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Linking weather and habitat to population dynamics of a migratory farmland songbird

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Although factors influencing population fluctuations of migrant birds have been studied intensively, few studies have applied autoregressive modelling in linking monitoring data to essential factors from both breeding and wintering areas. We studied the effects of temporal variation in habitat composition and weather conditions on population dynamics of the skylark *Alauda arvensis* in southern Finland in 1984–2003 through autoregressive modelling and Monte Carlo testing of simulated time-series. The amount of grassland habitats explained well the general trends in skylark population development. Rainfall had a negative effect on the population growth in breeding areas, but a positive effect in wintering areas. There was also evidence for first order negative density dependence. Our results suggest that intrinsic and extrinsic factors simultaneously included in a population dynamical model, can improve the statistical visibility of both factors. The Monte Carlo approach presented here can be useful in many studies involving strongly autocorrelated time-series.

Introduction

Understanding population dynamics is a central issue in ecology (Royama 1992, Bjørnstad & Grenfell 2001). Birds have intensively been studied in regard to factors influencing population fluctuations. In many studies, population density, habitat quality, food availability and weather have been reported to be important determinants of population growth (Korpimäki 1984, Nilsson 1987, Baillie & Peach 1992, Rotella *et al.* 1996, Yalden & Pearce-Higgins 1997, Watson *et al.* 2000, Jonzén *et al.* 2002b, Rodenhouse *et al.* 2003). However, although the recent amount of theoretical work on population dynamics has been extensive, the number of published studies that link bird population monitoring data to several ecologically essential factors from different stages of species' annual cycles is surprisingly scarce, especially for migrant species (but *see* e.g. Steenhof *et al.* 1999, Sæther *et al.* 2000, Krüger & Lindström 2001, Jonzén *et al.* 2002b). Particularly, more studies on high-quality long-term data sets, analyzed with carefully designed population models are needed in order to address the mechanisms underlying population fluctuations (Bjørnstad & Grenfell 2001). One major problem in these kinds of studies is to distinguish the roles of density-dependent and density-independent processes in determining the population fluctuations (*see* e.g. Royama 1992, Turchin 1995). As population fluctuations are caused by interactions between environmental variability and intrinsic (mostly density-dependent) processes depending on population characteristics (Turchin 1999, Newton 2004a), the separation of these two above-mentioned processes is often difficult or impossible (Ranta *et al.* 2000, Jonzén *et al.* 2002a). Nevertheless, accounting for both is often appropriate in population dynamical models (*see* Rothery *et al.* 1997, Dennis & Otten 2000).

A typical character of time series is that observations are dependent on each other. Furthermore, if a time series analysis includes hypothesis testing and makes use of classical methods, such as statistical tests based on the F-distribution in regression analysis, statistically significant interactions between autocorrelated variables may be spurious: there is often a risk for poor estimation of statistical significance. A common approach to account for autocorrelation in regression modelling is prewhitening of time series (*see* Chatfield 2004), i.e. removal of autocorrelation by some predefined technique. Another approach is adjustment of the effective degrees of freedom, to correspond to the amount of information in the time series. This can be done based on theory developed by Bartlett (1946), or even better with some modified adjustment methods (Pyper & Peterman 1998). The exact consequences of autocorrelated data can however be hard to predict, and consequently, one issue in this study is to handle the problem with autocorrelated time series with Monte Carlo tests by comparing observed data with simulated autocorrelated time series.

Here, we examine the population dynamics of a farmland bird species, the skylark *Alauda arvensis* L., using data from long-term farmland bird censuses performed in an agricultural landscape in southern Finland (Tiainen & Pakkala 2000, 2001). The skylark is an abundant species of open farmland landscapes all over Europe and it has shown a strong decrease in population size across central and western Europe since the 1970s (BirdLife International/European Bird Census Council 2000, Donald *et al.* 2001a, Gregory *et al.* 2004). It is a true field species, breeding, foraging and wintering in field areas (Cramp 1988). The decline of the skylark in central and western Europe has gathered great concern as it has been generally linked to the deterioration of breeding and wintering habitats caused by changes in farmland management and agricultural intensification (Wilson *et al.* 1997, Chamberlain *et al.* 1999, Chamberlain *et al.* 2000a, Donald & Vickery 2000, Donald *et al.* 2002). In Finland the skylark population has not declined over the same period. Rather it has been fluctuating with temporary increases during the country-wide set-aside schemes in the 1970s and early 1990s (Tiainen *et al.* 2001). In contrast to the situation in central and western Europe, the growing season in Finland is short and the landscape is constituted of relatively small patches of farmland usually surrounded by forests. Spring cereal cultivation dominates, while the cultivation of winter cereals is rare. Thus, as the skylark is a migrant in Finland, the majority of agricultural land is without any vegetative cover during the spring arrival in April. We suggest that in the northern agricultural ecosystem those fields with vegetative cover (i.e. cultivated grass, pasture, winter cereal and set-aside) are beneficial for the skylark because they offer better protection for nests and a more abundant food supply than ploughed fields (e.g. spring cereal, sugar beet and potato). Moreover, studies on skylark habitat associations in Finland have shown that the set-aside areas and agricultural grasslands are favoured by the species (Tiainen *et al.* 2001, Piha *et al.* 2003). Due to known habitat preference, the skylark may serve as a good model species when studying causes of population fluctuations in human managed agricultural habitats.

