

Multivariate State Space Modelling of Bird Migration Count Data

Jonas Knape, Niclas Jonzén, Martin Sköld, and Leonid Sokolov

Abstract We analyse 54 year long time series data on the numbers of common redstart (*Phoenicurus phoenicurus*), common whitethroat (*Sylvia communis*), garden warbler (*Sylvia borin*) and lesser whitethroat (*Sylvia curruca*) trapped in spring and autumn at Ottenby Bird Observatory, Sweden. The Ottenby time series could potentially serve as a reference on how much information on population change is available in count data on migrating birds. To investigate this, we combine spring and autumn data in a Bayesian state-space model trying to separate demographic signals and observation noise. The spring data are assumed to be a measure of the breeding population size, whereas the autumn data measure the population size after reproduction. At the demographic level we include seasonal density dependence and model winter dynamics as a function of precipitation in the Sahel region, south of the Sahara desert, where these species are known to spend the winter. Results show that the large fluctuations in the data restrict what conclusions can be drawn about the dynamics of the species. Annual catches are highly correlated between species and we show that a likely explanation for this is that trapping numbers are strongly dependent on local weather conditions. A comparative analysis of a related data set from the Courish Spit, Russia, gives rather different dynamics which may be caused by low information in the two data sets, but also by distinct populations passing Ottenby and the Courish Spit. This highlights the difficulty of validating results of the analyses when abundance indices derived by other methods or from other populations do not agree.

Keywords Trapping data · State space models · Migration · Bird · Seasonal

1 Introduction

Populations of organisms living in seasonal environments are exposed to different conditions during different parts of the demographic cycle (Fretwell 1972). For

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migratory organisms such as many bird species, the reproductive success may be mostly influenced by the conditions on the breeding grounds, whereas mortality is probably highest during migration and wintering (Silleet and Holmes 2002). Thus, different parts of the seasonal demographic cycle are affected by the conditions at geographically and environmentally distinct locations. Changes in the environment on wintering grounds, along the route of migration or on the breeding grounds may then have different implications for the dynamics of the species (Saether et al. 2004). Population dynamics of migratory birds is therefore interesting from an ecological perspective but just because of the long distances they travel, collecting appropriate data for analysing their dynamics is difficult.

Currently there is no general method for locating the same individuals or populations at the breeding and wintering grounds and analyses of population dynamics through the full seasonal cycle are usually restricted to count data or to mark-recapture data at either wintering or breeding grounds (but see Webster et al. 2002). Mark-recapture analyses of long distance migrants are often hard due to the possibility of birds returning to sites outside of the study area but can sometimes be used to estimate, e.g., effects of weather conditions on survival (e.g. Peach et al. 1991). Traditionally, data from counts at breeding locations such as the North American Breeding Bird Survey and the Common Bird Census in the United Kingdom have been used to compute indices of population sizes (e.g. James et al. 1996). Analyses of this type of data require care since the data often suffer from variation related to sources at different scales and levels, e.g., differences in skill between observers and differences in detection probabilities between types of habitats, and of biases due to biased selections of surveyed habitats (Thomas 1996; Nichols et al. 2008). Although some recent analyses have tried to take the most serious sources of variation in breeding bird survey data into account (e.g. Link and Sauer 2002), it would be helpful if other types of data could be used to confirm conclusions drawn from analyses of point count data (Dunn and Hessel 1995).

A complementary method for monitoring populations of migratory birds is to use visual counts or trapping numbers of birds at fixed locations during migration. Many bird observatories have data from standardised annual or even biannual catches of passerine birds during the periods of migration. Trapping data from bird observatories have recently been used to study phenology shifts in relation to climate change (e.g. Jonzén et al. 2006) and to estimate population trends and dynamics of passerine birds (e.g. Sokolov et al. 2001; Jonzén et al. 2002; Berthold et al. 2004). However, because of the high between year variation typically present in such data, the use of trapping data as indices of population size has been criticised (Svensson 1978). The day-to-day variation in trapping numbers is high and is influenced by local weather conditions. There are a number of studies analysing daily variation in migration count data with the aim of retrieving population abundance indices (e.g. Dunn et al. 1997; Francis and Hessel 1998). Most of these studies regress daily counts or log counts on sets of weather and time dependent variables and from this derive annual abundance indices. Here we take a different approach and analyse seasonal total trapping numbers using state-space modelling techniques. Thus, instead of accounting for weather effects by estimating adjusted annual indices we

deal with the problem of noisy data by integrating the noise in seasonal totals as part of the model.

We analyse trapping numbers from the Ottenby Bird Observatory (Sweden) and from the Courish Spit (Russia) on common redstart (*Phoenicurus phoenicurus*), common whitethroat (*Sylvia communis*), garden warbler (*Sylvia borin*) and lesser whitethroat (*Sylvia curruca*). These species are thought to spend part of the winter in the Sahel area south of the Sahara desert. Previous studies of migrants that winter in the Sahel area have shown that winter survival is dependent on the amount of rainfall in the Sahel area (Peach et al. 1991; Szep 1995). Particularly, a severe drought in the Sahel in the late 1960s and early 1970s (Hulme 1992; Nicholson et al. 1998) is thought to have been the cause of a crash reported for UK populations of common whitethroat (Baillie and Peach 1992) and Hjort and Lindholm (1978) found a strong relationship between the water level in Lake Chad and the number of whitethroats caught at Ottenby the following autumn. With 30 more years of data, we try to verify the influence of conditions at the wintering grounds on the dynamics of this species and compare it to the effects on three other Sahel migrants. We do this using a state-space modelling approach to explicitly deal with the problem of extracting a dynamical process from data in the presence of sampling error. In order to try to determine the relevance of the derived abundance indices as measures of population change we compare an analysis of Ottenby data to an analysis of data from the Courish Spit and to indices from the Swedish Breeding Bird Survey.

2 Materials and Methods

State-space models (Durbin and Koopman 2001) are becoming a standard tool among ecologists working on models of population dynamics (Buckland et al. 2004; Jamieson and Brooks 2004), and have been extensively used in fisheries stock assessment (e.g. Millar and Meyer 2000). Sampling error is a common feature of data from surveys on wild animal populations and a state-space approach to analysing population dynamics time series data therefore seems natural. For the Ottenby time series on annual catches, there are reasons to believe that a large portion of the variation in trapping data on migratory birds is related to varying external conditions during migration and not to real changes in population sizes (Svensson 1978). This is further supported by the tendency for high between species correlations in total annual catches. The high correlations may be caused by the fact that the species experience similar external conditions during their migration. Because of these potential problems we model multivariate observation disturbances within the state space framework.

Since we are interested in comparing the population dynamics between breeding and wintering seasons we construct a model with two simple dynamical components, one for the breeding season and one for the wintering and migration seasons. Both spring and autumn trapping numbers are inputs for this model which will henceforth be referred to as a seasonal model. The model will allow us to ask questions about how strong forces of density dependence are during summer and

winter respectively (Stenseth et al. 2003) and what effect conditions on the wintering grounds have on the winter season population dynamics. We further evaluate if there is any gain in terms of improved parameter estimates and abundance indices in including both spring and autumn data in the same model and in modelling correlated observation disturbances. The results from fitting the model are therefore compared to results from fitting models with uncorrelated observation disturbances and with models where spring and autumn data are included separately (referred to as non-seasonal models).

