954, and the majority was significantly smaller than the index for 1971. The indices starting from 1987 were not significantly larger than the index for 1986 (Fig. 9a–c). In general, the observed starling indices starting from the early 1970s were significantly smaller than the indices for the 1950s and 1960s (Fig. 10). The start of the collapse can be dated to the year 1972, since the series with the base year of 1971 are almost throughout significantly negatively labelled. The year 1972 was also the year when labels denoting a significant decline started to become more and more common. In 1975 all of the comparisons showed a significant decrease (Fig. 10).

The comparisons give a general view of the significances of continuous patterns in the

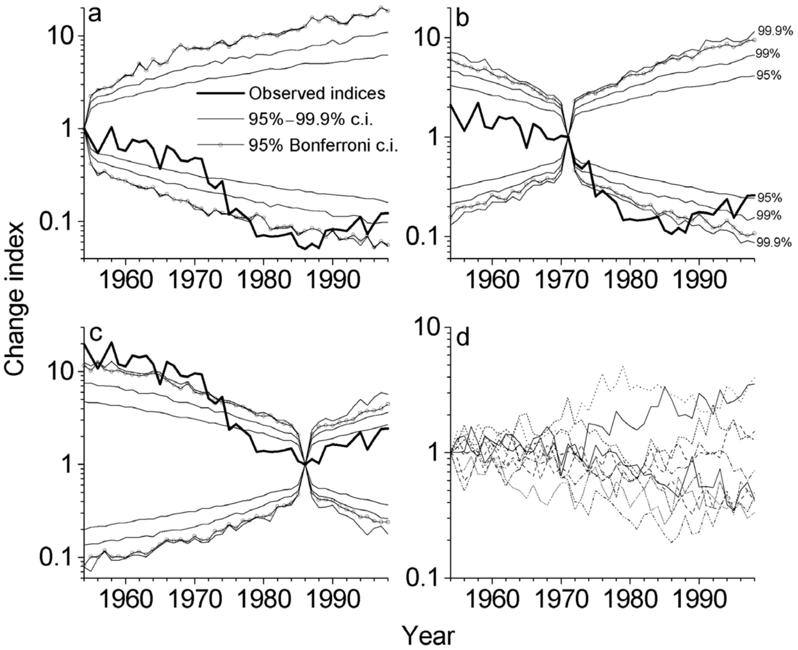

Fig. 9. The observed change indices of the starling population with their simulated upper and lower 95%, 99%, and 99.9% confidence intervals and 95% Bonferroni-corrected confidence intervals, 1954–1998 (**a**–**c**). The base years of the indices are set at 1954 (**a**), 1971 (**b**), and 1986 (**c**). For instance, the lower Bonferroni-corrected percentile has been calculated forward and backward from the base year by 2.5%/(1998–base year) and 2.5%/(base year–1954), respectively. Thus, the longer time the interval, the greater the Bonferroni correction. If the indices are outside a certain confidence belt, they are significantly smaller or larger than the index for the base year of the series in question. Ten examples of the individual random index series based at 1954 are also shown (**d**). Because of the two-year time-lag in the starling variable (Table 2), the actual simulation starts at 1955. Randomisations were initiated by assuming the first two values (1953 and 1954) of the transformed numbers of starlings, Y_t of Eq. 7 to be independent random numbers with mean and standard deviation equal to the observed average and standard deviation during 1953–1998. Thus, in the initiation period, indices were not subject to model parameters. Similarly, simulation of passerine totals started at 1954.

indices, e.g. situations when indices are, for relatively long periods, below the lower confidence intervals (Fig. 10). If we are testing individual indices then Bonferroni-corrected significance levels should be preferred (Fig. 9a–c); this is because significant results may occur by chance when a large number of comparisons are performed on the same series. Continuous trends and occasional peaks tended to occur in the simulated series (Fig. 9d). In certain years peaks in the observed indices were significantly different (at 5% level) from base years according to conventional confidence limits, but not according to Bonferroni-corrected limits: e.g. 1965, 1973, 1995 (Fig. 9a), 1973, 1992, 1995 (Fig. 9b), and 1976 (Fig. 9c). Overall, the Bonferroni-corrected comparisons showed significant decreasing index patterns in the long term, but not as clearly as the uncorrected confidence lines. Even after the Bonferroni correction, the drop in the indices in comparison to 1971 was almost significant in 1972, and from 1975 it was significant until 1988.