We investigated how temporal variation in breeding and wintering conditions has affected the dynamics of our study population. The factors studied are thought to affect: (1) breeding performance (the previous year's amount of preferred habitat and weather conditions of breeding areas), (2) adult and first-year survival (weather conditions of breeding and wintering areas), and (3) habitat attractiveness (amount of preferred habitat in the breeding season). The model is without doubt a simplification, but it summa-

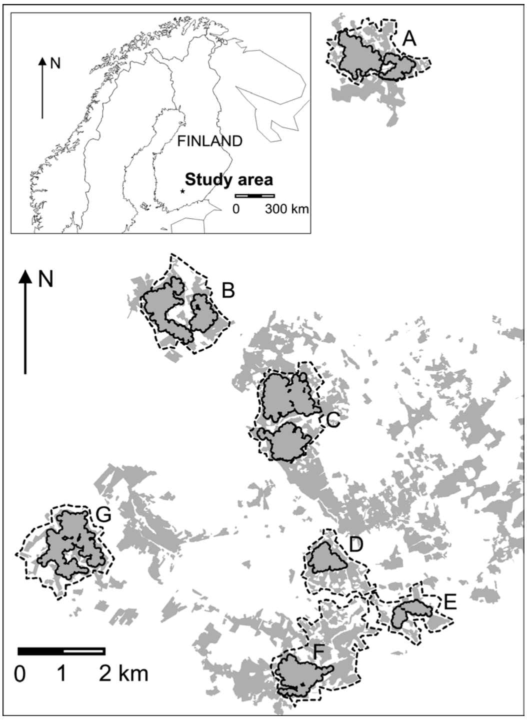

Fig. 1. The study area. The grey areas represent fields, dashed lines are the borders of the permanent bird census areas (subareas A–G). The areas with solid black border are the important skylark areas that were used in the analysis. The location of the study area is shown in the inserted panel (top left).

rizes the available, and, we propose, essential information about important conditions for the species. The aims of this study were to investigate how human-induced variation in farmland habitat composition and weather conditions in both breeding and wintering areas affect the population dynamics of the skylark. In addition, we present a useful approach how environmental effects can be detected from strongly autocorrelated time-series using simulation methods. Furthermore, we address the statistical visibility of density dependence and environmental variables when using a synthetic model of population regulation.

Material and methods

Study area and data collection

The study area is located in the municipality of Lammi, southern Finland (61°05´N, 25°00´E; Fig. 1). The agricultural landscape is rather fragmented consisting of relatively small patches (mostly < 0.2 km^2) of farmland. The total area of arable land in the annually studied permanent study plots was 1120 ha. The dominating crop types during the study period were spring cereals, cultivated grass and sugar beet.

Skylark territories were censused annually between 1984 and 2003 using a two-visit mapping method, which has been shown to be a reliable and accurate method for territory mapping of the skylark in southern Finland (Tiainen & Pakkala 2000). According to a study by Tiainen *et al.* (1985) two visits accounted for 98% of the territories found in five visits. The first visits were made between 5 and 20 May and the second between 1 and 20 June. Special attention was paid to recording simultaneous observations of singing males, as these are important for the identification of the correct number of territories. During each field visit, several observations of the same individuals were gathered; thus the interpretation of territories and the definition of territory centres were based on more than just single observations from the two visits. The interpretation was made according to a standard practice developed for studies on agricultural birds in Finland (cf. Tiainen & Pakkala 2000, 2001). The positions of all defined 3133 skylark territories were stored in a GIS database, as well as the boundaries and land use of the studied fields, which were mapped during and after the field visits. The land use of the fields was classified in two categories: (1) fields with over-winter vegetative cover i.e. grasslands, set-asides and winter cereals, and (2) fields without vegetative cover i.e. all spring-sown crops. For further analysis, a habitat variable that measures the amount of preferred habitat was then calculated as the arcsin-transformed proportion of field area covered with overwinter vegetation.

In the further analysis, the study area was selected to include only those field areas that were considered to be important for the skylark by using the following criteria: all skylark territory positions (N = 3133) defined during 1984–2003 in permanent study plots (total area of 1120 ha) were surrounded by zones with a radius of 50 metres and outer borders of these buffer zones in each study plot were used as borders of the respective study plots (*see* Fig. 1). Areas smaller than 20 hectares, which are of marginal importance for the population were excluded from the analysis. As a result, 2935 territories (94% of all territories) with total area of 620 ha were included in the further analysis. The skylark densities in seven sub-areas (indicated as A–G in Fig. 1) fluctuated synchronously (analysis of concordance: $W = 0.38$, $\chi^2 = 50.56$, df = 19, $p < 0.001$) and the distances between the sub-areas were relatively small in relation to the scarce available information of the species' natal dispersal (Donald 2004). Consequently, here we considered the sub-areas as belonging to the same population, and the used variables were pooled over the study area.

