Dynamics of Finnish starlings in 1951–2005: from monitoring to population modelling

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Academic dissertation

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This thesis is based on the following articles, which will be referred to by their Roman numerals in the text:

I   Rintala, J., Tiainen, J. and Pakkala, T. 2003. Population trends of the Finnish Starling *Sturnus vulgaris*, 1952–1998, as inferred from annual ringing totals. — Annales Zoologici Fennici 40: 365–385.

II   Rintala, J. and Tiainen, J. 2007a. Indexing long-term regional bird population dynamics with nestling ringing data. — Annales Zoologici Fennici 44: 115–140.

III   Rintala, J. and Tiainen, J. 2007b. A model incorporating a reduction in carrying capacity translates brood size trends into a population decline: the case of Finnish starlings, 1951–2005. — Oikos in print.

IV   Rintala, J. and Tiainen, J. 2007c. Age-structured modelling of a passerine bird: delayed density-dependence turns into ten-year cyclic dynamics as documented in national ringing data, 1951–2005. — Submitted.

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Importance of authors' contributions to publications indicated by ascending order of appearance. Articles referred to by their Roman numerals I — IV.

Contribution to [1]	Publications			
	I	II	III	IV
Original idea	JT, JR	JR	JR, JT	JR, JT
Methodological design	JR, JT, TP	JR	JR	JR
Execution of analyses	JR	JR	JR	JR
Written form	JR, TP, JT	JR, JT	JR, JT	JR, JT

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III A model incorporating a reduction in carrying capacity translates brood size trends into a population decline: the case of Finnish starlings, 1951–2005.

IV Age-structured modelling of a passerine bird: delayed density-dependence turns into ten-year cyclic dynamics as documented in national ringing data, 1951–2005.

SUMMARY

1 INTRODUCTION

Several farmland bird species have been declining in Europe over more than three decades (Gregory et al. 2005). These declines have coincided with reductions in quality of farmland habitat, resulting of general intensification of farming practices (Chamberlain et al. 2000, Siriwardena et al. 2001, Newton 2004, Donald et al. 2006). In Finnish farmlands, replacement of small-scale mixed farming areas, including rotational pastures and short-cut grasslands, with specialized cultivation has been one of the most drastic changes in agricultural landscapes from the 1960s until the 1990s (Tiainen 2004). As these environmental changes often process during several decades, it is important for species conservation that farmland bird monitoring programs, which are used for evaluating population statuses, are regionally adequate and long enough for reliable inferences of population processes (Chamberlain et al. 2000, Paradis et al. 2002).

Annual monitoring censuses of Finnish farmland species do not cover the history that turned cattle farming into the modern farming, but were commenced in the end of the 1970s (Väisänen et al. 1998), which is far too late for understanding a species dynamics that is strictly tied on the disappearance of pastoral farming, such as the Finnish starling *Sturnus vulgaris*, the target species of this thesis. The species, which used to be common in the Palaearctic between 40° and 70°N (Tiainen and Pakkala 1997, Väisänen et al. 1998), has suffered greatly from habitat deterioration caused by changes in farming practices (Tiainen et al. 1989, Solonen et al. 1991, Robinson et al. 2005). The decline in starlings was first noticed in Finland (Orell and Ojanen 1980, Solonen et al. 1991) and later in other parts of Europe (Møller 1983, BirdLife International 2004, Svensson 2004a, Robinson et al. 2005).

Because of the long-term nature of habitat change, other data, apart from national censuses, for a study of long-term regional population dynamics, were needed. Finnish nestling ringing data (and nest-card data) provided a useful source material for an analysis, which covered more than five decades from quite original mixed farming to modern intensified cultivation. My approach into the population dynamics resembles that of integrated population monitoring (Baillie 1990, Siriwardena et al. 2000, Freeman et al. 2002), which in addition to the estimation of indices of population change, acknowledge also demographic measures of the focal population. The combination of these measures contributes to our understanding of the underlying factors that determine population dynamical process.

Finnish starlings are migratory, the over-wintering grounds being in western Europe, extending from England to northern France (Fliege 1984, Valkama and Haapala 2007). Starlings produce only one brood per season (Berthold 1969, von Haartman 1969), so each ringed brood represents one breeding starling pair. This feature also improves the usefulness of the data in estimating annual patterns of per capita reproduction rate. Starlings have been ringed extensively ever since the earliest years of intensive ringing in the 1950s, as the species easily accepts nest-boxes near to human habitation.

1.1 Local population aspects

As mentioned briefly above, Finnish

farmlands have undergone great changes, especially of the parts that are connected to the types of land-use, which is especially well illustrated by the declined numbers of cattle farms (Fig. 1). These numbers have declined especially in southern and western Finland (Fig. 2). The diversification of the production substance of farms towards more specialized cultivation is the main determinant of large-scale decline of total diversity in farmland habitats (Tiainen 2004).

Tiainen et al. (1989) studied nestling production of starling in southern Finnish colonies. They found that nestling survival was higher in breeding colonies in the vicinity of mixed and cattle farming areas than in the specialized cultivation areas (Fig. 3). Similar results were found also from Sweden (Olsson et al. 2002, Smith and Bruun 2002). Pastures and short-cut grasslands are preferred feeding habitats by starlings (Feare 1984, Olsson et al. 2002, Källander 2004). The distance of nests relative to good quality habitat is the key factor in starling nestling survival, the quality of food that parent starlings feed their young being the ultimate factor affecting nestling survival (Tinbergen 1981, Tiainen et al. 1989, Varjonen 1991).

Tiainen (1989) hypothesized that the average reproduction rate of the whole population would have decreased along with the large-scale deterioration of habitats, which would have caused the overall drastic decline. In order to study this possibility, Solonen et al. (1991) monitored twenty local populations from southern to northern Finland starting from the late 1960s. The declines were asynchronous in southern Finland, being accentuated in those localities where pastures were recently replaced with specialized cultivation. In northern Finland, all local populations declined independently of the type of farming. Solonen et al. (1991) found that average brood size was lower in northern than in southern Finland, suggesting that populations in the northern region would have been supported by
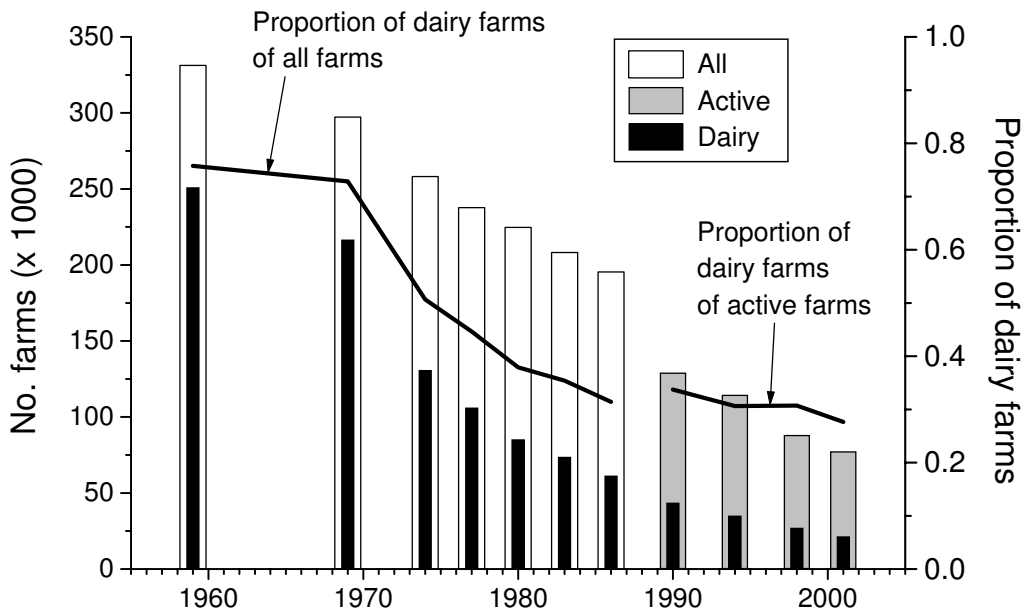

Fig. 1. Number of all farms and dairy farms in Finland (Anonymous 1962, 1971, 1986) and Annual yearbooks of farm statistics (adopted from Tiainen 2004).

immigrants from southern, highly-productive populations. As a consequence to overall population declines, immigration from the south would have ceased causing the decline of local populations in the north. I assume that the annual survival of starlings is the same in both regions or that it is lower in the north. Parallel to the overall population decline, mean brood size (measured from nestling ringing data from 1968 onwards) increased (see also Paradis et al. 2002), which was explained with a disappearance of local populations from poorly-productive habitats (Solonen et al. 1991).

1.2 Monitoring of farmland birds in Finland

Finnish farmland birds have been monitored annually for more than two decades. The general land-bird monitoring scheme, started in 1978, covers all terrestrial habitat types with single-visit line transect censuses (Väisänen 2006). The data useful for farmland bird monitoring are restricted to about 10 species, since the observations are not recorded by habitat.

Many species occur in many kinds of open habitats (farmland, mires, clear-cuts), and the farmland part of observations cannot be distinguished from others.

A second scheme is targeted explicitly for farmland birds and delivers high-quality data on 30–40 species. The scheme was initiated in 1984, but originally it was restricted to one region in southern Finland (Lammi). From the 1990s the scheme has expanded in geographical range, being representative for the southern part of Finland from 2000 onwards (Tiainen et al. 2007).