Discussion

Evaluation of the methods

Using ringing totals in population monitoring is complicated, since the annual variation in numbers of ringed birds is dependent not only on variations in population size, but also on variations in the ringing effort that usually cannot be estimated directly (e.g. Ginn 1969, Österlöf & Stolt 1982). Indirect estimates of ringing effort, such as those which use the ringing totals of passerines as a standard, are inaccurate if (and when) the abundance of the species used as standards fluctuates, or alternatively, in cases where ringers concentrate on a particular (target or standard) species, but this specialisation is unknown (e.g. Ginn 1969, Bibby *et al.* 1992). Another problem is how well the geographical distribution of ringers corresponds to that of target species in cases where there are geographical differences in the population trends of the target species. This is perhaps not a problem in our results, since ringing activities and starlings occur mainly in the south of Finland (*see* Saurola 1985, Väisänen *et al.* 1998).

Despite these problems, the estimates of starling population trends have been consistent with the available census data since the end of the 1960s (Solonen *et al.* 1991, Väisänen *et al.* 1998, later discussion). Ginn (1969) studied the ringing numbers of sixteen British farmland species and found that the annual variation in the numbers of nestlings corresponded well with the numbers estimated from common bird census (CBC) data during the 1960s. Based on those observations, Ginn (1969) concluded that ringing data could be useful as an additional confirmation of changes in population size, especially when large-scale fluctuations are involved (*see* also O'Connor & Mead 1984). The long-term trends of several passerine species, as estimated from Swedish standardised ringing numbers, corresponded to other monitoring results, and for those species migrating through Sahara, the trends could be explained by drought in the Sahel zone (Österlöf & Stolt 1982). More restricted ringing data from bird observatories have also been shown to be valuable in monitoring bird populations (Hjort & Lindholm 1978, Berthold *et al.* 1999).

The effect of the population fluctuations of standard species on the change indices for starlings could also be calibrated with available census data on passerines (since the late 1970s, Väisänen *et al.* 1998). However, this would not be straightforward, since the ringing of passerines is biased towards more or less densely populated human settlements in southern Finland (*see* Saurola 1985, Haapala & Saurola 1995) while national census data are unrepresentative of those areas (Väisänen *et al.* 1998). Looking at the numbers of passerines ringed in Finland (Fig. 1), no major changes can be observed that stem from reasons other than the general increase in ringing activity (Fig. 2). Because the error structure of the starling indices is probably due mainly to uncontrolled ringing activities, we decided not to consider calibrations with all available passerine census data.

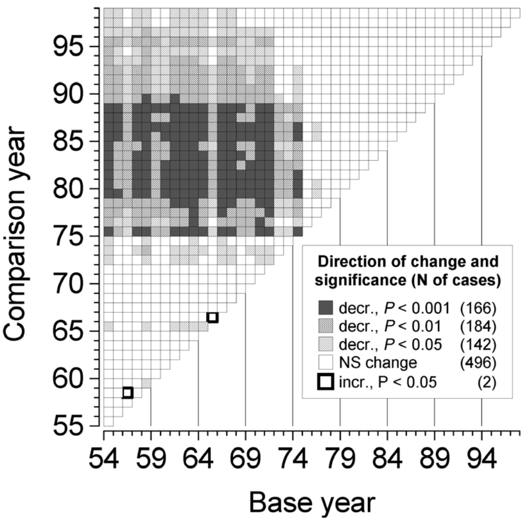

Fig. 10. Statistical significances of the differences of all possible annual index pairs (1954–1998) for the starling population based on the simulation data (cf. Fig. 9). The shading of the cells indicates whether the annual indices of the comparison year (*y*-axis) are significantly decreased, increased, or non-significantly (NS) different from the corresponding base-year index (*x*-axis).