Weather data

Although extreme weather conditions might in some cases be biologically more relevant, we chose average temperature and total amount of rainfall to approximate general weather conditions in the breeding and wintering areas. We assume that these fundamental weather variables also indirectly cover some of the (unknown) extreme weather conditions through correlation between average and extreme conditions. However, opposite to the situation when using large scale climate indices, we are still able to separate effects of temperature and rainfall in different areas.

Weather data of the breeding season consisted of records from the official weather station at Lammi Biological Station (located within the study area) collected between 1984 and 2003. We used two variables measuring the weather conditions during the breeding period: mean daily temperature and total amount of rainfall between May and July. In addition, we used the melting date of permanent snow cover as a variable describing the advance of spring (standardized as 1 March = 1).

According to the archives of the Ringing Centre of the Finnish Museum of Natural History the majority of Finnish skylarks winter in lowland France. To describe the weather conditions in wintering areas, we used the weather records of seven French weather stations located in lowland France (Toulouse-Blagnac 43°37´N, 1°22´E; Bordeaux-Merignac 44°49´N, 0°41´W; Nantes-Bouguenais 47°09´N, 1°36´W; Orleans 47°59´N, 1°46´E; Clermont-Fd 45°47´N, 3°09´E; Poitiers-Biard 46°35´N, 0°18´E; Limoges-Bellegarde 45°52´N, 1°11´E) between 1984 and 2003 provided by Meteofrance (http://www.meteo.fr/meteonet_en/index.htm). The mean temperature and mean cumulative rainfall between December and February of the seven weather stations were used.

Data analysis

The skylark time series

In this study we used annual estimates of breeding population densities, taken as the number of skylark territories per km^2, expressed as N_t. Natural logarithm transformation ($L_t = \ln N_t$) was used for further analysis of the time series.

To describe the properties of the time series, we analyzed the autocorrelation function (ACF), the partial autocorrelation function (PACF) and the more ecologically explicit partial rate correlation function (PRCF), that shows the strength and order of negative density-dependence (*see* e.g. Berryman & Turchin 2001). As seen from the ACF and PACF (Fig. 2), the skylark series was significantly positively autocorrelated at lag 1, but not at any greater lags in the PACF. This indicates a first order autoregressive process. In the ACF, significant negative autocorrelations of greater lags (7 and 8), reflect mostly the humped character of the skylark series. The PRCF shows that there is a nearly significant negative feedback (density-dependence) in the time series.

If a population is strongly age-structured and environmental variation is selectively affecting only some age classes, the effects of this variation on the population size may disappear (Kaitala & Ranta 2001). The skylark is a relatively short-lived bird that breeds already at an age of one year (Cramp 1988) so it is probable that the population age-structure has here only minor effects on main patterns of the results.

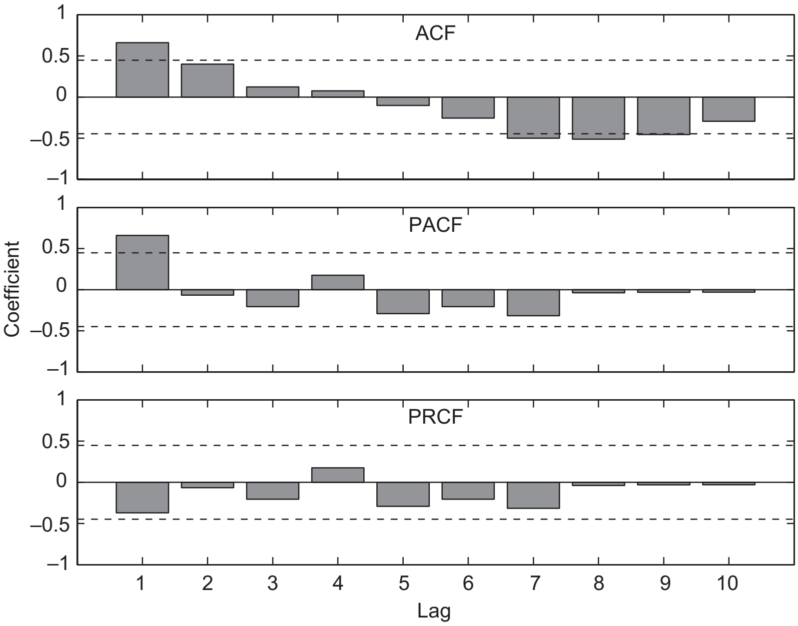

Fig. 2. The autocorrelation function (ACF), partial autocorrelation function (PACF) and partial rate correlation function (PRCF) of the logarithm transformed skylark time series. The dashed lines represent 95% confidence limits ($\pm 2N^{-0.5}$).

Complete model

We constructed a biologically feasible multiple regression model, where we included the intercept, the first order autoregressive component and seven extrinsic factors that could have an impact on skylark demography. As the response variable we used the rate of population change of the logarithm transformed population density, $r_t = L_t - L_{t-1}$. Hereafter we call the model with the total set of variables our *complete model*. Estimation of statistical significance of the complete model, as well as partial tests for the single variables, were done using Monte Carlo methods (as described in section "Simulated time series and Monte Carlo testing of the models").