From starling-monitoring point of view, the general land bird monitoring data (Väisänen 2006) are most likely insufficient, as the census is carried out between 1 to 20 June in southern Finland (somewhat later in northern Finland). The starlings fledge during this period, which subjects their census to random errors. Springs have arrived earlier as a response to the climatic change (e.g. Gilbert 2007), to which the starlings probably respond with earlier breeding (Svensson 2004b). Hence, in a time series, an increasing proportion of broods have fledged during
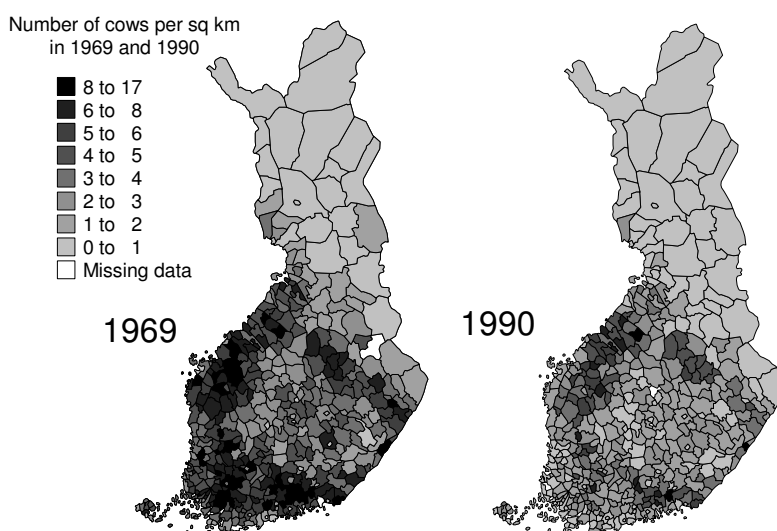

Number of cows per sq km in 1969 and 1990

- 8 to 17
- 6 to 8
- 5 to 6
- 4 to 5
- 3 to 4
- 2 to 3
- 1 to 2
- 0 to 1
- Missing data

1969   1990

Fig. 2. Number of dairy cattle km^{-2} among communes in 1969 (Anonymous 1971) and 1990. The Information Centre of the Ministry of Agriculture and Forestry in Finland delivered the data for 1990.

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the dates of censuses.

The farmland bird-monitoring scheme (Tiainen et al. 2007) relies on a mapping method currently based on three visits (two visits until 2000), which are timed properly for starling monitoring, and starling nests are likely to be found during the nestling period.

The monitoring schemes suffer, however, from late initiation in relation to the major change of Finnish farmland and most part of the starling decline. The national ringing archives, however, posses an extensive data-set, as all ringing information is available (in paper archives until 1972, in a database from 1973) with a record of brood numbers, brood size and location.

1.3   Modelling framework

The concept of population regulation is a causal to non-linear responses of per capita growth rate to population density, i.e. negative density-dependence, or simply, density-dependence (reviewed e.g. by May

1976, Sinclair 1987, Hanski 1990, Ranta et al. 2006). Density-dependence itself, due to lack of empirical support, has been a controversial issue in population ecology (Hassell 1986, Turchin 1995, 1999, Ranta et al. 2006). On the basis of census data, a great problem has been related to the weak statistical power of detecting the alternative hypothesis (density dependence) from the null hypothesis (density independence) (e.g. Slade 1977, Hassell et al. 1989, Hanski 1990, den Boer 1991). However, density-dependence is undeniably logical: assuming population growth rate as $R \neq 1$ and density-independence, a population would eventually either multiply to infinity or become extinct.

In recent literature, the controversy is smoothed to a more flexible state, in which density-dependence is a relative measure with respect to density-independent stochastic regulation (Sæther et al. 2002, Lande et al. 2003). The increasing degree of density-dependence tends to increase the tendency of a population to fluctuate regularly around the long-term mean
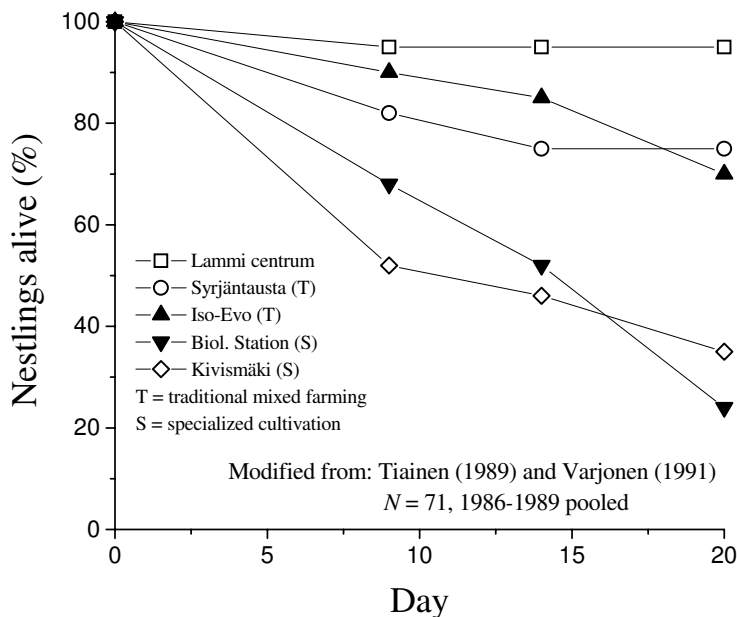

Fig. 3. Nestling survival of starlings in various southern Finnish farmland habitats in Lammi municipality.

density, i.e. carrying capacity (Lande et al. 2003). Intrinsic regulation together with stochastic processes are probably the major determinants of cyclic population dynamics as has been demonstrated in Finnish wood-grouse species (Lindström et al. 1995, Kaitala et al. 1996, Lindström et al. 1997). However, the ecological function behind a model such as an autoregressive process (e.g. Royama 1992) is not always clear — is the regulation due, for instance, to predator-prey interactions or to reproduction inhibition?

There are lots of examples of relationships between individual vital rates and population density (e.g. Newton 1998). In recent literature, there is evidence of density-dependent regulation of per capita reproduction rate in birds at a regional (Paradis et al. 2002) and local scale (Sæther et al. 2000, Hario and Rintala 2006). A demographic study of a small passerine population indicated that the growth rate of the population is density-dependent, and that a certain predictable change in carrying capacity would have a profound effect on the future population size, a phenomenon that could easily be extended to a larger spatial context (Sæther et al. 2000).

The concept of carrying capacity is fundamental in population ecology (e.g. May 1976, Sinclair 1987), but I have not found more than the one (Sæther et al. 2000) empirical evidence of a system, in which a large-scale deterministic change of carrying capacity would have been denoted to be the key-factor determinant of a population trend. However, there are quite a lot of studies that show direct relationships between temporal variation in a limiting resource and population density (see e.g. Newton 1998). Delayed density-dependence regulation and its function in fluctuating dynamics is a well-stated phenomenon in theoretical population ecology (May 1976, Royama 1992, Lande et al. 2003, Ranta et al. 2006). I acknowledged delayed density-dependence in order to investigate shorter-term regulation in starlings (IV).

As I had, in addition to long-term monitoring data of population counts, extensive data of per capita reproduction, it was quite clear that demographic matrix modelling would be the modelling tool (III, IV). Age-structured matrix models are widely used by ecologists (Emlen 1977, Caswell 1989, Lebreton and Clobert 1991, McDonald and Caswell 1993, Lindström et al. 1997, Kokko et al. 1999, Ranta et al. 2006). Density-dependence is easy to incorporate into a projection matrix, including all demographic parameters, where the regulatory function is free to vary from a simplistic overall effect to the regulation of one or more age-specific vital rates (Caswell 1989).

2 AIMS OF THE THESIS

As the main aim of the thesis, I quantified population patterns of Finnish starlings within three (II) or five (III, IV) geographical regions (south/north and west/east aspects) in 1951–2005. This required developing specific methods for the estimation of confidence limits of estimates based on the data (still to some degree scattered, despite of large total volume), a rather unconventional source for monitoring purposes (I, II). In addition to the analysis of long-term trends (I, II, III), spatial distribution (II), and density-dependent regulation of the population (IV), I used demographic matrix modelling in order to synthesize the population dynamical patterns, originally often verbally put, in a mathematical form (III, IV), which corresponds to structures in theoretical population ecology. As an ultimate aim, this work should encourage usage and further development of integrated monitoring projects, including the massive database of nestling ringing,

which might be of unprecedented value in future population ecological research of also other species than the starling.

In this integrated analysis, I introduce methods for indexing temporal population changes among varying regional scales (I, II), and for the estimation of spatial distribution of breeders (II). The annual mean brood sizes, integrated to annual indices of population change, are the basis for the analysis of long-term dynamics. Assuming delayed density-dependence in reproduction and environmental stochasticity (e.g. Lande et al. 2003), sustained ten-year cycles, observed from the actual population series, or at least strong tendency to cyclicity was evident with quite moderate vital parameters (IV). Nest-survival probabilities (during egg and nestling periods) estimated from the Finnish nest-card data, contributes to our understanding of the long-term patterns of brood size (III).

3   STARLING DATA AND STATISTICAL ANALYSES

Nestling ringing data from 1951–2005 (The Ringing Centre of Finnish Museum of Natural History), i.e. the number of nestlings within a brood, the base unit of observation, were projected into geographical information system according to Finnish uniform grid. The annual records were finally pooled within 2 km × 2 km grid squares to form the base spatially-structured data source (II, III). The base spatial unit is hereafter referred to as "site".