The confidence intervals of indices estimated with a generalised linear model (Fig. 4h) are too narrow, since in addition to the effect of having large numbers of starlings ringed, the model also assumes that the ringing effort for starlings (the weight factor, *see* Pannekoek & van Strien 2001) is known precisely; this cannot be the case with our data, since they lack any direct measures of ringing efforts. Serial correlation is a typical feature of time series data (e.g. Chatfield 1989). This was true also for the ringing data as shown by the analyses. Thus, standard regression analyses considering the running slope coefficients (Fig. 5) are probably also robust. It was for this reason that we considered the Monte Carlo simulation approach (*see* Manly 1997) to be the most appropriate, even if it is rather complex, and not a standard method for estimating the confidence of change indices. On the other hand, we recommend the use of generalised linear models in the analysis of ringing data based, for example, on standardised mist-net projects for which the precise ringing effort is known (e.g. Bairlein *et al.* 1994, Haapala & Saurola 1995, Karlsson *et al.* 2002); this also applies to ordinary census data (e.g. Väisänen *et al.* 1998).

Standardisation

The first principal component of the eight index series (Fig. 4) correlated better with the index series based on totals (Fig. 4e–h) than with the corresponding indices based on nestlings (Fig. 4a–d). This suggests that indices derived from totals are more consistent, and thus probably more reliable than indices based on nestlings. Regarding the various standard groups of totals, we propose that the ringing totals of all passerines are the most relevant standard, in preference to the smaller passerine groups, since they have a high correlation with the first principal component of three groups of totals (PC1; Table 1 and Fig. 7). PC1 was also an important (positive) factor in regression models, explaining well the relative changes in the numbers of ringed starlings and all passerines (Table 2).

Nestlings were not a useful standard, since there were uncertainties in the estimation of the nestling numbers up to 1967 (Figs. 1 and 3). The rate of increase of ringed adult passerine birds (other than hole-nesters) was probably overestimated; this may have diminished the rate of increase of ringed nestlings in comparison with the unknown real adult-to-nestling ratios. A possible reason for this could be that natural nests are generally more difficult to find (or reach) than the man-made nest-boxes preferred by starlings (whose adult-to-nestling ratios were used as the basis of the estimates, Figs. 1 and 3). Perhaps due to the increasing experience of ringers during the early years, the ringing effort on birds nesting in locations other than artificial nest-boxes increased. This could not have been the case for the starlings, as only a minority of pairs breed in natural holes, and these are also largely inaccessible to ringers. For instance, the declining numbers of ringed nestlings of the chaffinch during 1952–1994 (more nestlings were ringed even in the early 1950s than in the 1980s and 1990s, Fig. 1f) support the idea that the numbers of nestlings of open-nesting passerine birds generally were overestimated in the early 1950s. Any possible (but not very realistic) bias in the other direction, i.e. that the real rate of increase for full-grown birds was higher than the estimated one, would not have seriously affected the abundance index trends (Fig. 4a–d), since only a minor part of the estimated total number of the passerines consisted of adult birds at the start of the 1950s (about 5%, Fig. 1).