The basis of our model is a regression of r_t on the raw population density in the previous year N_{t-1} representing density dependence in the population. The extrinsic factors in the model are thought to exclusively affect the logarithmic rate of change (r_t) additively within one year, via births, deaths, immigration and emigration. This translates into a multiplicative effect on the population size. Our complete model was:

$$r_t = a_0 + a_1\mathrm{AR}(1) + b_1\mathrm{HAB}_{t-1} + b_2\mathrm{HAB}_t + b_3\mathrm{STEMP} + b_4\mathrm{SRAIN} + b_5\mathrm{MELTD} + b_6\mathrm{WTEMP} + b_7\mathrm{WRAIN} + \varepsilon_t \quad (1)$$

where:

AR(1) = First order autoregressive component $= N_{t-1}$.
HAB_{t-1} = Proportion of preferred habitat ($t - 1$), arcsin transformed.
HAB_t = Proportion of preferred habitat (t), arcsin transformed.
STEMP = Mean summer temperature (°C), Lammi ($t - 1$).
SRAIN = Total amount of summer rainfall (mm), Lammi ($t - 1$).
MELTD = Melting date of permanent snow cover, Lammi (t).
WTEMP = Mean winter temperature (°C), France (t).
WRAIN = Total amount of winter rainfall (mm), France (t).
ε_t = Normally distributed error term (t).
a_0, a_1, b_1, …, b_7 refer to the intercept and regression coefficients, respectively.

All environmental variables were normalized to zero mean and unit variance to make the effect sizes comparable.

Our regression model can be directly derived from Ricker's model of population renewal (Ricker 1954). With multiplicative effects of environmental variables and an error term the model is:

$$N_t = N_{t-1} \exp[r(1 - N_t K^{-1}) + \boldsymbol{X}_t \boldsymbol{b} + \varepsilon_t] \quad (2)$$

$$\Leftrightarrow$$

$$L_t = L_{t-1} + r - rN_t K^{-1} + \boldsymbol{X}_t \boldsymbol{b} + \varepsilon_t \quad (3)$$

$$\Leftrightarrow$$

$$r_t = r + rN_t K^{-1} + \boldsymbol{X}_t \boldsymbol{b} + \varepsilon_t \quad (4)$$

Here r is the intrinsic rate of increase, K is the carrying capacity, $\boldsymbol{b}$ is a column vector containing the regression coefficients and $\boldsymbol{X}_t$ is a row vector containing the observed values of the explanatory variables at time t. As our explanatory variables were normalized, the intercept term in the regression model will be an estimate of the parameter r, i.e. the intrinsic growth rate in absence of competition and in average environmental conditions. Without the AR(1) component, our model would equal exponential growth plus environmental effects.

The explanatory variables in the complete model are thought to act on r_t (*see* Eq. 4) via rates of birth, death, immigration and emigration. AR(1) stands for the eventual first order density-dependence and may act on any of the per capita rates, but the reason of statistical density dependence is not investigated here. Variables HAB_{t-1}, STEMP and SRAIN are related to the breeding conditions in the study area during previous year and can thus be thought to affect the breeding performance. Variables WTEMP and WRAIN describe the weather conditions at the main wintering grounds in France, and can be thought to have a direct impact on mortality. Mortality of breeding adults and fledglings can also be affected, especially by STEMP and SRAIN. Variables HAB_t and MELTD describe the conditions in the breeding grounds at the time of arrival in spring i.e. the habitat attractiveness or suitability for territory establishment. Thus, the variation explained by these variables could be connected to immigration and emigration. HAB_t could also affect the number of non-territorial floaters that were not recorded in the census that is based only on territorial individuals.

Reduction of the model

For a statistically significant complete model, an interesting aspect is which explanatory variables or which sets of variables offer the best fit for the data. Furthermore, in order to estimate the effect sizes of the important variables, it is appropriate not to include any unnecessary variables. We compared the models with the small sample unbiased Akaike information criterion ($\mathrm{AIC_c}$), which is a reliable method to select the most appropriate model (Johnson & Omland 2004). $\mathrm{AIC_c}$ is preferred unless the number of observations is at least 40 times the number of explanatory variables (Anderson *et al.* 2001). $\mathrm{AIC_c}$ evaluates models due to their residuals, in relation to the number of estimated parameters. We evaluated all possible model combinations and the model that received the lowest score was considered to be the most parsimonious one.

The five most parsimonious models were calculated to get some idea of the robustness of the best selected subset of variables. Variables may have entered the reduced model partly as a consequence of possessing a strong autocorrelation. Therefore we adjusted the standard errors of the regression coefficients by Monte Carlo methods (*see* below).