In the new ringing data starting from 1973 onwards, ringers used geographical coordinates in a precision of minutes and, of major commonness, uniform coordinates in precision of 1-km or even 100-m when recording the original ringing locations. These data are stored in the database of the Ringing Centre.

The old data from 1951 to 1972 were not stored into an electronic database, so, they had to be computerized from the original ringing reports left by ringers. In these reports, the locations of ringed broods were expressed verbally by names of communes, villages, farms, and so on, which were finally positioned from maps, and consequently, coordinates were determined for each ringing record. If no specific location was mentioned, the coordinates of centre of communes were registered (II).

In many of the statistical hypothesis testing, I preferred distribution free bootstrap and permutation methods (I – IV) instead of standard statistical tests. Randomisation methods are reviewed e.g. by Manly (1997).

3.1   Estimation of long-term trends

Statistical inference of population trends on the basis of monitoring data have undergone remarkable advances as the census programs have advanced (Crawford 1991, Bibby et al. 1992, Underhill and Prýs-Jones 1994, Thomas 1996, Siriwardena et al. 1998, Fewster et al. 2000, van Strien et al. 2001, Gregory et al. 2005). The main demand in developing indexing methods has been to solve how to deal with incomplete census data — incomplete, since these kind of site-by-year count matrices collected by voluntary field-ornithologist, may contain substantial amounts of missing counts (ter Braak et al. 1994, Thomas 1996, van Strien et al. 2001). When used as a site-by-year structured census data, nestling ringing data are really far from being geographically complete, demanding a lot of methodological power in order to produce plausible indices of population change (II, see also I).

Log-linear modelling (assuming Poisson errors) of site-by-year structured count data (ter Braak et al. 1994, Pannekoek and van Strien 2003) has become a standard in indexing of European bird population trends (van Strien et al. 2001, Gregory et al. 2005). Modelling is based on year-effects and site-effects on counts. Site-effects level counts among sites and year-effects denote annual trends. Year-effects can be formulated in various ways from annual effects to one overall or several sequential log-linear trends within the total period. An increasing proportion of missing counts limits the maximum usable number of year-effects (Pannekoek and van Strien 2003). Models

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are optimized following the statistical theory of generalized linear models, GLM (McCullagh and Nelder 1989). On the basis of the same rules, standard errors of indices can be estimated. Indices are calculated from a site-by-year count matrix, in which originally missing counts are imputed with model-based estimates. Modelling allows implementation of covariate effects (Pannekoek and van Strien 2003), which enables modelling of, for instance, regionally divergent trends within the total data (II, III).

One could think that the starling data are too sparse for the purpose of monitoring (annually 1–19% [mean = 11%] of all sites included sites from which brood count was recorded, II). The total volume of the data, however, was enough for yielding indices that quite confidently illustrated long-term dynamics of starlings among several regions (II, see also III).

Some fundamental methodological questions in estimating the indices arose. Firstly, the huge increase of ringing effort (increase in number and per capita effort of ringers) especially during the 1950s (I) could have caused underestimation of index numbers in the earliest years of the data. This possible bias was minimized by pooling the annual observation within as small spatial unit (2 km × 2 km squares, sites) as possible in respect of the precision of originally determined coordinates. It was possible to show that the general increase of ringing effort (I) was largely due to introducing new ringing sites especially during the earliest years of ringing (II). By choosing the smallest possible spatial unit for the basic unit of observation, the effect of the regionally extended ringing on counts per site should be minimized (II). It was basically realistic to assume that ringers, who had specialized to ring starling broods, could have, even alone,

been capable of ringing majority of starling broods from a site.

Secondly, it was generally unrealistic to assume that ringing effort had stayed, even in average terms, unchanged within sites during the total period 1951–2005. In addition, the precision of original coordinates of ringing locations within the "old" (1951–1972) and the "new" (1973–) sets of data diverged from each other. This could have meant that, when pooling observations per a site, a ringing location recorded to the old and the new sets of data could have been judged to belong to two different sites just because of the methodological constraint. This is why the old and the new sets were treated separately in the calculation of indices of regional population change. The years of the sets were designed at 1951–1973 and 1973–2005. The base index (Pannekoek and van Strien 2003) in both sets was set at 1973, allowing inference of trends over the total period 1951–2005 (II, see also III). After all these treatments, I still have to admit that indices in the first years of the data might be, to a some degree, downward biased due to the strong increase of ringing effort in the 1950s (I, II).

Thirdly — the trickiest issue to solve — ringing data did not offer a straightforward clue to distinguish actual zero counts from missing counts (no record made). In other words, the detection of the case "not any broods ringed" at certain site/year was due to disappearance of starlings or to lack of ringing activity, was practically impossible to be confirmed manually (ca. 1400 sites of which 90% missed annual record). Basically, it would have been possible to scale ringing activity towards starlings indirectly on the basis of other hole-nesting passerines that are found from the same habitats as starlings. This would have meant recruitment of a huge

amount of extra data, and probably in vain, because a ringer seeking, for instance, pied flycatchers does not inevitably ring starlings. Furthermore, ringing of most abundant hole-nesters, such as the pied flycatcher and some tit species, have been occasionally restricted by ringing rules (Saurola 1985).

Zero is an important count, since it may indicate a local extinction, and thereafter it also contributes negatively to annual index. The original "uncorrected" format of the data did not include registered zeros, but comprised only of counts greater than zero or "missing counts" (II). A data correction was made in order to predict probable zero counts apart of the missing count set. Prediction of zero counts was based on small count estimates (< 1) of a log-linear model on the original uncorrected data. A missing count was eventually judged as zero after a random procedure, which was built and tested on the basis of quantitative Monte Carlo simulations (Manly 1997) approach. A data matrix, in which a certain part of missing counts is implemented with zeros, is called "corrected data" (II).

The correction method is reported briefly in the following: log-linear estimates μ_{ij} were fitted on the uncorrected data m_{ij} (i = site identifier, j = time-point identifier). Small Poisson-distributed random counts (usually zero, expected mean = 0.01) were incorporated into the corrected data set m'_{ij} (correction of m_{ij}) if (1) a count was missing, (2) μ_{ij} was smaller than one, and (3) a uniform random number between 0 and 1 was less than, or equal to, the probability of the ringing effort $P_{(\text{EFFORT})ij}$ — otherwise, original values of m_{ij} were retained in m'_{ij}. Annual $P_{(\text{EFFORT})ij}$ estimates were estimated as

$$P_{(\text{EFFORT})ij} = \frac{\sum_i m_{ij}}{\sum_i \text{IMPUTED}_{ij} \mid \text{if IMPUTED}_{ij} \geq 1, \text{ else not summed}}$$

where IMPUTED_{ij} is the combination of observed counts m_{ij} and estimated counts μ_{ij} (cases that replace missing counts in m_{ij}). The summation of IMPUTED_{ij} was performed for only those values that were greater than or equal to one. This ought to focus better on sites where a local population could have existed, and hence, the summations would express the annual total population potentially available for ringing.

National indices of population change were studied also with a so-called standardisation method (Hjort and Lindholm 1978, Österlöf and Stolt 1982, O'Connor and Mead 1984). An annual index is calculated by dividing the annual ringing total of starlings with the total of other passerines. Strictly, this is the index of starling ringing totals in respect of the totals of other passerines. This quantity can index population change, provided that the total sample of passerines is the index of ringing effort. And again, in order to arrive at true index, we have to assume that starlings are ringed in proportions corresponding to the amounts they are represented in field. Monte Carlo simulation (e.g. Manly 1997) model was constructed in order to estimate the confidence limits of annual indices (I).

Daily survival rates of nests, during egg and nestling stage, were estimated from Finnish nest-card data (Finnish museum of Natural history) on the basis of Mayfield methodology (Mayfield 1961, Mayfield 1975, Johnson 1979). In these data, the base unit of observation is a nest that is visited at least twice during egg and/or nestling periods. Daily failure rate is the binomial odds that nest fails during a unit exposure day. The number of exposure days of nests is the midpoint of the period from the first to the last visit to a nest (Johnson 1979). For the analysis,

nest data are organized into two vectors, of which the first one comprise the fates of nest in binary 0/1 format (1 indicating failure), and the second one comprises the corresponding nest-specific exposure days. These data can easily be analysed basing on the framework of GLM (McCullagh and Nelder 1989); in this special case, logistic regression (Aebischer 1999, Siriwardena and Crick 2002) was used (III).

3.2 Spatial and time-series analyses

I estimated abundance distribution of breeding starlings in the total arable and human habitation area in Finland basing on presence/absence information of ringed broods and environmental variables within all possible sites. Data from 1951 to 1975, when starlings still were relatively abundant, were pooled for the analysis. At least one ringed brood during the period was an indication of within-site breeding population (II). For the estimation of spatial distribution, I used resource selection functions (RSF) for animal populations (Boyce and McDonald 1999, Manly et al. 2002, Keating and Cherry 2004).