The restrictions and guidelines for the ringing of nestlings of certain species (Saurola 1985) may also have skewed the indices based on nestlings. A restriction on ringing pied flycatcher nestlings was announced in 1984. In order to ring nestlings, 90% of females and 50% of males of the ringed broods had to be ringed or retrapped (Saurola 1985), and this most probably caused the sudden decrease in the ringing of nestlings of this species from 1984 on. The total numbers of ringed pied flycatchers also dropped, but not to the same extent as the numbers of nestlings (Fig. 1b and Appendix 1). Ringing projects for the nestlings of open-nesting passerine species (*Saxicola rubetra*, *Luscinia svecicus*, *Emberiza rustica*, *Sylvia communis*, *Carpodacus erythrinus*, *Lanius collurio*) were undertaken during the late 1970s and the 1980s (Saurola 1985); probably this was at least partly responsible for the coinciding increase in the numbers of ringed passerine nestlings. The total number of passerines ringed did not increase as strongly as that of nestlings during the start of the ringing projects (Fig. 1g and Appendix 1).

Certain projects have also been established for the ringing of full-grown birds; these include the "Acroproject" for the sedge warbler *Acrocephalus schoenobaenus* which has been going on since the beginning of the 1980s (Saurola 1981, Koskimies & Saurola 1985). These kinds of activities may have skewed the estimates for ringing effort when the ringing totals of all individuals were used as standard. Nevertheless, no apparent relative effect on the total number of ringed passerine birds has been observed since the start of the Acroproject (Fig. 1g and h, Appendix 1). Standardised mist-netting projects, or constant effort sites (Peach *et al.* 1998), have been used for monitoring purposes in Finland from 1986 onwards (Bairlein *et al.* 1994, Haapala & Saurola 1995). These activities may, at least to some extent, have affected the ringing of starlings as well as the ringing of passerines in general. Yet overall, the bias in index estimates due to the monitoring projects is probably negligible. It is, however, worth noting that there were increasing efforts to ring roosting starlings in reed beds when starlings were still abundant in the late 1960s and early 1970s; these activities may have caused an extra jump in the population estimate based on totals as standards (cf. Fig. 4d and h, Appendix 1). To sum up, we consider the ringing totals of all passerines to be the best standard currently available. Thus, in the following discussion, more attention will be paid to the indices based on standardisation with passerine totals than to the other indices.

Simulations

The models explained annual variations in the ringing numbers of starlings and passerines fairly well (Table 2 and Fig. 8). The error variation, i.e. the excess or deficit in the observed numbers in relation to fitted values, was due to annual variations in the availability of birds for ringing. The availability changes were due to unquantifiable human and ecological factors such as the movements and actions of ringers, the spatial and temporal dynamics of bird populations, weather conditions during ringing, the timing of migration, and so on. The model fits were better for all passerines than for starlings (Table 2 and Fig. 8), which seemed quite logical, since the ringed totals of a large bird group are probably not as sensitive to random factors as are the numbers of just one species. We must bear in mind that the statistical significances of the population changes among starlings are on the conservative side, since the error variation in indices is due not only to the stochastic-like population dynamics of starlings, but also to the dynamics of the other passerines and to the unknown decisions of the ringers.

The autoregressive parameter with lag two in the starling model (Table 2) is explainable by population dynamics. The partial autocorrelation functions suggested density-dependent population regulation by a second-order autoregressive process (Chatfield 1989). The aim of this work was not to analyse whether the dynamics of Finnish starlings are cyclical in nature; we would merely point out the index estimates (Fig. 4) that could indicate such dynamics, involving a four-year cycle, especially during the times before the collapse. Based on the significance of partial autocorrelations, we assume that delayed density dependence is present in starling dynamics, and that this may have led to population cycles. It has been shown that cyclic population dynamics, resembling e.g. those of Finnish grouse species, can be generated with density dependent autoregressive models (e.g. Kaitala *et al.* 1996).

It is unclear why passerine totals were negatively affected by a one-year lagged autoregressive variable (Table 2). The phenomenon may have been due to the density-dependent dynamics of the most abundant passerine species, or else due to the effect of very efficient ringing years, which were followed by less efficient years with lower numbers of birds ringed.