For all models we make the assumption that the disturbance terms in the process part of the state-space model are independent between species. This assumption may not be entirely satisfying since species having similar life-histories and geographical distributions may well have correlated dynamics even when covariates suspected to influence the dynamics are included in the model. On the other hand, we expect errors in observations to be large and potentially influence similar species in a similar manner.

To get an idea about the validity of the population abundance indices that are derived from the state part of the models as measures of larger scale population change we compare our results with patterns reported for other European populations. We also compare population indices estimated from our model with indices derived with the same analysis of similar data from the bird station at the Courish Spit and with indices from the Swedish Bird Survey which are computed using another type of data (see the Data section below). Both the Courish Spit and the Swedish Breeding Bird Survey may however cover populations distinct from the ones passing Ottenby and therefore comparisons between these indices are not very informative unless results agree.

2.1 Data

Ottenby Bird Observatory (56°12'N, 16°24'E) is situated at the southernmost point of Öland, a 137 km long island ca. 10 km off the coast of south-eastern Sweden. The trapping area in the observatory garden is 1.2 ha and contains most of the higher vegetation within the nearest 2 km, and therefore attracts migratory birds. Birds have been caught at Ottenby in funnel traps of Helgoland-type (Bub 1991) since the first year of trapping in 1946. Since 1960 birds have also been caught in mist nets and to avoid a potential increase in trapping numbers due to the increase in the number of traps we only use data between 1960 and 2005. The start of spring trapping varied considerably between 1952 and 1979, whereas from 1980 onwards, the spring trapping started on March 15 and ended on June 15. The spring passage of the species analysed in this paper is mainly in May, which has been well covered in all years except for 1966 and 1967 when there were no spring trappings. These years are treated as missing data points. The spring data we use is the total number of birds caught per year between March 15 and June 15 in the Helgoland traps and in the mist nets. The autumn trapping season starts on July 25 and ends on November 15. In some years the season ended before November 15, but very few

birds of the species studied in this paper are trapped after mid October. By using the total number of individuals trapped per year between July 25 and October 25 during 1960–2005 we include 99.9% of all trapped individuals of the species studied here. Both juveniles and adult birds are caught in autumn but there is an over representation of juveniles for most species. Since age classification were not complete for all years, both adults and juveniles are included in our data. For more details about the trapping conditions, see Stervander et al. (2005).

Data from the Courish Spit consist of the number of birds caught in two traps between 1977 and 2005. The project was carried out by the Biological Station Rybachy of the Zoological Institute, Russian Academy of Sciences (Sokolov et al. 2000). Index values from the Swedish Breeding Bird Survey (SBBS) (Lindström and Svensson 2005) are available from 1975. These indices are derived from point counts along routes freely chosen by observers and are therefore potentially subject to biases such as habitat bias, differences in skill between observers, etc. (Thomas 1996). Annual Sahel rainfall indices were obtained from the web-page of the Joint Institute for the Study of the Atmosphere and the Ocean, http://jisao.washington.edu/data_sets/sahel, and are computed as the mean of monthly rainfall indices from June through October. The annual indices were standardised for the period 1950–2004.

2.2 Models

A (rather) general definition of a multivariate linear Gaussian state-space model with covariates can be given as

$$\begin{aligned} \mathbf{y}_t &= \mathbf{Z}_t \mathbf{x}_t + \boldsymbol{\epsilon}_t, & \boldsymbol{\epsilon}_t &\sim N(0, \boldsymbol{\Omega}_t) \\ \mathbf{x}_{t+1} &= \mathbf{T}_t \mathbf{x}_t + \mathbf{W}_t \mathbf{c} + \boldsymbol{\eta}_t, & \boldsymbol{\eta}_t &\sim N(0, \boldsymbol{\Sigma}_t) \end{aligned} \quad (1)$$

for $t = 1, 2, \dots, n$, where all $\boldsymbol{\epsilon}_t$ and $\boldsymbol{\eta}_t$ are independent (the parameters of the $N(\boldsymbol{\mu}, \boldsymbol{\Sigma})$ -distribution denote the mean vector and variance matrix respectively, vectors are denoted by bold face and matrices by capital letters). The first state vector, \mathbf{x}_1 , also needs to be defined to complete the model specification. This can be done in various ways, and in our models described later in this section the initial vector is treated as a parameter with an informative prior. An interpretation of the model is that the vectors \mathbf{y}_t represent the data which are noisy observations of linear transformations (\mathbf{Z}_t) of hidden state vectors \mathbf{x}_t which need not be of the same size as the vectors of observations. The hidden state is a linear normal stochastic process with autoregression coefficient matrix \mathbf{T}_t . The matrix \mathbf{W}_t contains covariates for the transition from t to $t + 1$ and their (linear) effect on the process is measured by the regression coefficients in the vector \mathbf{c} . Depending on the setting, the elements of the matrices of the model may either be completely specified or may depend on unknown parameters.

All our models of the bird observatory data are special cases of the more general model defined above. To find out if anything is gained by using both spring and

autumn data in the same model we used both a seasonal and a non-seasonal version of the state space model. For the non-seasonal model, the data are arranged so that the vectors \mathbf{y}_t contain the log of the total seasonal trapping numbers in year t in either spring or autumn for the four species. The system is modelled on the log scale in line with common practise in studies on population dynamics. The log transformation also had the effect of making the data appear more Gaussian. The non-seasonal model is a simplified version of the model in (1):

$$\begin{aligned}\mathbf{y}_t &= \mathbf{x}_t + \boldsymbol{\epsilon}_t, & \boldsymbol{\epsilon}_t &\sim N(0, \boldsymbol{\Omega}) \\ \mathbf{x}_{t+1} &= \mathbf{a} + B\mathbf{x}_t + r_t\mathbf{c} + \boldsymbol{\eta}_t, & \boldsymbol{\eta}_t &\sim N(0, \boldsymbol{\Sigma}).\end{aligned}\quad (2)$$

The vectors \mathbf{a} and \mathbf{c} of length 4 contain parameters a_i and c_i respectively on position i . The autoregression coefficient matrix B is diagonal with parameter b_i on position (i, i) . All the regression parameters a_i , b_i and c_i are different between species so that there are no shared parameters between species in the deterministic part of the model. The hidden state vector \mathbf{x}_t of length 4 should be interpreted as the logarithm of population indices for the species in year t . The scalars r_t are indices of mean Sahel rainfall during the wet season (June–October) in year t . The amount of rainfall here serves as a surrogate for availability of food and water for the populations during the winter, which in turn might affect winter survival (Peach et al. 1991). The process disturbance variance matrix $\boldsymbol{\Sigma}$ was constrained to be diagonal with entries σ_i^2 on the diagonal. We consider two models for the observation disturbance variance matrix $\boldsymbol{\Omega}$. In the first $\boldsymbol{\Omega}$ is allowed to be non-diagonal and all elements of the matrix are estimated. In the second model $\boldsymbol{\Omega}$ is constrained to be diagonal, meaning that we have a set of four independent models for the species.