Firstly, the area of all available units, in which ringing activity could have been possible, was determined. On the basis of the sample of available units, a relative probability estimator $\mathbf{w}$ (w_1, w_2…w_N) of occurrence of starlings among N available units was produced by optimisation of a logistic regression model, incorporating the starling data and environmental variables. Secondly, the optimized logistic regression model, or RSF, was used to extrapolate (predict) $\mathbf{w}$ over all possible starling habitats in Finland, $\mathbf{w}_{(extrapolated)}$. Thirdly, $\mathbf{w}_{(extrapolated)}$ was scaled so that vector values summed up to unity $\mathbf{w}_{(scaled)}$. Finally, $\mathbf{w}_{(scaled)}$ was used to allocate

the population, 200 000 breeding pairs (Väisänen et al. 1998), over Finland, simply as 200 000 $\mathbf{w}_{(scaled)}$.

Density-dependent population regulation and cyclicity were studied on the basis of stationary time-series (Box and Jenkins 1970, Chatfield 1989, Royama 1992). In the stationary state, the long-term mean and variance of a population variable is stable. Time series of annual relative population density (POP), in relation to carrying capacity, and per capita reproduction rate (RR) were derived from (log) total brood counts and (log) overall mean brood sizes (IV). I fitted generalized additive models (Hastie and Tibshirani 1990, Fewster et al. 2000, R Development Core Team 2006) on each (log) series and used model residuals as the estimates of POP and RR. GAM smoothers are very suitable for this kind of purposes, because they are flexible, and thus, they do not restrict the shape of fit into any deterministic form, but the level of smoothing is purely based on scatter plot of the observed response variable (IV).

Despite the population density estimate based on the total count of broods may be, to some extent, scattered due to unpredictable changes in ringing activity, it is still very useful for the purposes of time-series analysis, because 55-year long series enabled powerful statistical analysis of population patterns, i.e. density-dependence and cyclicity. In addition to standard time-series techniques (Box and Jenkins 1970, Chatfield 1989, Royama 1992), I was able to perform analyses on several systematically sub-set samples of varying period lengths and year-combinations. This sub-setting method, I call "recursive" sampling or analysis (IV).

4   POPULATION MODELS

My general aim was to find out the population limitation mechanism that could have caused the population patterns measured from the actual data in south-west Finland (III, IV). An age-structured model, for the purpose, is written as

(2) $\mathbf{n}_{(t+1)} = \mathbf{A}\mathbf{n}_{(t)}$,

where the vector $\mathbf{n}_{(t)}$ comprises the number of 0-year old juveniles n_1 and at least one-year old adult birds n_2 at year t. The projection matrix

$$\mathbf{A} = \begin{pmatrix} c_{(t)}f_1s_1 & c_{(t)}f_2s_2 \\ s_1 & s_2 \end{pmatrix}$$

includes fecundity f_i (number of female fledglings produced per female per year) and survival s_i of females belonging to age groups $i = 1$ and $i = 2$. Note the design of post-breeding census (e.g. McDonald and Caswell 1993), meaning that in order to reproduce, individuals must survive over the forthcoming year after the census — that is why f_i is scaled with s_i. Delayed density-dependence was targeted to the reproduction term with a scaling factor

$$c_{(t)} = 1 - n_{2,(t-1)} / K,$$

where K is the carrying capacity of environment. Density-dependent regulation of the vital parameter is exerted by the adult population n_2 (IV).

In order to model the effect of environment change, K was set to decline by an approximate quantity of 80% (cf. I, II). Here, the scaling parameter $c_{(t)}$ is simpler than above (cf. IV): no delay and

density-dependence was exerted by the total population (young and adult stages together, III), rather than adult stage alone (IV).

The type of the projection matrix $\mathbf{A}$ is a stage-structured Lefkovitch matrix which, unlike the Leslie matrix, can contain non-zero values also in other cells than in the first row and sub-diagonal elements (see e.g. Manly 1990, Lindström et al. 1997). The model assumes that individuals die before the age of senescence (cf. Lande et al. 2003). Thus, the maximum life span of individuals is not strictly limited as in a Leslie matrix, but the probability of longevity of an individual is the annual survival probability s_2 powered to the time (years) spent in the second age group (IV).

I estimated the degree of density-dependence D in the south-west population density (POP, see above, IV) using a method by Lande et al. (2003). D is estimated as,

$$\hat{\mu} D = 1 - \sum_{i=1}^{\alpha} b_i,$$

where $\hat{\mu}$ is annual adult mortality rate, α is the age at first breeding, and b_i is the autoregressive coefficient of order 1 to α. D increases with increasing negativity of autoregressive terms and decreasing $\hat{\mu}$. I performed the analysis for successive ten-year periods starting from 1951. The same analysis was performed on a 1000-year simulation series of starling population dynamics, incorporating intrinsic regulation and environmental stochasticity in fecundity (IV).

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5   MAIN RESULTS AND DISCUSSION

5.1   *Population trends and spatial patterns*

According to the standardisation method (Fig. 4, I), the total population declined by 80–90% from the early-1970s up to the end-1980s or early-1990s. The decline was similar compared to the estimate for the total area based on site-by-year structured data (II). These patterns convinced me that there really had been a substantial long-term regional decline of the population, as
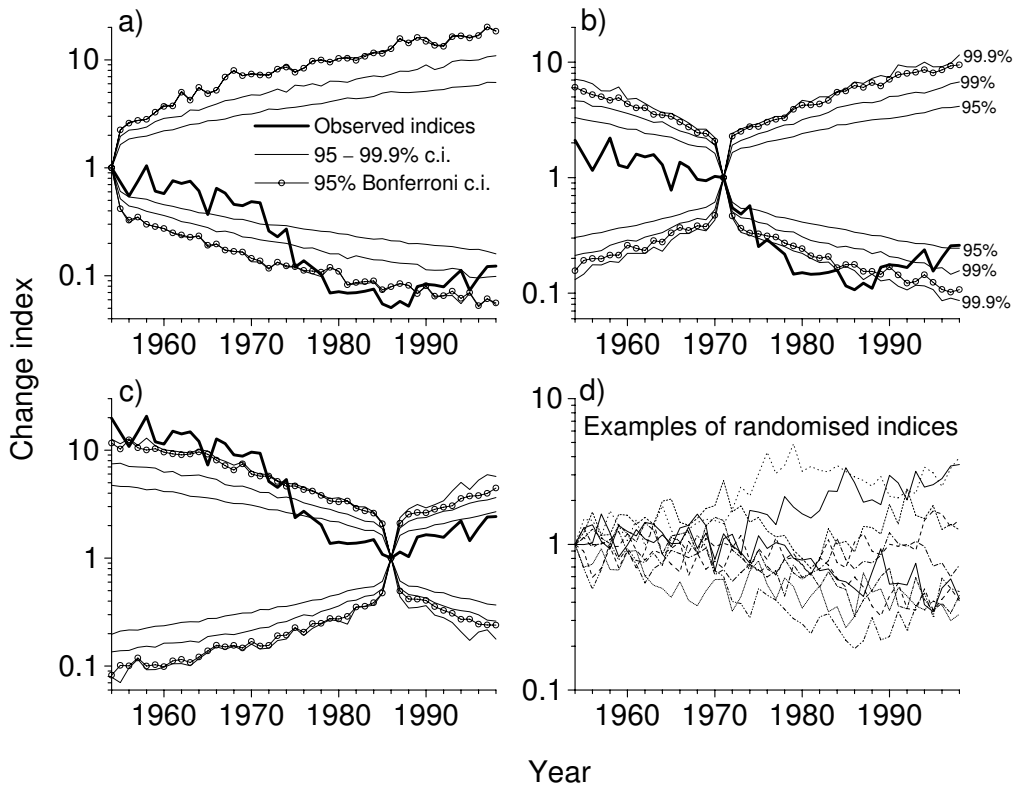

Fig. 4. Indices of population change of starlings in Finland (I). Monte-Carlo simulated upper and lower 95%, 99%, and 99.9% confidence intervals, as well as 95% Bonferroni-corrected confidence intervals (for the null model, assuming no long-term population change) are plotted for 1954–98 (a–c). Base years of the indices were set to 1954 (a), 1971 (b), and 1986 (c). For instance, lower Bonferroni-corrected percentile was calculated forward and backward from base year by 2.5% / (1998 – base year) and 2.5% / (base year – 1954), respectively. Thus, the longer time interval the more substantial is the Bonferroni correction. If indices are outside a certain confidence belt, they are significantly smaller or larger than the index at the base year of the respective series. Ten examples of the individual random index series based at 1954 are also shown (d). Because of the two-year time-lag in the Monte Carlo simulation model, the actual simulation starts from 1955. Randomisations were initiated by setting the first two values (1953 and 1954) to independent random numbers with mean and standard deviation corresponding the observed data, 1953–98. Thus, in the initiation period, indices were not subject to model parameters. Similarly, simulation of passerine totals (the standard) started at 1954.

suggested also by Solonen et al. (1991). The results also strongly suggest that population densities had been consistently high during the 1950s and 1960s (cf. Fig. 4 and 5). The estimates for the regional patterns indicated more severe declines in northern Finland than in southern and central Finland (Fig. 5). These trends, in addition to overall population decline, lead to a range contraction of the northern population (II, see also III).