Simulated time series and Monte Carlo testing

Due to autocorrelations in the time series under investigation, classical tests for statistical interactions may give inaccurate results, either through spurious correlations (error of type I), or in some cases failure in detecting an interaction (error of type II). These kinds of problems can be handled using various Monte Carlo methods (Pyper & Peterman 1998, de Valpine 2003), i.e. repeated simulation of a test statistic under a more specific null hypothesis ($\mathrm{H_0}$). In order to include the autocorrelation of the time series in $\mathrm{H_0}$, we generated simulated time series that had similar autocorrelation at lag 1 as the observed population density, but which were otherwise random. To generate the time series, we used a first order autoregressive process (*see* Ripa & Lundberg 1996) as described in Eq. 5, where W_t is the simulated population density in year t, α is the desired autocorrelation coefficient (with lag 1) and ε_t is normally distributed, uncorrelated random noise with zero mean and unit variance.

$$W_t = \alpha W_{t-1} + \sqrt{1-\alpha^2} \times \varepsilon_t \qquad (5)$$

We chose α to equal the autocorrelation coefficient of the detrended skylark series. As we knew the distribution of autocorrelations generated by the process with given α through simulation, we created an algorithm for acceptance/rejection, so that the accepted output fitted within a distribution with mean α and SD = 0.01 in detrended form. Finally, the observed linear trend in the skylark series was added also to the simulated time series. Thus we included the trend in H_0, rather than removed it. However, in our case the linear trend was so weak (*see* Results) that the approach in handling the trend was indifferent.

The Monte Carlo procedure was done by substituting the skylark series with W, which was then further analysed in the same way as the original time-series (*see* Eq. 1). In other words, we substituted the response variable with $\Delta \ln W$ and the AR(1)-component with W_{t-1}, in the simulations. To get the probability distribution for H_0 we repeated the process 100 000 times for every test. The statistical significance (p) of H_0 was then the proportion of those simulated test statistics that performed better than the observed test statistic. For the overall test of the complete model, we chose to use the coefficient of determination (R^2) as our test statistic.

We also performed partial tests of the explanatory variables in the complete model by similar methodology, by investigating the observed and simulated absolute values of partial correlation coefficients. Thus, we tested H_0 implying that removal of a variable does not impair the model fit, either because there is no genuine statistical interaction or because there is collinearity between explanatory variables. Standard errors of regression coefficients in all models were adjusted for autocorrelation, as derived from the Monte Carlo p-values by the inverse process of significance testing.

Statistical visibility of density dependence and environmental variables

The importance of having a synthetic approach, with both intrinsic and extrinsic factors in the model simultaneously, were investigated by an information theoretical approach. In these comparisons, we used the best subset of variables (with lowest $\mathrm{AIC_c}$) excluding AR(1) as our environmental set of variables. This was to exclude variables that were not important, e.g. due to collinearity, without favouring a set of environmental variables that fits with AR(1).

In order to measure if the effect of AR(1) changed when accounting for environmental variables, we compared the improvement in $\mathrm{AIC_c}$ when adding AR(1) to the best subset of environmental variables with the improvement when adding AR(1) to the model containing the intercept only. The differences in improvement of $\mathrm{AIC_c}$ and the Akaike weights (ω) were calculated to compare the two situations. Likewise, we compared the improvement in $\mathrm{AIC_c}$ when adding the best subset of environmental variables to a model containing AR(1) with that when adding the best subset to the intercept only.

Results

Mean observed density of the total study area varied between 18.9 and 35.9 territories per km^2 during the study period. There was no significant linear trend (regression on L_t against time: $y = 3.196 + 0.001x$, $R^2 = 0.0011$, df = 19, $p = 0.89$).

Correlations between variables

In this section we highlight problems with collinearity in our data. All correlations between variables are given in Table 1.

The proportion of preferred habitat occurs in the complete model with both lag 1 (HAB_{t-1}) and lag 0 (HAB_t), and as this variable was strongly autocorrelated (α = 0.84), we have a problem with collinearity. Also AR(1) was strongly correlated with HAB_{t-1} and HAB_t. Collinearity between the variables makes it more difficult for the habitat related variables and AR(1) to enter the same reduced model. There was also a significant negative correlation between HAB_{t-1} and SRAIN (total amount of rainfall in breeding areas at lag 1), and a significant positive correlation between the variables WTEMP and WRAIN

Table 1. Pearson's correlation coefficients of the predictor variables. Coefficients that are significant according to the *t* distribution (df = 17, $p < 0.05$) are given in boldface.

	AR(1)	HAB$_{t-1}$	HAB$_t$	STEMP	SRAIN	MELTD	WTEMP
HAB$_{t-1}$	**0.77**						
HAB$_t$	**0.58**	**0.84**					
STEMP	–0.33	–0.26	–0.16				
SRAIN	–0.12	**–0.48**	–0.32	–0.32			
MELTD	0.10	0.07	–0.06	–0.42	0.10		
WTEMP	0.13	0.23	0.17	0.11	–0.21	–0.07	
WRAIN	0.02	0.20	0.02	–0.15	0.01	0.34	**0.49**

Table 2. Complete model: regression coefficients (*b*), standard errors adjusted for autocorrelation (SE$_{\text{adj}}$) and partial *p* values for the variables. SE$_{\text{adj}}$ for the intercept is not adjusted for autocorrelation.

	b	SE$_{\text{adj}}$	Classic *p*	Monte Carlo *p*
Intercept	0.362	0.203	0.105	–
AR(1)	–0.015	0.008	0.100	0.099
HAB$_{t-1}$	–0.086	0.105	0.279	0.431
HAB$_t$	0.108	0.053	0.031	0.071
STEMP	–0.031	0.023	0.238	0.213
SRAIN	–0.112	0.035	0.006	0.010
MELTD	–0.015	0.020	0.508	0.477
WTEMP	–0.010	0.020	0.676	0.645
WRAIN	0.087	0.027	0.010	0.009

that describe weather conditions of the wintering areas. Although the former does not make any sense, it introduces some further collinearity in the data. The correlation between STEMP and SRAIN is negative, but surprisingly not very strong.