Based on the above definition, the process part of the model for species i can be written as:

$$x_{it+1} = a_i + b_i x_{it} + c_i r_t + \eta_{it},$$

where subscripts i refer to element i of the vectors. Thus the processes are $AR(1)$ -processes with covariates and since the model is defined for the log of the data, this can be seen as a Gompertz model for the population dynamics (see e.g. Royama 1992).

The quantities $1 - b_i$ in the Gompertz model can be interpreted as measures of density dependence in growth. The log-linearity of the process guarantees that the coefficients b_i are invariant to multiplying the population process $\exp(x_i)$ by a constant. More specifically, if

$$N_{t+1} = \exp(x_{t+1}) = \exp(a + bx_t + \eta_t) = N_t^b \exp(a + \eta_t),$$

and the population size is rescaled to an index $M_t = kN_t$, then

$$M_{t+1} = kN_{t+1} = (kN_t)^b \exp(a + (1 - b) \ln k + \eta_t) = M_t^b \exp(a' + \eta_t),$$

where $a' = a + (1-b) \ln k$. Hence, the parameter b can be interpreted as a measure of density dependence regardless of the value of the constant of proportionality implied by the index interpretation of $\exp(x_i)$. The parameter a on the other hand depends on the constant and is thus of little interest to us. A critical assumption of the model is that k , the proportionality constant linking the trapping numbers to the “true” population size is constant through time. In fact, the same interpretations of the model parameters hold if the assumption is lightened by letting $\ln k$ be independent and identically distributed according to a normal distribution since the terms then can be seen as a part of the disturbance terms η_t . If however k is not independent over time or if k depends on population size it might well affect estimates of e.g. density dependence and abundance indices.

For the seasonal model, both spring and autumn trapping numbers are included simultaneously. We let \mathbf{y}_t^a be vectors containing the log of autumn trapping numbers for the four species and \mathbf{y}_t^s be vectors containing the log of the spring trapping numbers. Using sub- and superscripts b and w referring to breeding and winter season respectively and sub- and superscripts a and s referring to autumn and spring, the model is defined as:

$$\begin{aligned} \mathbf{y}_t^a &= \mathbf{x}_t^a + \boldsymbol{\epsilon}_t^a, & \boldsymbol{\epsilon}_t^a &\sim N(0, \Omega_a) \\ \mathbf{x}_t^a &= \mathbf{a}_b + B_b \mathbf{x}_t^s + \boldsymbol{\eta}_t^b, & \boldsymbol{\eta}_t^b &\sim N(0, \Sigma_b) \end{aligned} \quad (3)$$

$$\begin{aligned} \mathbf{y}_t^s &= \mathbf{x}_t^s + \boldsymbol{\epsilon}_t^s, & \boldsymbol{\epsilon}_t^s &\sim N(0, \Omega_s) \\ \mathbf{x}_t^s &= \mathbf{a}_w + B_w \mathbf{x}_{t-1}^a + r_{t-1} \mathbf{c}_w + \boldsymbol{\eta}_t^w, & \boldsymbol{\eta}_t^w &\sim N(0, \Sigma_w). \end{aligned} \quad (4)$$

In the same way as for the seasonal model, the vectors \mathbf{a}_b , \mathbf{a}_w and \mathbf{c}_w contain species specific parameters and the matrices B_b and B_w are diagonal with species specific autoregressive parameters for measuring seasonal density dependence. Again, two versions of observation disturbance variance matrices are considered, in the first these are non-diagonal and in the second they are diagonal. The process disturbance variance matrices are diagonal. This model is also included in the general definition in (1), but here the index t refers to year.

Similarly to the non-seasonal model, $\exp(x_t^s)$ and $\exp(x_t^a)$, should be interpreted as indices of spring and autumn population sizes respectively. However, since it may well be that different populations or parts of populations pass the observatories in spring and in autumn respectively, the spring and autumn indices may not share the same constant of proportionality to the “true” population size. In the same way as above, the parameters b_w and b_s are invariant to multiplying the population time series by a constant.

To try to validate the assumption of correlated observation disturbances we compared the estimated correlation matrices of the observation disturbances to a heuristic estimate calculated from the amount of overlap in migration between the species. The sum of daily catches over the years from 1950 to 2005 for each species was divided by the total number of catches for the species. The heuristic estimate

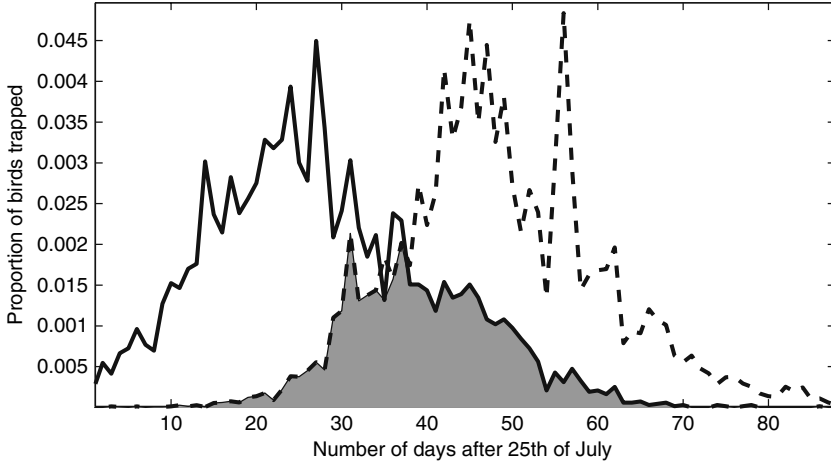


Fig. 1 Autumn phenology curves for whitethroat (*solid line*) and redstart (*dashed line*) and the amount of overlap in migration period (*shaded area*)

of the correlation was then computed as the area under the overlap of the curves (Fig. 1). The correlation of the observation disturbances between species i and species j was estimated as the posterior mean of element (i, j) of the Ω matrix divided by the square root of the product of the posterior means of the elements (i, i) and (j, j) of the same matrix.

2.3 Priors

The model was fitted to data from 1960 to 2005 for Ottenby and from 1977 to 2005 for the Courish Spit. The state vectors of the seasonal model were initialised by putting normal priors on x_{i1}^s with means equal to the mean of the log of spring data between 1950 and 1959 and with prior standard deviations set to 1.5 times the empirical standard deviations over these periods. Analogous priors were used for the initial states of the non-seasonal models. Courish Spit data between 1957 and 1976 was used as prior information for the initial state of the model of the Courish Spit data.

For the other parameters we used vague priors (given below) since there was no obvious a priori information available. To improve convergence of the Gibbs sampler (see Section 2.5), the regression was centred around $m_x = 5$, i.e. the model in (2) was reparametrised as

$$\mathbf{x}_{t+1} = \mathbf{a}' + B'(\mathbf{x}_t - m_x \mathbf{1}) + r_t \mathbf{c} + \boldsymbol{\eta}_t,$$

where $\mathbf{1}$ is a vector of ones. This parametrisation gives the same interpretation of B' as of B . The components of the regression parameter vectors \mathbf{a}' and \mathbf{c} were then given independent $N(0, 100)$ -prior distributions. When $|b'_i| > 1$, the model is

non-stationary and there is no reason to expect extreme non-stationarities of the population indices. The autoregression parameters b'_i were therefore given slightly more informative $N(0, 10)$ -priors. The stationarity argument does not translate directly to the seasonal model in 3, but to simplify comparisons between the models we used the same priors for the corresponding parameters a'_b , a'_w , b'_b and b'_w .