On the basis of a resource selection function, RSF (II), the distribution of breeding population was south and south-west weighted. However, the RSF predicted population existence also to
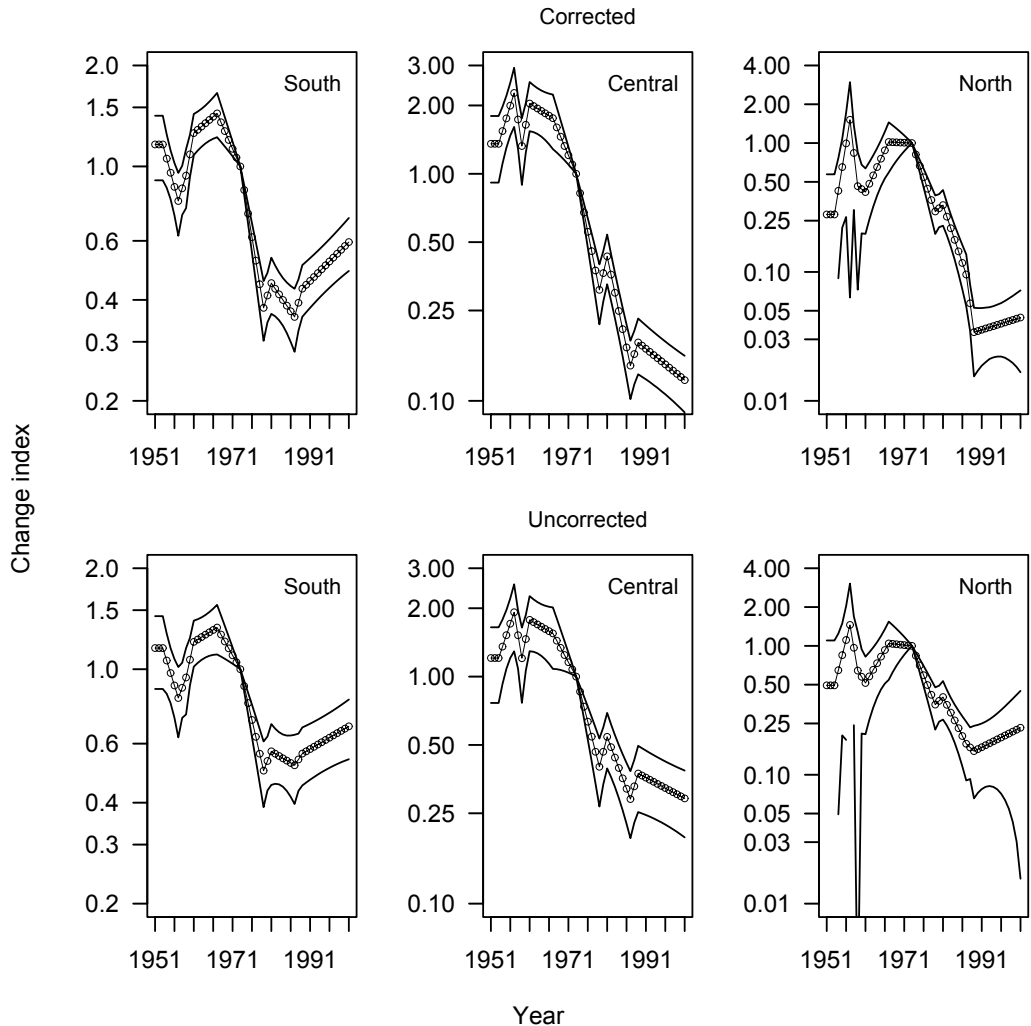
Fig. 5. Index series with 95% confidence belts estimated on the basis of log-linear models for regional starling populations (South, Central, and North) for the period 1951–2001. Each time-series consists of two data sets (periods 1951–1973 and 1973–2001; the base year is 1973 whose index was set to one). Calculations were based on corrected and uncorrected data sets (see methods). Unreasonable negative lower confidence limits of indices (a consequence of insufficient data for certain years) were not drawn because of the logarithmic scale. Note varying scales in *y*-axes.

northern breeding grounds (Fig. 6), which converge with observations based on breeding bird atlas (Väisänen et al. 1998). The RSF generated density hot-spots especially around southern Finnish towns and villages. These areas, during the 1950s and 1960s, actually provided a lot of pastoral habitats and artificial nest-places for breeding starlings. The commonness of cattle farming and its disappearance from the surroundings of towns was explored from farm statistics of Finland (see details in II). These well-documented environmental changes are straight proves of the drastic environmental changes that took place since the end of the 1960s until the end 1980s (Tiainen 2004), which caused the population decline (III).

5.2 Demography of starlings

Mean brood size exhibited significant lows during the period of population decline, a phenomenon that was most evident for southern and also western areas of Finland (III). Similar dynamics was not found on the basis of Mayfield estimates of nest failures (III), suggesting that the population was regulated by density-dependent fecundity. Actually, of all parameters implemented into the projection matrix (see model section above), the young-bird fecundity had the greatest relative effect on population growth rate (IV).

As the reproduction of starlings was density-dependent (IV), I was able to assume that the long-term trend of mean
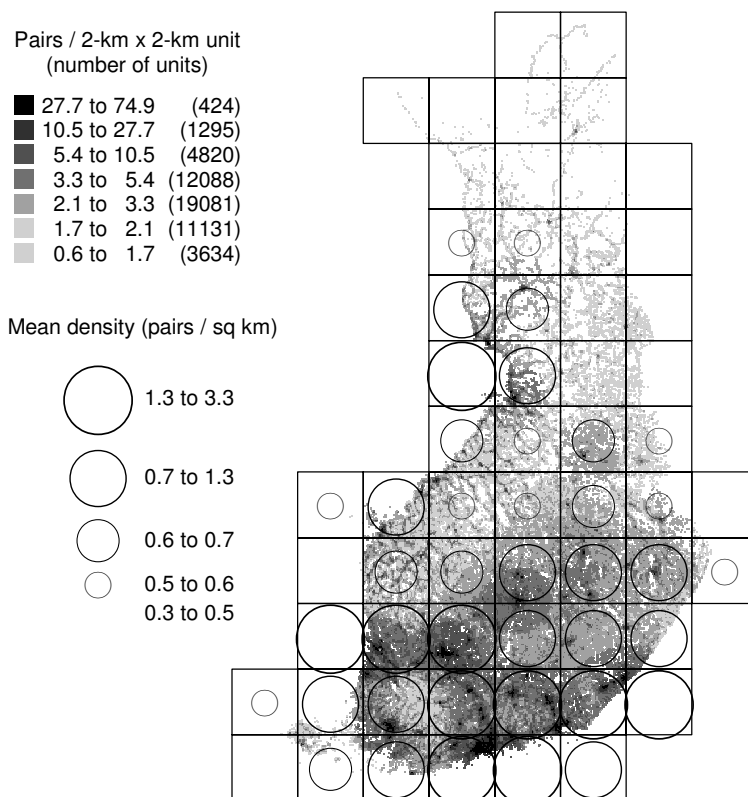
Fig. 6. Numbers of breeding starlings in Finland, as estimated with the RSF on the basis of ringed broods in 1951–1975. The base habitat-unit is a 2-km grid square. Mean densities (pairs km^{-2}) are given for the habitat units within 100-km grid squares.

brood size could have been a causal to large-scale deterioration of farmland habitats, i.e. deterministic decline of carrying capacity *K* (III). A demographic matrix-model was used to simulate the response of a population to declined *K*. Because of the delay, density-dependent regulation of per capita reproduction rate increased during the decline of *K* (Fig. 7), a dynamical feature, which can be used for explanation of the observed patterns, too (III).

It is worth noting that the reductions in habitat quality have been a region-wide process (drastic in southern and western parts of Finland, Fig. 2). However, all environments did probably not suddenly turn from a good state into poor quality, but the deterioration of sites occurred in a varying spatiotemporal sequence along with the agricultural intensification (cf. Solonen et al. 1991). These changes were up to the decisions of individual farmers and their personal objectives. From the starling point of view, this means that during deteriorations, increasing proportions of farms turned the production from mixed farming (good habitat with pasturing livestock and mown grassland) to specialized cultivation (bad habitat without livestock). During the fastest phase of the population decline (Fig. 7),
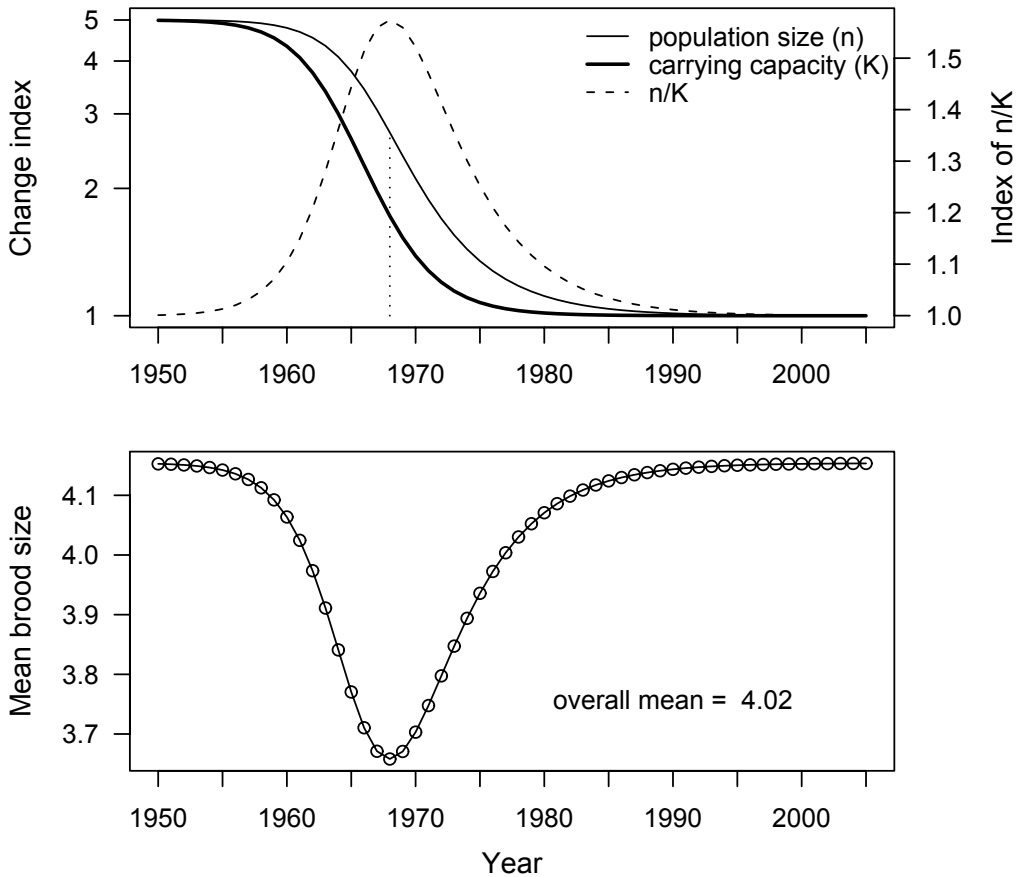
Fig. 7. Population model: the effect of declining carrying capacity on population dynamics. In the simulation, the carrying capacity of the environment has been adjusted to decline by 80%. In the simulation, the long-term pattern in the annual mean brood size is due to the changing ratio of n/K. In 1968, there were 1.6 times more breeders than could be maintained by the current carrying capacity (see the vertical dotted line).