Model explanation of population change

The Monte Carlo test for the complete model produced a highly significant result, even though there were highly intercorrelated explanatory variables. The observed coefficient of determination was $R^2_{\text{obs}} = 0.861$ and the simulated models provided mean $(R^2_{\text{sim}}) = 0.579$; SD $(R^2_{\text{sim}}) = 0.138$; $p < 0.01$ (Table 2). In the partial tests of the complete model, the total amount of rainfall at Lammi in the previous breeding season (SRAIN) and the total amount of rainfall in the wintering area (WRAIN) were statistically significant. The effect was negative at breeding areas and positive at wintering areas. HAB$_t$ showed a tendency towards a positive effect on population rate of change. The effect sizes of all mentioned external variables (HAB$_t$, SRAIN and WRAIN) were about equal: around 10% of population increase per standard deviation of change towards better conditions in each environmental variable.

The reduced model with the best AIC$_{\text{c}}$ score among all model combinations (*see* Table 3 for the statistics and variable coefficients of the complete and five best reduced models) explained the observed variation well ($R^2 = 0.830$). The best model included the AR(1) component, HAB$_t$ and the same weather variables (SRAIN and WRAIN), that were significant in the partial tests. The adjusted standard errors for the regression coefficients in the best reduced model (Table 4) revealed that the model parameter estimates were reasonably robust. The signs of the regression coefficients were the same as in the complete model, and the effect sizes of the environmental variables were still about equal, but marginally smaller than in the complete model, being around 7% of increase per standard deviation of change towards better conditions in each environmental variable. The considerable difference in AIC$_{\text{c}}$ for the best model compared with that of the second best ($\Delta\text{AIC}_{\text{c}} = 4.255$) reveals that the variables excluded from the best reduced model are not really needed to improve the explanatory power of the model. Further, as AR(1) and HAB$_t$ are included in all reduced models, these variables seem to be important indeed, despite the quite weak evidence in the partial tests of the complete model. To visualize the apparent connection between the skylark density and the proportion of preferred, grassland habitats, the time series are compared in Fig. 3.

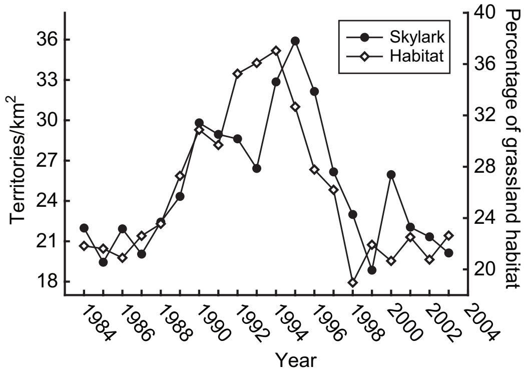

Fig. 3. Skylark density and proportion of preferred, grassland habitats in Lammi study area.

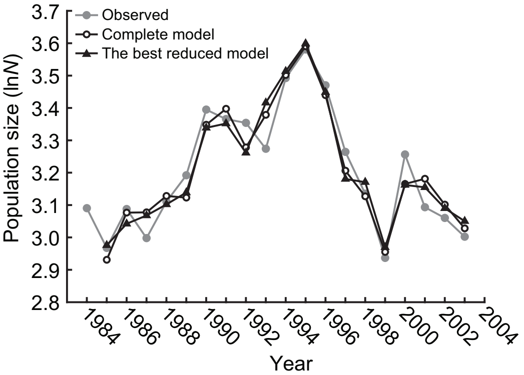

Fig. 4. The observed skylark time series and the predictions of the complete- and the best reduced model. Predictions equal one-year forecasts.

Table 3. Complete model and the five best reduced models, their coefficients of determination (R^2), AIC$_c$-scores and regression coefficients. The difference in AIC$_c$ between the best and the second best reduced model is 4.255.

	Complete	Reduced 1	Reduced 2	Reduced 3	Reduced 4	Reduced 5
R^2	0.861	0.830	0.839	0.836	0.831	0.831
AIC$_c$	–63.169	–87.857	–83.602	–83.295	–82.785	–82.736
Parameters						
Intercept	0.362	0.531	0.557	0.433	0.529	0.527
AR(1)	–0.015	–0.021	–0.022	–0.017	–0.021	–0.021
HAB$_{t-1}$	–0.086	–	–	–0.042	–	–
HAB$_t$	0.108	0.070	0.068	0.090	0.070	0.069
STEMP	–0.031	–	–0.016	–	–	–
SRAIN	–0.112	–0.076	–0.082	–0.087	–0.077	–0.076
MELTD	–0.015	–	–	–	–0.006	–
WTEMP	–0.010	–	–	–	–	–0.004
WRAIN	0.087	0.066	0.064	0.073	0.069	0.067

Model fit and predictions of the models

A general rule in fitting a statistical model is to test if the residuals are approximately normally distributed and not autocorrelated. We tested the normality assumption with Lilliefors' test (Lilliefors 1967). In our case, the residuals of the complete and best reduced models did not differ significantly from a normal distribution, nor were they significantly autocorrelated (Table 5). At least on these criteria, we have no reason to doubt the fits of our models.