Trends in abundance

The index estimates mainly showed decreasing or fairly stable trends in the starling population during the 1950s and 1960s (Fig. 4). The confidence limits of the indices based on totals as standard suggested no long-term trends preceding the collapse (Figs. 9 and 10), i.e. the statistical null hypothesis (no change at all) was retained. According to the line-transect censuses, starlings increased by one third from the mid-1950s to the mid-1970s (Väisänen *et al.* 1998), but these results are not very convincing since they are based on small and geographically restricted data. During 1952–1963 (data from eight years) the number of census routes varied between 1 and 34 with an average of 16 routes; during 1973–1991 (data from eleven years) the number of routes varied between 7 and 296 with an average of 117 routes (Väisänen *et al.* 1998). In comparison to the line-transect census data, the ringing data are very large, especially when the data from the 1950s and 1960s are considered: considering starling nestlings alone, the number of ringing localities (with precise locations established to within minutes of degrees in geographical coordinates) has varied between 40 and 298, with an average of around 170 during 1952–1998. Since 1954 the number has been at least 90.

The availability of pastures is important for the persistence of starling populations (e.g. Feare 1984, Tiainen *et al.* 1989, Solonen *et al* 1991, Robinson *et al.* 2002, Smith & Bruun 2002). The number of cattle farms in Finland declined by one third during 1959–1969 (Official statistics of Finland). This supports the idea that starlings barely increased during the 1960s (cf. below).

The suggested timing of the start of the collapse varies according to the standardisation method applied, but is close to the turn of the 1960s, moving into the 1970s. The simulation model suggests the year 1972 for the starting point of the collapse. Indices based on the log-linear model date the statistically significant turning point towards decline at 1971 (Fig. 4h), and thus the starting of the collapse at 1972. In the literature, the first reports of the collapse came as late as the end of the 1970s (von Haartman 1978, Ojanen *et al.* 1978, Orell & Ojanen 1980). Solonen *et al.* (1991) found that among twenty local populations from southern to northern Finland, the decline started in 1970, which is very close to our estimate.

The simulation model suggested a highly significant population decline during the 1970s and 1980s (Figs. 9 and 10). On the other hand, we cannot make accurate inferences regarding the amount of the decline owing to the wide confidence belts of the indices (Fig. 9). According to the indices based on totals as standard, the population declined on average by 90% (the average from the numbers in Fig. 4e–h) during 1967–1986. A calculation based on Solonen *et al.*'s (1991) local population data indicates an 85% decline over the same period. From 1976 to 1988, the indices (Fig. 4e–h) show an average decline of 51% while indices based on the line-transect censuses show a decline of 75% (Väisänen *et al.* 1998). Each of these sets of data may have its own source of bias. Solonen *et al.*'s data are quite small, and local processes may have biased the estimate for regional population development. The national census data cover all kinds of environments, but occasionally they may have been unrepresentative of the starling population. The timing of transect counts is not optimal and the data are not entirely representative of the farmland areas and human settlements that form the main breeding environments of starlings (Väisänen *et al.* 1998). Unfortunately, ringing data are also biased, for example by variations in the ringers' activities and routines. Nevertheless, the indices based on the census data (Solonen *et al.* 1991, Väisänen *et al.* 1998) and the ringing data are all in general agreement regarding the collapse, making it easier to claim that the decline was a reality, and that it was registered within the ringing data.

The decline of the starling (Fig. 4) coincided quite closely with the widespread abandonment of cattle farming that has taken place in Finland since the end of the 1960s. In the period 1969–1990, the number of cattle farms fell by 75%, and the number of dairy cows fell by 50%. Over the same period, the area under pasture fell by 50% (Information Centre of the Ministry of Agriculture and Forestry in Finland). Tiainen *et al.* (1989, *see* also Smith & Bruun 2002) showed that the nestling mortality of starling populations in southern Finnish agricultural areas was much lower in mixed farming areas containing cattle than it was in root crop and cereal cultivation areas, i.e. in those areas which represent typical specialised farmland after dairy farming is abandoned. Solonen *et al.* (1991) suggested that the disappearance of pastures from breeding habitats was the reason for the decline of several local starling populations in Finland. The relationship between declining starling populations and the disappearance of pastures has also been suggested with regard to other northern and western European areas (e.g. Møller 1983, Robinson *et al.* 2002, Smith & Bruun 2002).