mean brood size was at lowest, but as population density was still decreasing towards the new lower stable level, a large amount of individuals were forced to breed within sub-optimal habitats. This explains why the coefficient of variation in brood size peaked during the fastest phase of the population decline (III).

The south-west starling population exhibited ten-year cyclic periodicity, as recursively repeated autocorrelation function ACF clearly indicated (Fig. 8, IV). The damped pattern of autocorrelations can

be explained with stochastic perturbations that interference the intrinsic regularity (Royama 1992, Lande et al. 2003), but also with the fact that the intrinsic dynamics does not maintain sustained cyclicity (Fig. 9). The sustained fluctuation pattern of population size, however, can be maintained by environmental stochasticity, that is incorporated into fecundity parameter (Fig. 10).

In the age-structured modelling approach (Fig. 9) with second-order density-dependence (one-year delay) in
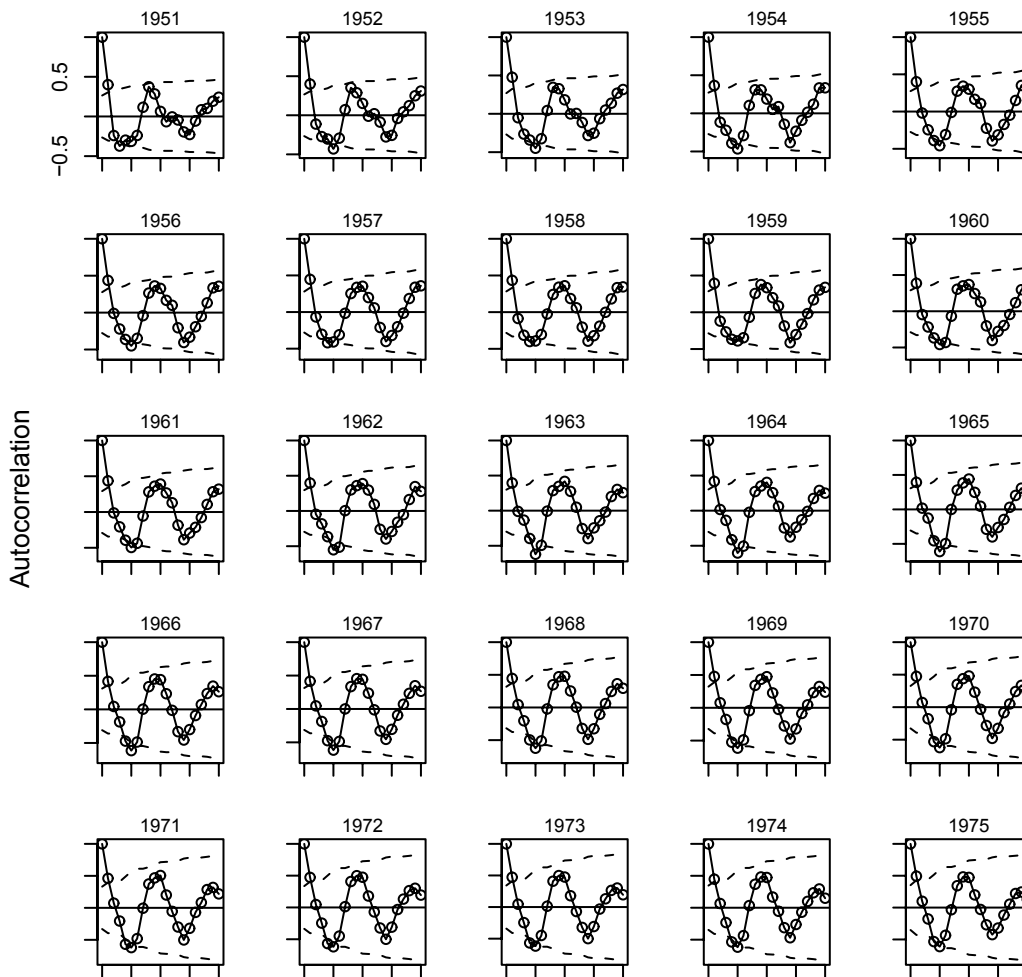
Fig. 8. Recursive autocorrelations (starting from 1951…1975 onwards [to 2005]) based on relative population-density series (POP) in south-west Finland. Dashed lines denote the 95% confidence belt for the null-hypothesis assuming no autocorrelations.

fecundity (cf. starlings in Paradis et al. 2002) is exerted by the adult-stage only (cf. Lande et al. 2003). The biological function is analogous to a classical "predator–prey" situation, in which the predator follows the prey with a lag. During low overall population densities, the young-cohort reproduces and increases quickly, as the regulatory adult-cohort is at lowest. Thus, during the fastest increase and aging of young, the adult-cohort also starts to increase fast, but with a lag. During the maximum density, the adult-cohort exerts the strongest inhibition on young-bird fecundity (and also on adults

themseves). The growth rate of population is most sensitive to variations in first-year fecundity, which thus is the key-factor in determination of population dynamics (IV). It is possible that old breeders dominate over the first-year breeders in the competition of possessing the best habitats, which could explain the higher density-dependence of the young-stage.

I found that the total density-dependence (Lande et al. 2003) of starlings was not constant during the early years of the time-series (Fig. 11) corresponding to the period at which the carrying capacity most probably started to decline (III).
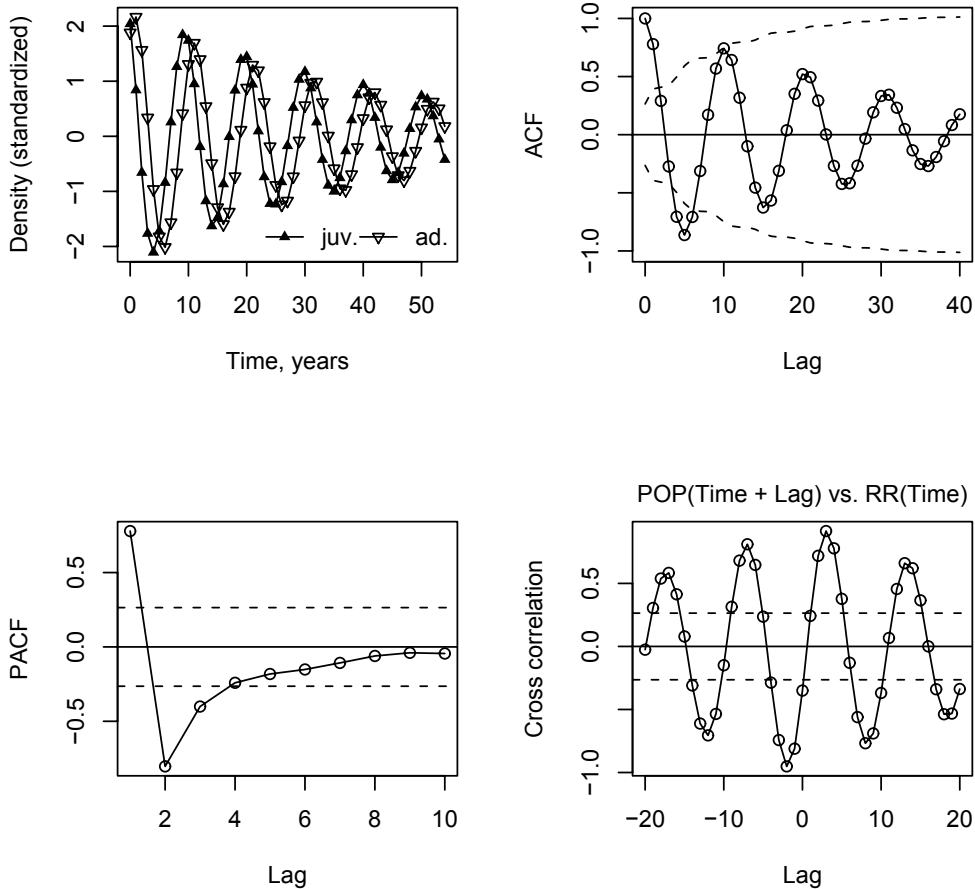
Fig. 9. Simulated population dynamics based on the matrix model. Population trajectories are shown for juvenile and adult birds (top left graph); autocorrelations (ACF, PACF) for the corresponding total population, and cross correlations for population density (POP) vs. reproduction rate (RR). Dashed lines denote the 95% confidence band.