Table 4. The best reduced model: regression coefficients (*b*) and standard errors adjusted for autocorrelation (SE$_{adj}$). SE$_{adj}$ for the intercept is not adjusted for autocorrelation.

	b	SE$_{adj}$
Intercept	0.531	0.107
AR(1)	–0.021	0.004
HAB$_t$	0.070	0.035
SRAIN	–0.076	0.015
WRAIN	0.066	0.017

For comparison, we plotted the observed skylark time series and the predictions of the complete and best-reduced models (Fig. 4). The fit between the observed time-series and the predictions seems good except for some inaccuracy in 1990–1994 before the maximum of 1995.

Visibility of density dependence and environmental variables

The best set of environmental variables, chosen in absence of AR(1), was HAB_{t-1}, HAB_t, SRAIN and WRAIN, hereafter denoted ENVSUBSET. Adding AR(1) to ENVSUBSET improved AIC_c more than adding AR(1) to the intercept only (Table 6). The Akaike weight $\omega = 0.74$ for the former case, suggests some improvement in visibility when accounting for environment, but the evidence is not very strong. Similarly, adding ENVSUBSET to the AR(1) component is slightly better than adding ENVSUBSET to the intercept only, suggesting that accounting for density dependence can improve the visibility of environmental effects. The two comparisons are in fact equivalent in terms of $\Delta\Delta AIC_c$ and ω (Table 6).

Discussion

Many studies on European farmland bird populations' trends have described the population changes and shown correlations between the trends and agricultural intensification (reviewed by Newton 2004b), but studies integrating density-dependence and several environmental determinants with population changes through autoregressive time-series modelling have not been published. A synthetic view of population regulation including endogenous and exogenous factors to explain population fluctuations might be of particular importance in research of migrant birds, as they confront a wide range of spatially and temporally variable extrinsic factors limiting population size (*see* e.g. Newton 2004a). Our study integrated multiple factors plausibly affecting population dynamics. The modelling approach was based on simulating autocorrelated time-series and Monte Carlo testing. The best determinants of changes in skylark population density were the first order autoregressive component, referring to negative density dependence, amount of preferred habitat in breeding areas and rainfall both in breeding and wintering grounds.

Results of tests for detecting patterns similar to density dependence from annual abundances collected from a natural population cannot reveal causal processes (Wiens 1989, Shenk *et al.* 1998). According to Wolda and Dennis (1993) these tests rather look for a "return tendency", a tendency for population sizes to return to some intermediate range of values. The observed pattern similar to negative density dependence can be caused by intrinsic regulation or by other density-related processes, for example the variation in habitat availability which also has similar return tendencies as pointed out by Wolda and Dennis (1993). In our case, a clear return tendency was observed when accounting for environmental variables in the model.

In Finland skylarks prefer grassy agricultural habitats (set-asides, pasture and cultivated grass) (Piha *et al.* 2003) probably because these habitats offer better safety for breeding and more

Table 5. Tests for normality and autocorrelation of model residuals. Lilliefors' test statistic critical value is 0.195 at the significance level 0.05 ($N = 19$).

	Complete model	Best reduced model
Lilliefors' statistic	0.089	0.093
Significance (*p*)	> 0.10	> 0.10
Autocorr. coefficient	–0.169	–0.181
Significance (*p*)	0.503	0.472

Table 6. Statistical visibility of AR(1) and environmental variables when the other aspect is present and absent. Visibility is measured as the improvement in the model (ΔAIC_c) and the difference in improvement is compared in terms of $\Delta\Delta AIC_c$ and Akaike weights (ω).

Present variables	Added variables	ΔAIC_c	$\Delta\Delta AIC_c$	ω
Visibility of AR(1)				
Intercept, ENVSUBSET	AR(1)	–1.666	0.000	0.736
Intercept	AR(1)	0.388	2.054	0.264
Visibility of environmental variables				
Intercept, AR(1)	ENVSUBSET	–15.285	0.000	0.736
Intercept	ENVSUBSET	–13.232	2.054	0.264

abundant invertebrate food supply (Poulsen *et al.* 1998, Wilson *et al.* 1999, Kinnunen *et al.* 2001, Jeanneret *et al.* 2003). The results of this study show that the variation in availability of these habitats is of importance in population fluctuations of the skylark. The role of preferred habitat could be related to population size by two main mechanisms: (1) enhanced breeding success at the population level, when the amount of preferred habitat increases (effect on population size with a time lag), and (2) increased habitat attractiveness i.e. more settlers when the amount of preferred habitat increases (effect on population size without a time lag). The best reduced model included only the amount of preferred habitat at lag 0. However, it is possible that the habitat availability at lag 1 (HAB_{t-1}) is also of importance due to better breeding performance, but not visible as it was collinear with both AR(1) and the habitat variable without a lag (HAB_t). Likewise, HAB_{t-1} may possibly have played the same role as the AR(1) component. It is however impossible to distinguish the possible causal effect of HAB_{t-1}, from the effect of AR(1). Had habitat availability been important only by way of habitat selection, the gain in population size would have resulted mostly from immigration from other areas. This is not necessarily the case here, as in Finland both skylark population densities and habitat changes are relatively synchronous over large areas (Väisänen 1999, Tiainen *et al.* 2001, Tiainen 2004 based on official statistics of Finland). Instead, the proportion of non-territorial floaters, which were not recorded in the census, may vary with the proportion of suitable habitat. In any case, it is evident that variation in the size of the skylark population is strongly affected by the availability of grassy habitats, although it is difficult to explicitly separate the effects of breeding performance and habitat attractiveness with the methods we have used.