For the variances of the observation and state disturbances, the information in the data on separating the two can be low (Dennis et al. 2006). Therefore, if there is no prior information on the relative size of these it is desirable to give them similar priors. The variances of the state disturbances, σ_i^2 , were given conditionally conjugate improper inverse gamma distributions with shape parameter 0 and inverse scale parameter 0.01, $IG(0, 0.01)$ (Fig. 2). In the models with diagonal observation error variance matrices, Ω , the elements on the diagonal were also given $IG(0, 0.01)$ -priors. When the matrices Ω , Ω_s and Ω_a were allowed to be non-diagonal we gave them improper inverse Wishart priors with 3 degrees of freedom and scale matrix $0.02I$ where I is the identity matrix. Since the marginal distribution of the elements on the diagonal of a matrix having an inverse Wishart distribution with scale matrix V of size $p \times p$ and ν degrees of freedom is an $IG((\nu - p + 1)/2, V_{ii}/2)$ -distribution, the marginal prior distributions for the elements on the diagonal then also correspond to $IG(0, 0.01)$ -distributions.

We analysed sensitivity to priors by changing the prior distribution for the σ_i^2 parameters to an improper $IG(-0.5, 0.001)$ distribution and at the same time

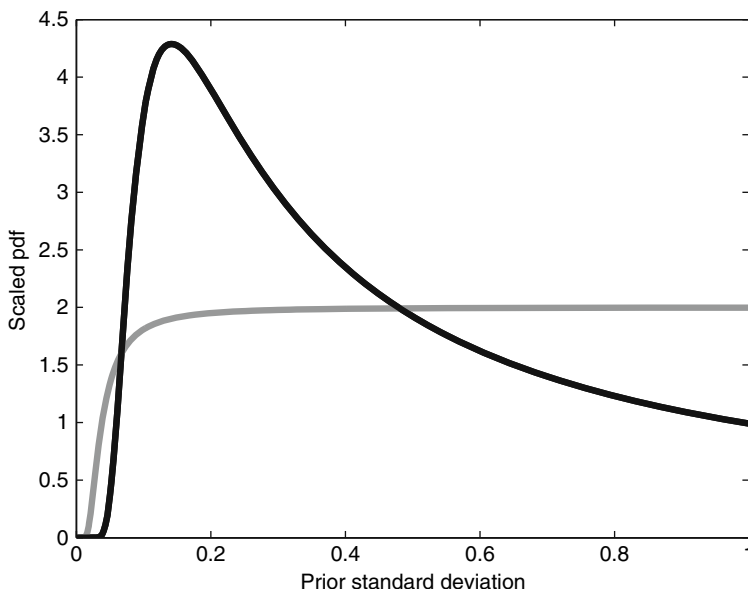


Fig. 2 The pdf (scaled) of the prior distribution of the standard deviations of the observation and process disturbances (*black line*) and of the alternative prior used for sensitivity analysis (*grey line*). The priors on the standard deviations correspond to $IG(0, 0.01)$ and $IG(-0.5, 0.001)$ prior distributions on the variances respectively

changing the parameters of the inverse Wishart distribution to 2.5 degrees of freedom and scale matrix equal to $0.002I$. In this way the priors on the variances of the process disturbances and on the variances of the observation disturbances are kept identical. The $IG(-0.05, 0.001)$ distribution on the variances is close to a uniform distribution on the standard deviations except that it has low support for small values (Fig. 2). It also lacks the peak of the $IG(0, 0.01)$ probability density function.

2.4 Goodness of Fit

Bayesian p -values build on some measure of discrepancy between the model and data and is the posterior probability that a replicate data set yields a larger value of this measure. We used the deviance, i.e.

$$D(y, \theta) = -2 \log f_{Y|\theta}(y)$$

where $f_{Y|\theta}(y)$ is the likelihood of the data given the vector θ containing the regression parameters and the parameters of the variance matrices of the observation and process errors, as a measure of discrepancy. The likelihood was computed using the Kalman filter (see e.g. Durbin and Koopman 2001).

Goodness of fit was also checked by analysing the residuals of the models. Residuals in the state space model, $\hat{\epsilon}$ and $\hat{\eta}$, can be defined as the expected value of ϵ and η given the data and given the parameters θ equal to their posterior marginal mean. The residuals were analysed by computing their correlation, autocorrelation and by qq-plots.

2.5 Fitting the Models

The model was fit by implementing a Gibbs sampler in the program Matlab. In each iteration of the sampler, all the state vectors \mathbf{x}_t^s and \mathbf{x}_t^g were updated simultaneously using the Kalman simulation smoother of Durbin and Koopman (2002). All the regression parameters a , b and c for all species and both seasons were updated as a block according to their multivariate normal conditional posterior. The inverse Wishart prior is conditionally conjugate for the observation variance matrices Ω . When these matrices were allowed to be non-diagonal, they were therefore updated by simulating a draw from the inverse Wishart posterior. For the diagonal variance matrices, each diagonal element was updated with a draw from the inverse gamma conditional posterior. The Gibbs sampler for the non-seasonal models was constructed in a similar manner but is even more simple since the regression parameters a , b and c then are the same for each time step of the state space model.

The sampler was run with a single chain for half a million iterations where the first 20,000 iterations were discarded as burn. Every 20th value of the output was then used as a draw from the posterior. Convergence and mixing of the MCMC's

were investigated by looking at trace plots and autocorrelation functions of the thinned chains. Visual inspection revealed no sign of poor mixing and all autocorrelations of the thinned chains were below 0.15 at lag 5. All chains seemed to have converged after just a few iterations.

Starting values of the MCMC were chosen at least a small distance away from the expected region of high posterior density. Specifically, the state vectors were initialised to 1 for all species, all the regression parameters, a , b and c were initially set to 2 and all variance matrices were initialised as identity matrices.

Although we have not done so, we believe all our models could be implemented and fit in e.g. the program WinBUGS if the priors on the variance matrices are changed to proper ones. The non-seasonal model with uncorrelated observation disturbances is especially simple and parameter estimates can be obtained using maximum likelihood or REML methods (see e.g. Dennis et al. 2006). These methods can probably also be used for estimating parameters of at least some of our more complex models.