Indices based on ringing data suggest some degree of population increase since the middle of the 1980s. Without the sudden drop and recovery of the indices during 1984–1989 (Fig. 4), the total increase up to 1998 would not have been as striking as it appeared to be. Whether the starling population has really started to increase or not remains a somewhat open question, since, for example, the trend inferred from ringing data conflicts with Väisänen *et al.*'s (1998) indices from line-transect census data that indicate declining trend up to 1995. If there has been a true increase, it has so far been too small to be confirmed by statistical tests on the data collected.

Conclusions

Despite many uncertainties in the methodology, the standardised starling ringing data do give us some crucial information regarding the long-term development of the starling population in Finland. We conclude that (*i*) the population size was fairly stable during the 1950s and 1960s, (*ii*) the national decline started at the end of the 1960s or at the beginning of the 1970s, and the population was stabilised by the end of the 1980s, (*iii*) the decline of the population was statistically highly significant, and could be estimated at around 90% from the late 1960s up to the mid-1980s.

Ringing is a common and widespread activity in Finland. Hundreds of volunteer ringers invest much effort in ringing both nestling and adult birds. If this annual effort could be fully quantified and documented, bird ringing would complement other annual bird census work extremely well. Moreover, it is entirely plausible that general ringing data could be used to study the past population development of species other than the starling, although the methods would have to be adjusted separately for each species.

Nevertheless, caution is needed. In order to attain realistic abundance indices using ringing data, a target species should be at least relatively common and widely ringed. Furthermore, on the basis of this study, without improvements in controlling the ringing effort, we cannot recommend this method as a standard tool for bird monitoring, since there is too much error variation in the indices due to unknown patterns in the ringing activity. This might mean that characterising the population status of a species is possible only if large changes in the population size have already occurred. It is far from sure that we could detect relatively small changes in population density — in other words, the kinds of changes which are important, for example, in species conservation, where we often need to get accurate estimates of population size before drastic decreases become apparent.

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Appendix 1

Original numbers of passerine birds ringed in Finland during 1952–1998. Sv = starling *Sturnus vulgaris*, Fh = pied flycatcher *Ficedula hypoleuca*, Pm = great tit *Parus major*, Pt = willow warbler *Phylloscopus trochilus*, Ti = redwing *Turdus iliacus*, and Fc = chaffinch *Fringilla coelebs*, Oth = all passerines except previous species, All = all passerines except the starling. N refers to nestlings and T to the total number of individuals ringed.