Weather conditions of both breeding and wintering areas affected population fluctuations. Rainfall, rather than the temperature, seemed to be of importance in the model. In the breeding areas, the amount of rainfall during the previous breeding season had a negative effect on the population growth rate. Avian reproduction may be highly influenced by rainfall and temperature (e.g. Wingfield 1984, Newton 1998), which has also been shown to be the case with the skylark (Donald *et al.* 2001b, 2002). Weather can affect nestling development by chilling the nestlings, reducing the feeding time of the female and by reducing invertebrate density and activity and hence their availability (*see* e.g. Newton 1998). Interestingly, the precipitation in wintering areas had a positive effect on population growth rate. As there was a significant positive correlation between rainfall and temperature at wintering grounds, rainfall may in fact suitably well describe the overall weather conditions, as temperature alone does not provide any relevant information. The effects of cold winters on adult survival can be quite striking (*see*. e.g. Dobinson & Richards 1964, Cawthorne & Marchant 1980). Wintering conditions may also affect the subsequent breeding success through effects on body reserves or spring arrival date (Marra *et al.* 1998, Currie *et al.* 2000, Newton 2004a).

Factors that were not investigated in this study might also be of some importance for skylark population fluctuations, although model fit does not indicate lack of any key variables. However, these factors include e.g. densities of predator populations (*see* e.g. Tryjanowski *et al.* 2002), quality of wintering and stopover habitats (Wilson *et al.* 1996, Perkins *et al.* 2000, Siriwardena *et al.* 2000, Moorcroft *et al.* 2002), and, the ongoing illegal hunting of migrant and wintering skylarks in southern Europe (McCulloch *et al.* 1992). However, the effect of predation in breeding areas might be indirectly included in the model via the availability of grassland habitat, in which nests are assumingly better protected against predation.

Rothery *et al.* (1997) showed by simulation methods that the statistical power for detecting density dependence increase when accounting for environment. In the theoretical study by Lundberg *et al.* (2002), loss of statistical visibility of environmental effects was probably a consequence of omitting density dependence. Empirical support for these findings was provided by Dennis and Otten (2000), using information theoretical comparisons on kit fox *Vulpes macrotis* population dynamics. Our study explicitly gives further empirical support to the importance of having density dependence and environmental variables simultaneously in the model, in this case with a migratory songbird. The result would probably have been even more pronounced without the earlier described collinearity problems. However, we cannot make *a priori* assumptions that the autoregressive component is the important variable, rather than amount of preferred habitat with a time lag.

The skylarks within the whole study area were here treated as one population. We emphasize that density dependence as well as habitat and weather effects, may be scale dependent. Especially density dependence, arising from intraspecific competition, may be stronger on a more local scale.

Conclusions

According to our results, the synthetic view of population regulation i.e. both intrinsic and extrinsic factors are usually simultaneously important in determining population dynamics, is supported. Leaving out either one had a negative effect on the statistical visibility of the other aspect. In addition, among the extrinsic factors, there were significant environmental ones from both the breeding and wintering grounds. Migrant birds are likely to be affected more by extrinsic factors in one area than another, although the relative importance of breeding or wintering areas may change through time (*see* e.g. Newton 2004a). During our 20-year study period, factors in both breeding and wintering areas were important, although we didn’t have data on temporal variation in wintering habitats. As migrant birds face variable ecological conditions, it is important to study population fluctuations in the light of species’ annual cycles.

Farmland biodiversity in Europe and North America has markedly declined due to a general loss of habitat heterogeneity at various spatial and temporal scales (reviewed by Benton *et al.* 2003). Agricultural intensification has been a cause of many bird declines and range contractions, declines being greatest in countries with more intensive agriculture (Chamberlain *et al.* 2000b, Donald & Greenwood 2001, Donald *et al.* 2001a). Thus, agri-enviromental schemes and land-use planning of field areas are important for sustainable development of farmland bird populations. In addition, ecological responses to recent climate change are already clearly visible (Walther *et al.* 2002). As the migrant skylark population is relatively strongly affected by weather conditions, the impact of climate changes may also be of importance.

We think that Monte Carlo methods making use of simulated autocorrelated time-series can be useful for making more accurate inference on population dynamics, whenever the used time-series are strongly autocorrelated. The specific method used here is only one possibility, but the approach can be refined to fit the properties of different data sets. Naturally, the species responses to environmental changes differ, so extrapolating the methodology to various species requires basic studies on e.g. the species habitat associations. Further studies integrating detailed breeding biology data and time-series analysis are needed for a better understanding of the relative importance of intrinsic and extrinsic factors as underlying processes of population fluctuations.

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