3 Results

Unless otherwise stated, the results below refer to the Ottenby data. Tests always refer to the informal test of whether or not 95% credible intervals contain the value of the null hypothesis. Estimates of abundance indices from the non-seasonal model on autumn catches with observation disturbances allowed to be correlated across species are shown in Fig. 3. A comparison with estimates from spring catches (Fig. 4) shows that on a coarse (long term) scale, the indices for the two data sets have similar tendencies with sample correlations 0.8, 0.6, 0.3 and 0.5 for redstart, whitethroat, garden warbler and lesser whitethroat respectively. (Note that the sample correlations should be interpreted with care as the indices are autocorrelated.) The estimated whitethroat indices show declines in the early 1970 and 1980s which roughly coincide with droughts in the Sahel area. Declines in numbers of whitethroats following these droughts have been reported in the UK. A decline by the time of the first drought was reported for redstarts in the UK (Gibbons et al. 1993) and the indices derived here decline at about the time of the start of the drought in the late 1960s but this result is weaker than for the whitethroat indices. Any trends in the garden warbler and lesser whitethroats indices are less clear although there was a drop in autumn catches of lesser whitethroats in the early 1970s and a sudden drop in both spring and autumn catches of garden warblers around 1990. The regression coefficient for Sahel rainfall, c , is only significantly larger than zero in the model of whitethroat autumn data (Table 1). Estimates of parameters representing density dependence, b , all had wide credible intervals that don't allow us to make any comparisons between species or seasons (Table 1). However, the credible intervals of b for whitethroat and garden warbler are well separated from one. Since b equal to one represents density independence this could be an indication of some degree of density dependence, but because of the wide credible intervals we avoid drawing any firm conclusions.

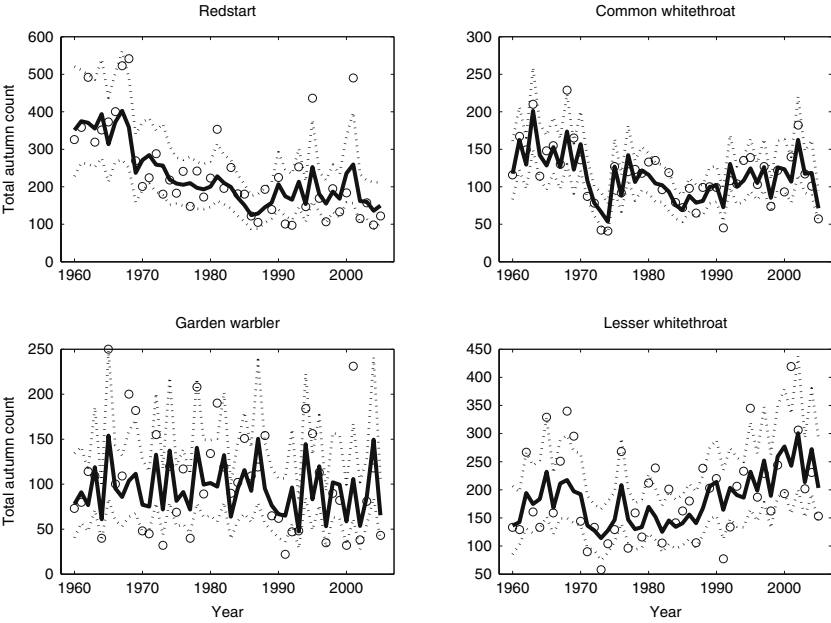


Fig. 3 Posterior mean abundance indices from the non-seasonal model of Ottenby autumn data (black lines) with 95% credibilty bands (dotted lines). The circles denote the observed data

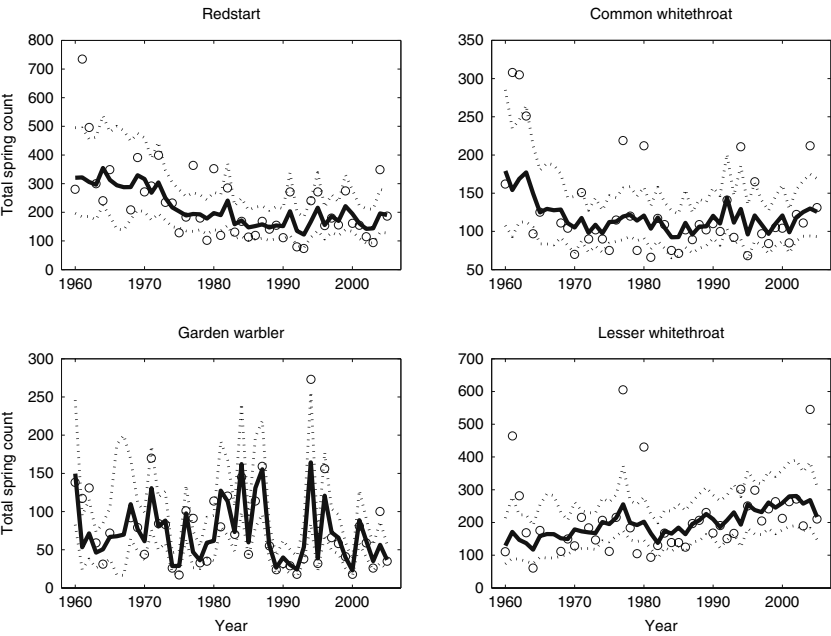


Fig. 4 Posterior mean abundance indices from Ottenby spring data (black lines) with 95% credi- bility bands (dotted lines). The circles denote the observed data

Table 1 Parameter estimates and 95% credibility intervals for the non-seasonal models applied to autumn and spring data at Ottenby and to autumn data at the Courish Spit. Estimates of the square root of the elements on the diagonal of the observation disturbance variance matrix Ω are denoted ω_i . Indices refer to redstart, r , whitethroat, w , garden warbler, g , and lesser whitethroat l . All models in the table have correlated observation disturbances

Parameter	Ottenby spring		Ottenby autumn		Courish spit autumn	
p -value	0.62		0.51		0.51	
b_r	0.58	(−0.06, 0.96)	0.63	(0.20, 0.94)	0.24	(−0.45, 0.76)
b_w	0.25	(−0.63, 0.82)	0.11	(−0.27, 0.45)	0.35	(−0.17, 0.78)
b_g	0.13	(−0.26, 0.51)	−0.30	(−0.90, 0.22)	0.02	(−0.52, 0.54)
b_l	0.57	(−0.27, 0.98)	0.43	(−0.11, 0.93)	0.65	(0.11, 1.07)
c_r	0.08	(−0.05, 0.22)	0.10	(−0.03, 0.24)	−0.19	(−0.48, 0.08)
c_w	0.07	(−0.05, 0.20)	0.27	(0.15, 0.39)	0.05	(−0.21, 0.32)
c_g	−0.17	(−0.44, 0.09)	−0.01	(−0.26, 0.25)	−0.18	(−0.50, 0.12)
c_l	0.02	(−0.10, 0.17)	0.13	(−0.01, 0.28)	−0.13	(−0.47, 0.19)
σ_r	0.22	(0.07, 0.40)	0.24	(0.08, 0.41)	0.37	(0.23, 0.58)
σ_w	0.16	(0.07, 0.28)	0.20	(0.09, 0.29)	0.42	(0.22, 0.62)
σ_g	0.57	(0.41, 0.75)	0.36	(0.12, 0.55)	0.41	(0.13, 0.66)
σ_l	0.19	(0.08, 0.32)	0.22	(0.10, 0.34)	0.41	(0.13, 0.66)
ω_r	0.39	(0.25, 0.52)	0.32	(0.19, 0.42)	0.41	(0.17, 0.69)
ω_w	0.34	(0.24, 0.45)	0.23	(0.13, 0.33)	0.35	(0.14, 0.61)
ω_g	0.39	(0.19, 0.62)	0.48	(0.30, 0.68)	0.50	(0.24, 0.78)
ω_l	0.42	(0.30, 0.56)	0.34	(0.23, 0.47)	0.45	(0.18, 0.76)