As estimated for south-west Finland, the strength of density-dependence increased clearly (about 0.3 units) from the mid-1950s to the mid-1960s followed by a sudden drop to a constant level at the beginning of the 1970s. The observed density-dependent pattern supports the idea that the carrying capacity of farmland habitats declined, and that the population responded to the decline with a delay (III).

During the simulation period of 1000 generations, the level of density-dependence stayed relatively constant most of the time, as measured consecutively for population densities within ten-year periods. Increasing (or decreasing) trends of more than 0.1 units of density-dependence were not yielded (Fig. 10). However, substantial increases were observed from the actual data (0.3-unit increase until the mid-1960s, Fig. 11). Within the random dynamics some disturbances in density-dependence (exceptional high values) occurred, for instance, at about 75 generations preceding the end of the simulation (Fig. 10).
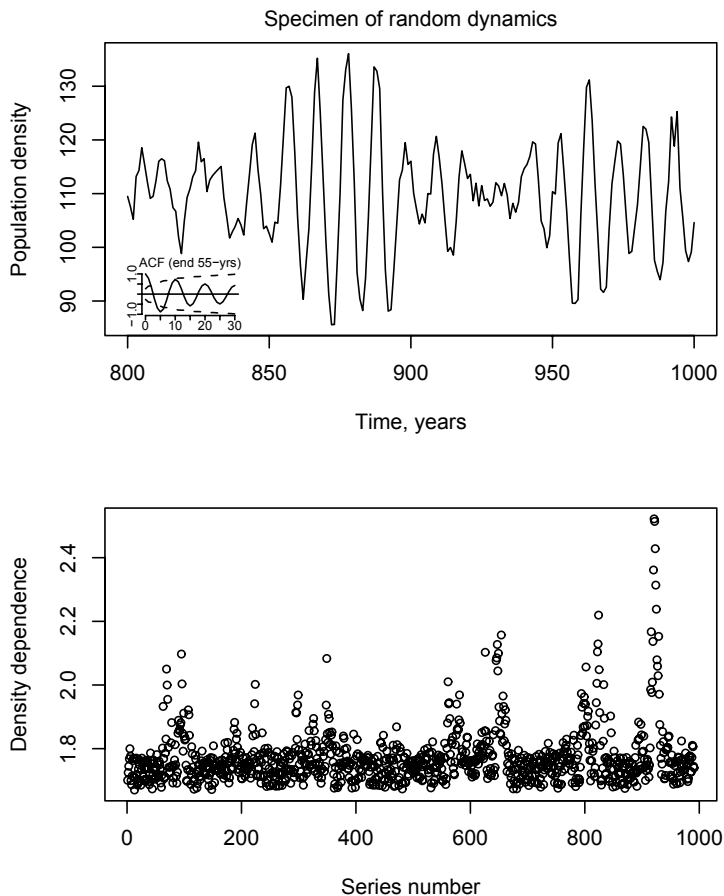
Fig. 10. Population dynamics based on the matrix model (cf. Fig. 9) perturbed with an environmental stochasticity of 5% SD in fecundity terms. Fluctuations of population density are shown for the last 200 generations and ACF (insert graph) for the last 55 generations of the total simulation period (1000 generations). Variation in density-dependence during the total simulation period was derived on the basis of first-order autoregressive terms successively estimated for sliding ten-year periods (the same routine as for the actual data, Fig. 11).

6   IMPLICATIONS

6.1   *Conservation of starlings*

The starling decrease observed in Finland (80% in two decades, II) should have been a conservation biology issue, but what could have been done? The decline was due to a large-scale decrease of carrying capacity (III). The only way to prevent the starling decline would have been stopping the decreasing carrying capacity. In the present-day developmental stage of our society and in the context of agricultural policy implemented today, starling populations cannot be restored by restoring cattle farming. However, there may be compensatory measures for environmental management, which increase the carrying capacity.

Starlings may have benefited from annual set-asides which farmers are obliged to leave from cultivation each year (approximately 10 percent of their field area). Most of Finnish annual set-asides are stubble fallows, where the sward is not dense and high during the breeding season of starlings. Set-asides founded by dense sowing of a green-manure sward, are unsuitable for starlings.

The increase of southern Finnish starling populations (II, III) coincides with the set-aside policy carried out in Finland from 1989 (Tiainen 2004). Set-asides were initially founded by dense sowing of green-manure plants, but since 1995, as Finland became member in the European Union, about 10% of field area has been annual set-asides, without sowing green manure plants.

There are also other changes in land-use, which may have benefited the starling. For instance, the increasing popularity of horse keeping in the surroundings of big cities has increased the area of pastures, which offer feeding opportunities to starlings. These cannot restore the former situation where the number of farms was large (350 000 in 1959) and 80% of farms had cattle (cf. Fig. 1). In conclusion, the starling population has established a new population level at the present-day carrying capacity.

6.2   *Sources and sinks?*

In the 1960s, Finnish farmland area still largely consisted of a mosaic of various kinds of habitats where the land-use was dominated of mixed farming; half of the field area comprised rotational pastures and field grassland. During the 1960s cattle farming was gradually turning into specialized cultivation (Fig. 1), and
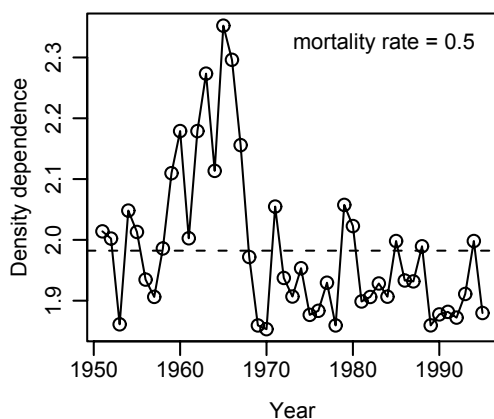

Fig. 11. Variation in density-dependence in starling population dynamics (POP, south-west Finland). Estimates were derived consecutively for sliding ten-year periods. The dashed line represents the total density-dependence estimated for the total period.

increasing parts of starling populations were forced to breed in sub-optimal habitats. Despite of the deterioration of habitats, starlings were abundant during the end of the 1960s and in the beginning of the 1970s. This can be explained with lags in population response to environmental change (III).

It is also possible that source–sink dynamics (e.g. Pulliam 1988) could have enabled the populations to persist among low-quality habitats (see discussions in II and III). Assuming that the source–sink aspect functions among local populations, it is possible, that starlings could have persisted despite of some deterioration of habitats. It is possible that the deterioration had not passed a certain threshold level for overall population persistence. However, per capita growth rates of individuals settled in various-quality habitats would have diverged so that without immigration/emigration movement of individuals, some of the local populations would have become extinct. The results indicate that the extinction rate of local populations increased towards north (II) and mean brood size decreased northwards (III). Based upon these findings, I suggest that during overall deterioration of farmland habitats (Tiainen et al. 1989) and partly because of pure random factors, emigration

from remaining source populations was insufficient of maintaining the most isolated and smallest sink populations (Gilpin and Hanski 1991, Newton 1998, Chamberlain and Fuller 2000, Foppen et al. 2000, Chamberlain and Fuller 2001, Svensson 2004a), leading to increasing risk of local extinctions and overall population decline, which was most drastically expressed in northern Finland (Fig. 5). The rapid and consistent deterioration of breeding habitats and the subsequent deficiency of reproductive output of starlings, as an ultimate reason, in wide farmland areas most probably caused the decline (III).

Environmental stochasticity, i.e. spatially autocorrelated random factors that affect demography of populations (Royama 1992, Lande et al. 2003), may lead to temporally synchronous population fluctuations among regionally separate populations (Ranta et al. 1995, Ranta et al. 2006). Environmental stochasticity increases the risk of small and isolated populations to become extinct (Lande et al. 2003). I found synchronous population dynamics in southern Finnish starlings (IV). Therefore, I suggest that environmental stochasticity, in addition to demographic reasons (III), might have affected the large-scale population crash of northern starlings (III, IV).

7   PROSPECT

There is a need for spatially explicit research of the possible source–sink dynamics of starlings, synthesizing the ideas presented in this thesis (especially II and III). This approach is not straightforward, since many demographic parameters are unknown, and thus a thorough attempt requires an extensive simulation design. Here, I formulated a candidate basis for such an inspection. I used the spatial RSF-estimates (cf. Fig. 6) in estimating the initial population. For the modelling approach, I pooled the site-specific counts within 10 km × 10 km squares, which I now call "units k". Spatially explicit discrete-time and age-structured model (cf. Ranta et al. 2006) is written as,

$$N_{k,t+1} = N_{k,t}s_2 + f_k N_{k,t} s_1 (1-m) + \mathbf{D}\mathbf{v}_t ,$$

where $N_{k,t}$ is breeding population size (number of females) per unit k in year t, s_1 and s_2 denote first-year and adult survivals, and m is the proportion of emigrating young of the cohort that survives to the following breeding season. Only a part of the juvenile-cohort is assumed to disperse, when they seek potential breeding sites in the forthcoming year following their birth. Unit-specific f_k is per capita reproduction in numbers of female fledglings. The last component of the model is the dispersal kernel. $\mathbf{D}$ is a square matrix of disperse probabilities between units i. The diagonal of the matrix comprise of zeros, and each column sums up to unity. A vector $\mathbf{v}_t$ is the same as

$$N_{k,t} f_k s_1 m .$$

The matrix-multiplication operation allocates individuals from units k to their surroundings by a probability, which is (inversely) weighted by the distance matrix of units k. $\mathbf{D}$ was predicted with a simple exponential-decay fit on numbers of recovered starlings found from various distances in respect of their birth-nest during breeding season (totally 121 recovered; ring recovery data, the Ringing Centre of Finnish Museum of Natural History).