Year	Sv N	Sv T	Fh N	Fh T	Pm N	Pm T	Pt N	Pt T	Ti N	Ti T	Fc N	Fc T	Oth N	Oth T	All N	All T
1952	446	447	–	381	–	1069	–	132	–	375	–	304	–	3990	–	6251
1953	1273	1310	–	649	–	1620	–	321	–	674	–	393	–	6311	–	9968
1954	1771	1939	–	1347	–	3240	–	423	–	757	–	567	–	8952	–	15286
1955	1443	1530	–	1206	–	2716	–	685	–	1054	–	589	–	10689	–	16939
1956	1295	1339	–	2143	–	2526	–	643	–	572	–	489	–	13850	–	20223
1957	1923	2050	–	2362	–	3090	–	1195	–	1255	–	830	–	15088	–	23820
1958	2102	2334	–	2044	–	2037	–	577	–	1337	–	526	–	12360	–	18881
1959	1848	2365	–	2591	–	4332	–	828	–	2135	–	1010	–	21792	–	32688
1960	2519	3175	–	4412	–	5066	–	1715	–	2263	–	2205	–	29896	–	45557
1961	4372	5411	–	5296	–	5920	–	2656	–	3763	–	3039	–	38048	–	58722
1962	4872	6376	–	6723	–	7666	–	4828	–	4839	–	4969	–	47506	–	76531
1963	4393	5128	–	8106	–	4900	–	4180	–	1802	–	2908	–	34134	–	56030
1964	3687	4094	–	7422	–	4840	–	3309	–	2130	–	3164	–	34554	–	55419
1965	3279	3830	–	7850	–	6381	–	6722	–	2749	–	2615	–	63179	–	89496
1966	4707	6138	–	6992	–	6016	–	7525	–	4785	–	4561	–	55978	–	85857
1967	5064	6028	–	8210	–	7029	–	7223	–	4452	–	3321	–	59734	–	89969
1968	3212	5405	2126	3458	5142	8734	1123	16152	2045	4810	459	4304	19875	72173	30770	109631
1969	4407	6843	10035	11909	6570	13466	1606	21356	2325	5285	491	9723	14531	72515	35558	134254
1970	4606	9824	13044	15189	9716	18153	1570	20410	2744	5164	598	7378	15815	102598	43487	168892
1971	3591	7149	12330	15218	11470	21682	1004	10143	1490	3236	439	3901	14435	78353	41168	132533
1972	3113	5246	15509	18997	14935	26845	724	7207	1645	3940	444	5704	13915	107536	47172	170229

Continues

Appendix 1. Continued.

Year	Sv N	Sv T	Fh N	Fh T	Pm N	Pm T	Pt N	Pt T	Ti N	Ti T	Fc N	Fc T	Oth N	Oth T	All N	All T
1973	2978	4704	17584	21783	20284	37694	539	6627	1691	4407	313	5950	15431	90322	55842	166783
1974	2235	3036	15700	18496	10863	17205	924	4003	1427	2667	157	1927	10440	56067	39511	100365
1975	1329	1631	15753	19221	17390	24903	521	5563	1598	2825	246	2598	13418	64832	48926	119942
1976	1157	1952	13911	16892	12863	19967	536	6102	1224	3085	200	4665	9851	71437	38585	122148
1977	1088	1626	12067	15101	8036	13313	910	7902	1556	4063	203	4106	8814	72762	31586	117247
1978	1028	1424	11767	14406	11050	15334	717	12007	1767	3502	246	2787	12634	64671	38181	112707
1979	995	1230	14483	16822	16065	25516	725	8269	1668	3789	422	3193	18464	82334	51827	139923
1980	1138	1625	17440	20491	18784	30192	1085	13850	2022	4597	594	4410	22510	116220	62435	189760
1981	1329	1587	17421	20562	15408	25491	1187	14229	3194	6080	464	5579	22479	116699	60153	188640
1982	1207	1437	17529	21455	9337	15904	1368	17206	2681	4124	338	2659	18987	97976	50240	159324
1983	1199	1659	20151	23456	12154	23404	1331	17528	2399	3218	290	3100	19521	105187	55846	175893
1984	1266	1508	9511	14113	9360	15368	370	11911	2046	3671	167	2528	20433	102663	41887	150254
1985	815	1095	10549	14740	9179	20497	483	13410	1403	2487	130	2790	17883	107555	39627	161479
1986	909	1136	11391	16047	9947	21943	676	17989	1266	2241	181	3019	19337	114673	42798	175912
1987	838	956	7473	11483	5829	13698	741	16319	1693	2494	161	2687	17944	78945	33841	125626
1988	1075	1136	6883	9744	7621	18622	649	20251	2314	3624	144	2186	20800	101902	38411	156329
1989	1583	1836	6848	9786	9114	20822	942	20672	2345	2991	120	1936	23242	115808	42611	172015
1990	1660	1752	6457	9352	7741	17980	918	19782	2529	3681	168	1783	24016	106080	41829	158658
1991	1563	1662	7264	10209	6398	16571	587	13925	2210	3251	178	2121	22627	110473	39264	156550
1992	1991	2011	8933	12365	9185	20537	687	15872	2125	2771	163	2405	24613	126750	45706	180700
1993	2261	2287	6914	9744	8343	13875	1039	19254	2364	3784	255	2224	31565	142731	50480	191612
1994	2227	2332	5564	8434	3952	10822	928	25365	2658	4163	229	2805	24599	130131	37930	181720
1995	1795	1888	5438	7910	4860	16459	727	18647	1865	2754	166	2071	23706	145884	36762	193725
1996	1999	2116	4988	7740	5428	16793	745	15204	1775	2826	150	2289	25309	118210	38395	163062
1997	1927	2065	5130	7406	4062	11805	756	13317	1045	1669	142	2138	23050	99691	34185	136026
1998	1990	2121	5069	7464	5250	12173	595	11479	780	1346	85	1475	26592	96193	38371	130130