When combining spring and autumn data in the seasonal model, the derived indices appear more similar to the indices from the non-seasonal model of autumn data than to the indices from the non-seasonal model of spring data (Fig. 5). This indicates that the information in the spring data is less than the information in the autumn data in agreement with a belief that spring ringing figures at Ottenby are more dependent on local weather than autumn figures (Hjort and Lindholm 1978). Estimates of the regression coefficients on standardised Sahel rainfall, c_i , are qualitatively similar between the seasonal and the non seasonal models with a positive effect for whitethroat (Table 2). There is however a stronger indication of a positive effect of Sahel rainfall for redstart in the seasonal model even though it is barely significantly larger than zero. As for density dependence the credible intervals are still very wide and not much can be said about differences between seasons. The whitethroat estimates of b are however lower in the winter season than in the breeding season although this is not significant at the 95% level. We therefore leave it as a hypothesis that whitethroats are more strongly regulated by density dependence in the period between leaving and arriving at the breeding grounds than in the period spent at the actual breeding grounds. As an indication of whether or not the combined model improved abundance indices we summed the lengths of the 95% credible intervals of the log abundance indices x_{it} for each species across time for spring and autumn indices separately. This was done for both the seasonal and the non-seasonal models. We then computed the percent reduction of these summed totals for the seasonal model compared to the non-seasonal models. The total lengths of the log spring index credible intervals were reduced by 10, 15, 13 and 9 percent

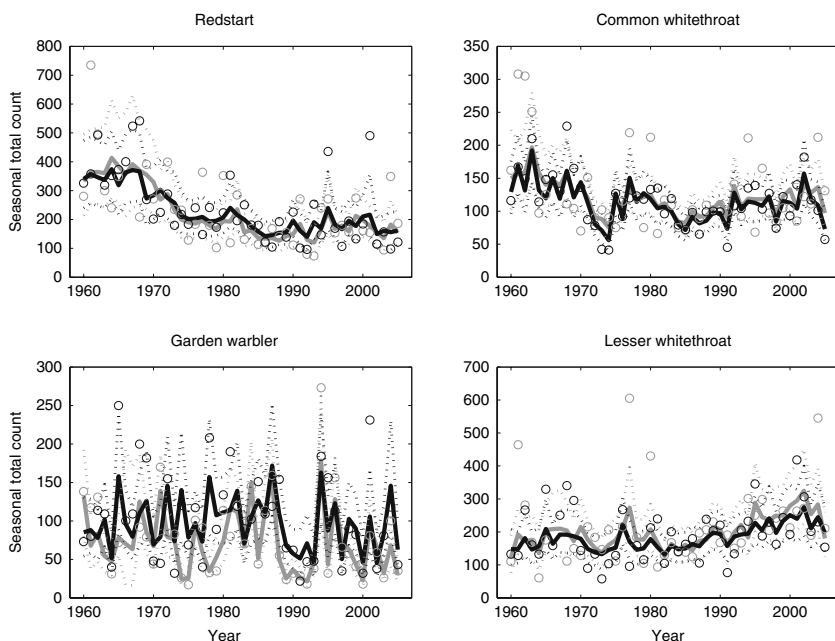


Fig. 5 Posterior mean abundance indices from the seasonal model of Ottenby data with 95% credibility bands (*dotted lines*). Grey lines denote spring indices and black lines denote autumn indices

for redstart, whitethroat, garden warbler and lesser whitethroat respectively. The analogous reductions in autumn were 6, 1, 9 and 4 percent. Hence in this sense the seasonal model performs slightly better than the non-seasonal models. The fact that the reduction is larger for the spring indices also supports the conclusion above that the spring data are less informative.

The reduction in total length (both spring and autumn) of log abundance credible intervals when moving from the seasonal model with independent observation disturbances to the seasonal model with correlated observation disturbances are 9% for redstart, 4% for whitethroat, 30% for garden warbler and 22% for lesser whitethroat.

The agreement between SBBS-indices and indices from the non-seasonal model of spring and autumn data is weak (Fig. 6). Sample correlations between SBBS-indices and autumn indices from the non seasonal model were 0.4, 0.2, -0.1 and 0.1 for redstart, whitethroat, garden warbler and lesser whitethroat. For indices from the non-seasonal model of spring data these correlations were 0.5, 0.3, 0.1 and 0.2. For the redstart, both the SBBS and our indices indicate a decline in the early 1980s but that is much more marked in the former. For the whitethroat no decline at all at this point is seen in the SBBS indices. A noticeable feature is that a sudden sharp decline in whitethroats in 1991 occurs in both autumn data at Ottenby and in the SBBS-indices and is further consistent with a drop in the British CBC-indices (Gibbons et al. 1993).

Table 2 Parameter estimates with 95% credible intervals for the seasonal model with correlated and uncorrelated* observation disturbances applied to data from Ottenby. First indices refer to breeding season *b*, winter season *w*, spring observation *s* and autumn observation *a*. Second indices refer to species as in Table 1.