I used demographic parameters, as tabulated below:

s_1	s_2	Mean of f_k	Max of f_k	Min of f_k	m
0.4	0.45	1.52	1.8	1.12	0.31

Vital parameters are somewhat based on earlier results (III, IV). The parameter m was straightforwardly determined from the proportion of individuals that had dispersed further than ten kilometres from their birth-nest. For the values of f_k, a decreasing northwards trend was modelled using a log-linear estimate $\exp(-0.0041) = 0.996$ (see Table 3 in III). In other words, each ten-kilometre step northwards decreased f_k by a proportion of $1 - 0.996$. In order to make the model a bit more realistic, unit-specific maximum carrying capacity of $K_{(\max)k} = 5 N_{k,t=0}$ was implemented to regulate f_k term (cf. IV). By the model, the total population exhibited a slight decreasing trend. I implemented the source–sink aspect with a vector of normally distributed random numbers (mean = 0, SD = 0.3) additive to f_k. Hundred-year simulations were run with and without dispersal.

The simulation approach indicated that dispersal is needed for maximal persistence of population. In the absence of dispersal, the poorly-productive populations faded quickly away, especially in northern region (Fig. 12 and 13). Local population numbers spread out more in the no-dispersal scenario than in the dispersal

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one, which was clearly visible at the points of fifty and hundred years of simulated dynamics (Fig. 12). In the absence of dispersal, highly-productive populations grew quickly at the local K while poorly-productive populations declined. In the source–sink situation, dispersal, via emigration, limited population growth and, via immigration, prevented some of the populations to become extinct. In this case, dispersal stabilized local population dynamics (e.g. Ranta et al. 2006). The
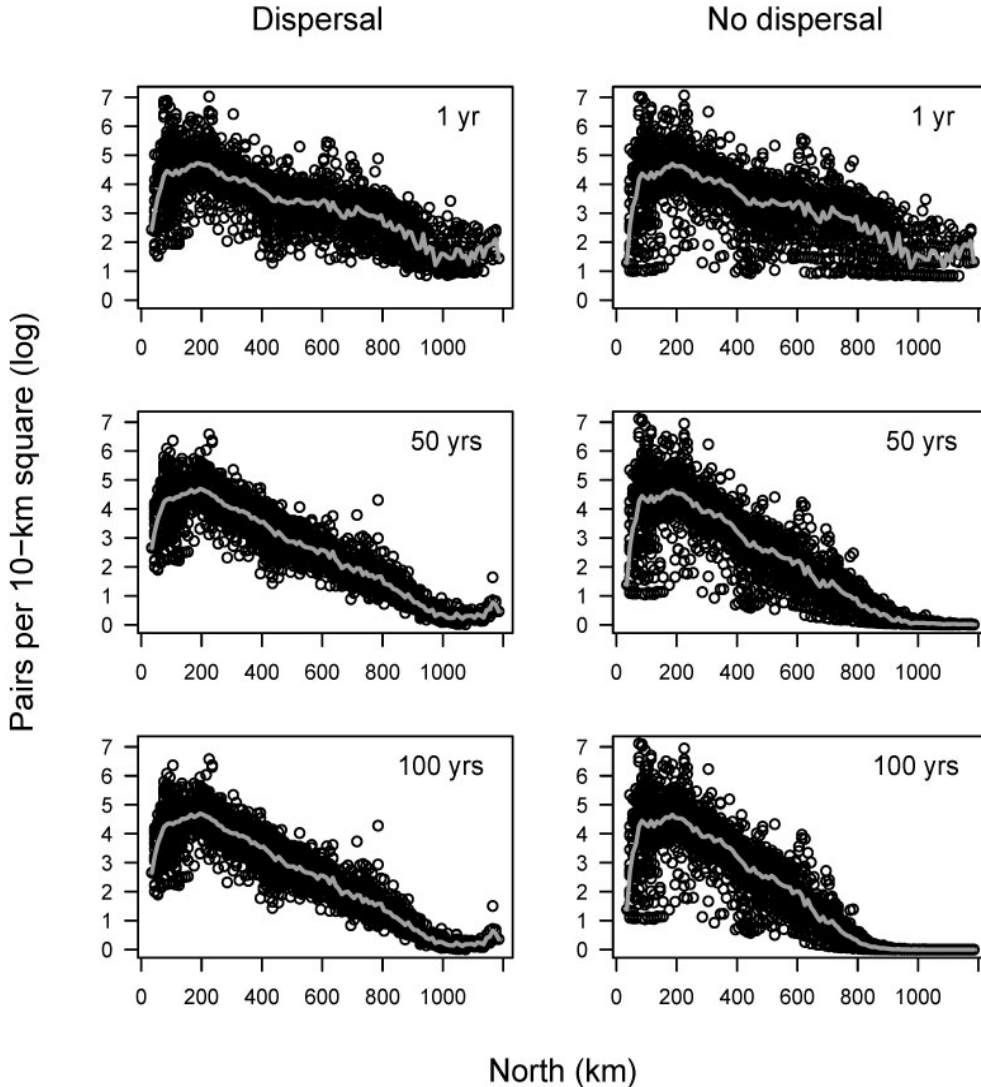

Fig. 12. Population dynamics of Finnish starlings, as generalized with an explicit source–sink model (Dispersal) and a corresponding model that does not assume individual movements between breeding units (No dispersal). Cross-section samples were taken from the population at the time-points of 1, 50, and 100 years from the start-year of each simulation, and log(number of pairs per unit + 1) were plotted against latitudinal coordinate. The lines show mean values according to the latitudinal coordinate.

smaller and the more isolated a population is the higher is the probability that a population becomes extinct (e.g. Gilpin and Hanski 1991, Lande et al. 2003). On the basis of the spatially explicit model, cessation of dispersal clearly increases the extinction-prone of populations especially in the north (Fig. 13). Better understanding of spatiotemporal dynamics involves modelling the effects of various scenarios of habitat change, stochasticity, regionally divergent survival, and wide continuum of dispersal patterns.
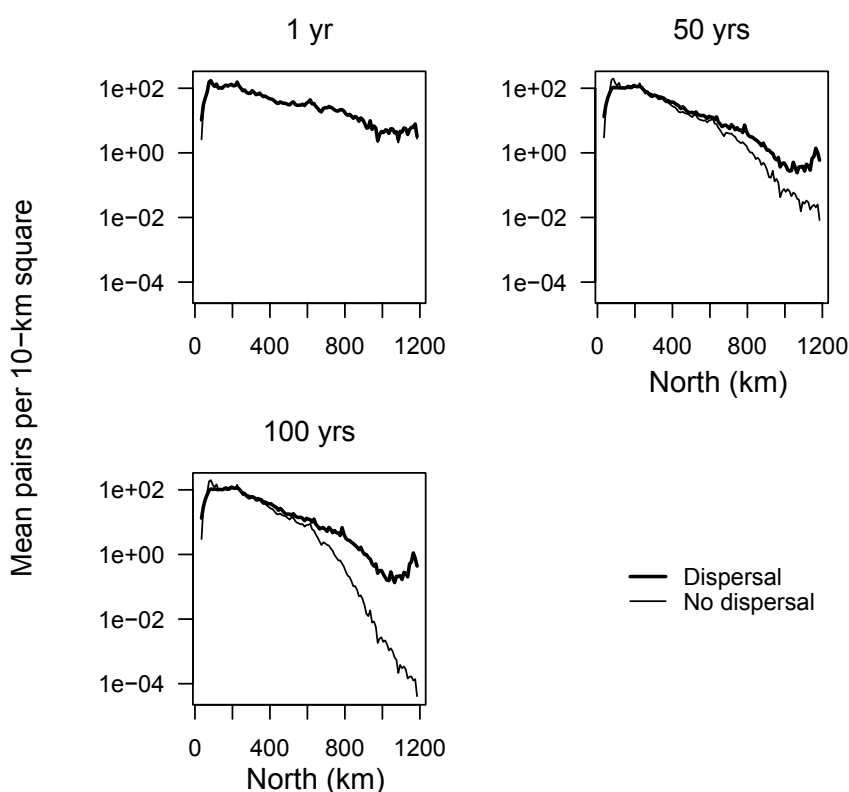
Fig. 13. Population dynamics of Finnish starlings, as generalized with an explicit source–sink model (Dispersal) and a corresponding model that does not assume individual movements between breeding units (No dispersal). Cross-section samples were taken from the population at the time-points of 1, 50, and 100 years from the start-year of each simulation, and the mean number of pairs per unit was plotted against latitudinal coordinate. Here, actual model-based mean numbers (not log[number + 1] as in Fig. 12) are shown, and the values ought to vary in inverse proportions to the extinction probability of unit populations (note logarithmic *y*-scale).

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