Appendix 2. Construction and main statements of the "null model" expressed schematically.

(*i*) Assume that there is a certain ringing activity variable X that to some extent explains both the total numbers of ringed starlings and all passerines (the standard). The time (t) trend coefficient, say b, may affect X. The trend does not explain all the variation in X, and a residual error e_x remains:

$$X = bt + e_x.$$

(*ii*) Imagine that the ringing history could be replayed. Due to random factors, the values in the "replayed" ringing activity variable X would not be exactly the same as those observed during 1952–1998. We can still try to define frames for random X, say $\hat{X}$, as:

$$\hat{X} = bt + \hat{e}_X,$$

where $\hat{e}_X$ is a normally distributed random error term with a mean of zero and standard deviation of e_x.

(*iii*) The numbers of starlings Y_{ST} and passerine totals Y_{ALL} are affected by their history, which is a common feature of time series data. This dependence may be characterised by variables $Y_{\mathrm{ST,\ BEFORE}}$, $Y_{\mathrm{ALL,\ BEFORE}}$ and coefficients r_{ST}, r_{ALL}. If we assume that in addition to these effects, Y_{ST} and Y_{ALL} are only affected by variations in X (other external factors such as changes in breeding habitats are excluded) we can formulate:

$$Y_{\mathrm{ST}} = X + r_{\mathrm{ST}} Y_{\mathrm{ST,\ BEFORE}} + e_{\mathrm{ST}}$$

and

$$Y_{\mathrm{ALL}} = X + r_{\mathrm{ALL}} Y_{\mathrm{ALL,\ BEFORE}} + e_{\mathrm{ALL}},$$

where e_{ST} and e_{ALL} are the respective residual errors.

(*iv*) If we again "replay" the ringing history, randomised numbers of starlings and passerine totals, $\hat{Y}_{\mathrm{ST}}$ and $\hat{Y}_{\mathrm{ALL}}$, respectively, can be formulated as:

$$\hat{Y}_{\mathrm{ST}} = \hat{X} + r_{\mathrm{ST}} \hat{Y}_{\mathrm{ST,\ BEFORE}} + \hat{e}_{\mathrm{ST}}$$

and

$$\hat{Y}_{\mathrm{ALL}} = \hat{X} + r_{\mathrm{ALL}} \hat{Y}_{\mathrm{ALL,\ BEFORE}} + \hat{e}_{\mathrm{ALL}},$$

where $\hat{e}_{\mathrm{ST}}$ and $\hat{e}_{\mathrm{ALL}}$ are normally distributed random error terms with a mean of zero and standard deviations of e_{ST} and e_{ALL}, respectively.

(*v*) All the parameters of the equations above can be measured from the available data, and these estimates represent the best available ones.