	Seasonal model		Seasonal model*		Prior sensitivity	
<i>p</i> -value	0.60		0.68		0.66	
<i>b_{br}</i>	0.72	(0.39, 1.13)	0.88	(0.38, 1.50)	0.68	(0.33, 1.13)
<i>b_{bw}</i>	1.05	(0.56, 1.79)	1.33	(0.65, 2.38)	1.08	(0.52, 1.99)
<i>b_{bg}</i>	0.28	(0.01, 0.54)	0.46	(−0.12, 1.50)	0.27	(0.01, 0.53)
<i>b_{bl}</i>	0.62	(0.19, 1.14)	0.57	(−0.39, 1.98)	0.55	(0.15, 1.04)
<i>b_{wr}</i>	0.92	(0.42, 1.49)	0.81	(0.36, 1.41)	0.83	(0.32, 1.48)
<i>b_{ww}</i>	0.20	(−0.13, 0.60)	0.22	(−0.04, 0.57)	0.16	(−0.15, 0.55)
<i>b_{wg}</i>	−0.03	(−0.73, 0.65)	0.26	(−0.83, 1.89)	−0.01	(−0.60, 0.54)
<i>b_{wl}</i>	0.68	(0.10, 1.55)	0.14	(−1.25, 1.67)	0.70	(0.08, 1.76)
<i>c_{wr}</i>	0.13	(0.00, 0.27)	0.09	(−0.02, 0.23)	0.14	(0.00, 0.31)
<i>c_{ww}</i>	0.19	(0.09, 0.31)	0.17	(0.07, 0.29)	0.19	(0.08, 0.31)
<i>c_{wg}</i>	−0.10	(−0.34, 0.15)	−0.12	(−0.37, 0.12)	−0.10	(−0.35, 0.16)
<i>c_{wl}</i>	0.10	(−0.03, 0.24)	0.09	(−0.08, 0.25)	0.10	(−0.04, 0.25)
<i>σ_{br}</i>	0.18	(0.07, 0.35)	0.18	(0.06, 0.40)	0.21	(0.04, 0.41)
<i>σ_{bw}</i>	0.16	(0.07, 0.25)	0.17	(0.07, 0.29)	0.17	(0.05, 0.27)
<i>σ_{bg}</i>	0.40	(0.17, 0.54)	0.31	(0.08, 0.62)	0.43	(0.27, 0.56)
<i>σ_{bl}</i>	0.16	(0.07, 0.28)	0.23	(0.07, 0.44)	0.17	(0.05, 0.30)
<i>σ_{wr}</i>	0.18	(0.07, 0.35)	0.15	(0.06, 0.33)	0.21	(0.04, 0.41)
<i>σ_{ww}</i>	0.14	(0.07, 0.24)	0.13	(0.06, 0.22)	0.15	(0.05, 0.26)
<i>σ_{wg}</i>	0.61	(0.46, 0.79)	0.49	(0.12, 0.79)	0.63	(0.49, 0.81)
<i>σ_{wl}</i>	0.20	(0.09, 0.31)	0.22	(0.07, 0.47)	0.23	(0.08, 0.34)
<i>ω_{sr}</i>	0.38	(0.26, 0.50)	0.39	(0.27, 0.51)	0.37	(0.22, 0.51)
<i>ω_{sw}</i>	0.35	(0.27, 0.45)	0.36	(0.28, 0.46)	0.36	(0.27, 0.46)
<i>ω_{sg}</i>	0.31	(0.13, 0.53)	0.42	(0.09, 0.75)	0.30	(0.10, 0.53)
<i>ω_{sl}</i>	0.41	(0.30, 0.53)	0.38	(0.12, 0.55)	0.40	(0.28, 0.53)
<i>ω_{ar}</i>	0.33	(0.21, 0.44)	0.32	(0.15, 0.45)	0.31	(0.16, 0.44)
<i>ω_{aw}</i>	0.23	(0.14, 0.34)	0.18	(0.07, 0.31)	0.22	(0.13, 0.33)
<i>ω_{ag}</i>	0.41	(0.24, 0.62)	0.43	(0.10, 0.68)	0.39	(0.21, 0.60)
<i>ω_{al}</i>	0.36	(0.25, 0.47)	0.31	(0.09, 0.49)	0.36	(0.25, 0.49)

Estimated abundance indices for the Courish Spit data show a quite different picture than the Ottenby estimates (Fig. 7). There is e.g. a decreasing trend in the lesser whitethroat and a drop in the number of whitethroats in the mid 1990s. No clear effect of Sahel rainfall is found for the Courish Spit data (Table 1). Credibility intervals for the parameter estimates are in most cases too wide to allow for comparisons with estimates from Ottenby data but, except for the garden warbler, estimates of state disturbance variances are less precise for the Courish Spit data.

A comparison between the heuristic correlation estimate and the estimate from fitting the seasonal model with correlated observation disturbances (Table 3) reveals, especially in autumn, a close agreement between the two. The estimates from the model are in general higher than the heuristic estimates, but sample correlations between the off diagonal correlation estimates were 0.99 in autumn and 0.76 in

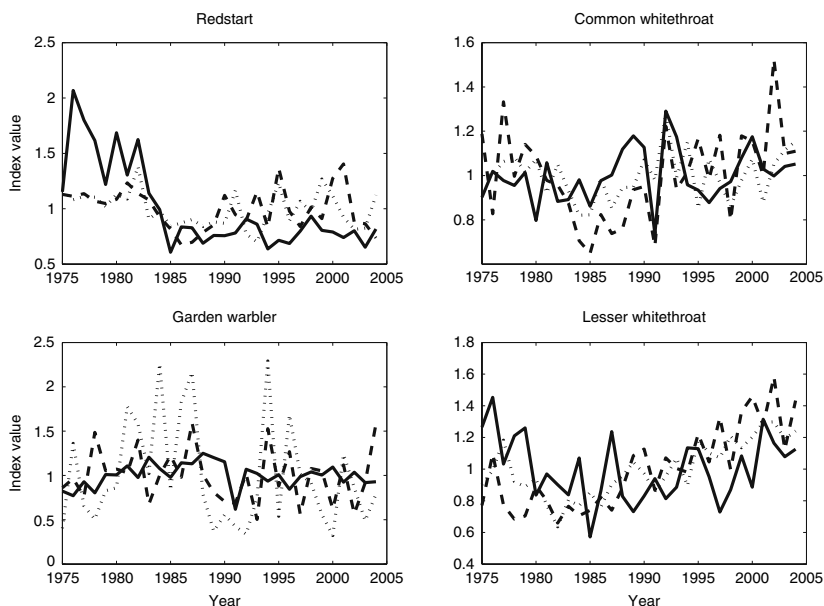


Fig. 6 Indices from the Swedish breeding bird survey (*solid line*) and from the non-seasonal model of data from Ottenby in spring (*dotted line*) and autumn (*dashed line*). The indices are scaled to have mean equal to one for the given time period

spring. A good estimate of the overlap in trapping season between the species can thus be computed from just total annual catches.

P-values did not indicate signs of bad fit for any of the models (Tables 1 and 2). Analysis of residuals showed that the model with correlated observation disturbances in total had somewhat less correlation and autocorrelation of the residuals than the model with independent observation disturbances. Also, the observation disturbance residuals of the seasonal model show that the fit is worse for spring than for autumn data (Fig. 8). None of the autocorrelations of the residuals at lag 1 were larger than 0.2 but correlations between residuals for different species were in some cases larger than expected. This was true for all of the models we considered.

Table 3 Estimates of correlations in observation disturbances from the seasonal model and the heuristic estimate. Upper right triangles show estimates from spring data and lower left triangles from autumn data

	Model estimate				Heuristic estimate			
	r	w	g	l	r	w	g	l
r	1.00	0.60	0.64	0.84	1.00	0.67	0.50	0.84
w	0.51	1.00	0.79	0.83	0.39	1.00	0.77	0.79
g	0.76	0.73	1.00	0.76	0.69	0.62	1.00	0.62
l	0.66	0.84	0.85	1.00	0.57	0.77	0.82	1.00

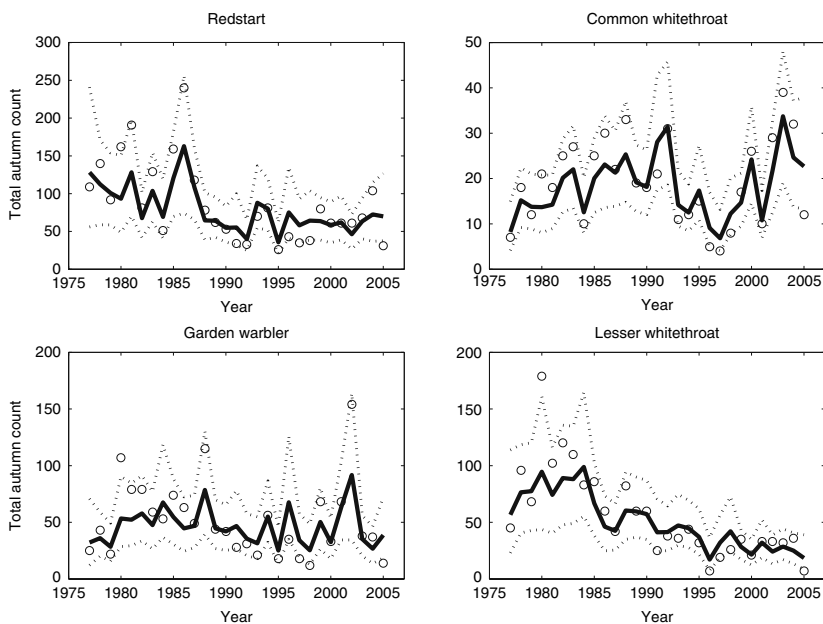


Fig. 7 Posterior mean abundance indices from autumn data at the Courish Spit spring (*black lines*) with 95% credibility bands (*dotted lines*). The circles denote the observed data

A reason for this might for example be that the correlations or variances of the disturbances are not constant through time as we assume in our models.

Residual analysis for the Courish Spit data also show a worse fit than Ottenby data for at least whitethroat and lesser whitethroat, which are the species that are caught in lowest numbers. Using the log of total counts is not very appropriate when counts are small and an overdispersed Poisson model of observations could have been a better alternative here.

4 Discussion

The linear dynamics derived from our state space model of trapping data is presumably a mix of “true” variation in population abundance, of weather dynamics or other external forces that influence migration patterns and of trapping probabilities and possibly also of dynamic changes in migratory routes. The relative influence of these processes determines the amount of information available in the data and the relevance of the data as indicators of population size. It is however hard to assess this amount of information unless there is a close agreement between analyses of various kinds of data at several locations. Different methods of recording and analysing data may give rise to different kinds of bias and geographically (or temporally) separated populations may experience different conditions that cause differences in

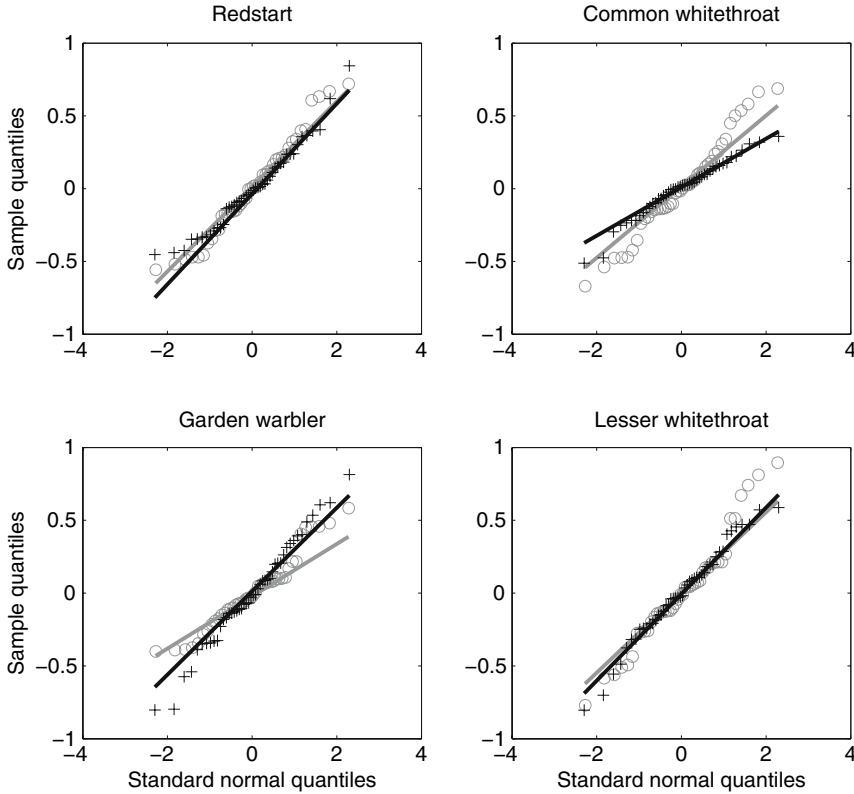


Fig. 8 Qq-plots of observation disturbance residuals for spring (*grey circles*) and autumn (*black crosses*) for the seasonal model with correlated observation disturbances

dynamics. The rough agreement between spring and autumn indices from Ottenby may thus indicate that there is a relation to changes in abundance but let alone can not exclude the possibility of e.g. dynamical changes in catching probabilities. The lack of agreement between indices from Ottenby, the Courish Spit and the SBBS on the other hand can not be taken as more than an indication that some of the indices are not very precise as there may well be differences in both breeding and wintering locations of the populations passing the stations. What can be done using statistical analyses of ringing figures is to set limitations to what information can be extracted from the data. This is exemplified by the fact that autoregressive parameters in our model could not be estimated with any reasonable degree of precision.

The good agreement between the heuristic estimates of correlations in observations and the matrices estimated from the model (Table 3) indicates that the assumption of correlated observation disturbances and independent population dynamics is reasonable. The relatively high variance of these disturbances in turn show that catches are highly dependent on extrinsic factors which has been hypothesised before (Svensson 1978). Ignoring effects of correlated measurement errors could

cause the dynamics between species that migrate during the same time period to appear overly coherent, if for no other reason, simply because the sample size is overestimated. There is not much sign of such an effect in this analysis but it is important to be aware of the correlations in the data, not only when analysing population dynamics or population sizes but in all analyses relying on ringing figures (e.g. analyses of phenology). We expect that the high correlation in catches is not a special feature of the Ottenby and Courish Spit data but rather is common in counts of populations during migration.

Despite the high variance in observation disturbances, there are still hints that there is some valuable information in the data, at least for some species. There is support for a positive effect of Sahel rainfall on between year fluctuations in abundance indices for whitethroats and weak support for the same effect on redstarts. Visual inspection of the abundance indices for redstart and whitethroat show declines following the Sahel droughts and give some support for the possibility of picking up clear population trends in the data for some species. When the purpose is to produce visual population trends, the state-space modelling approach could be used to produce more smoothed estimates than the ones given here. For example, a local linear trend model (Durbin and Koopman 2001) could be used instead of the autoregressive model.

Our analyses give some support to the view that spring catches at Ottenby are less informative about population sizes than autumn catches (Hjort and Lindholm 1978). The location of Ottenby at the southern tip of Öland may influence the dynamics of spring and autumn catches differently. In autumn, migrating birds may use Öland as a lead line on their southward migration whereas no such lead line is available for birds passing Ottenby in spring (Stervander et al. 2005). This can lead to spring catches being more dependent on local weather conditions (Hjort and Lindholm 1978).

Due to the high variance in observation disturbances, we believe that ringing figures from bird stations are not very suitable for picking up even drastic changes in population abundances. However, long term ringing figures on migrating birds from bird stations with carefully standardised trapping methods might in some cases be useful in recovering long term trends and biological information but any conclusions from such analyses need to be confirmed by independent data.

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