

Climate and spatio-temporal variation in the population dynamics of a long distance migrant, the white stork

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Summary

1. A central question in ecology is to separate the relative contribution of density dependence and stochastic influences to annual fluctuations in population size. Here we estimate the deterministic and stochastic components of the dynamics of different European populations of white stork *Ciconia ciconia*. We then examined whether annual changes in population size was related to the climate during the breeding period (the 'tap hypothesis' *sensu* Sæther, Sutherland & Engen (2004, *Advances in Ecological Research*, **35**, 185–209) or during the nonbreeding period, especially in the winter areas in Africa (the 'tube hypothesis').

2. A general characteristic of the population dynamics of this long-distance migrant is small environmental stochasticity and strong density regulation around the carrying capacity with short return times to equilibrium.

3. Annual changes in the size of the eastern European populations were correlated by rainfall in the wintering areas in Africa as well as local weather in the breeding areas just before arrival and in the later part of the breeding season and regional climate variation (North Atlantic Oscillation). This indicates that weather influences the population fluctuations of white storks through losses of sexually mature individuals as well as through an effect on the number of individuals that manages to establish themselves in the breeding population. Thus, both the tap and tube hypothesis explains climate influences on white stork population dynamics.

4. The spatial scale of environmental noise after accounting for the local dynamics was 67 km, suggesting that the strong density dependence reduces the synchronizing effects of climate variation on the population dynamics of white stork.

5. Several climate variables reduced the synchrony of the residual variation in population size after accounting for density dependence and demographic stochasticity, indicating that these climate variables had a synchronizing effect on the population fluctuations. In contrast, other climatic variables acted as desynchronizing agents.

6. Our results illustrate that evaluating the effects of common environmental variables on the spatio-temporal variation in population dynamics require estimates and modelling of their influence on the local dynamics.

Key-words: climate effects on population dynamics, density dependence, environmental stochasticity, population synchrony, white stork.

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Introduction

It has been known for a long time (Lack 1966; Lawton 1996), especially from studies of passerines (Curnutt, Pimm & Maurer 1996; Sæther *et al.* 2003) and game birds (Cattadori & Hudson 1999; Williams, Ives & Applegate 2003) that variation in population dynamics occurs within the distribution range of bird species. However, the mechanisms behind these patterns are poorly understood (Brown, Mehlman & Stevens 1995; Lawton 1996). We propose that such regional variation in population dynamics can arise in two different ways. First, the influence of variation in environmental variables on population dynamics may differ geographically. For instance, the influence of a large-scale climate phenomenon, the North Atlantic Oscillation (NAO), on fluctuations in the size of great tit *Parus major* and pied flycatcher *Ficedula hypoleuca* populations differ over short distances as well as shows gradients over larger geographical scales (Sæther *et al.* 2003). Secondly, spatial variation in the deterministic components of population dynamics, such as the strength of the density dependence may also induce regional patterns in population dynamics. Accordingly, assuming a logistic model of density regulation, large variation was found among populations of the great tit and the pied flycatcher in the specific population growth rate r (Sæther *et al.* 2003), which in this model determines the rate of return to equilibrium or the strength of density dependence (May 1981). Thus, an evaluation of these two hypotheses for intraspecific variation in population dynamics requires separate estimates of the parameters specifying the deterministic component of the dynamics as well as stochastic influences on local population fluctuations. Unfortunately, several studies of birds (Sæther *et al.* 1998, 2000; Sæther & Engen 2002) have shown that obtaining reliable estimates of those parameters even after neglecting the influence of age structure requires precise long-term population counts that are available only for a few species.

Comparative studies have shown that environmental stochasticity has a strong influence on the population dynamics of birds (Sæther *et al.* 2004a, 2005). Such stochastic fluctuations in the environment can influence fluctuations in population size in two different ways. As suggested by Lack (1966), environmental variation during the breeding season can affect the number of recruits produced, resulting in a change in population size the next breeding season. This was termed the 'tap hypothesis' by Sæther, Sutherland & Engen (2004b). Alternatively, according to the 'tube hypothesis', changes in population size from one year to the next may be affected by the number of birds that manage to survive during the nonbreeding season, which will be influenced by the environmental fluctuations during this time of the year. The relative contribution of the tube- and tap hypothesis for the effects of environmental stochasticity on the variability of bird populations is, however, poorly understood (Sæther *et al.* 2004b).

In 1953, Moran published a highly influential paper stating that common environmental noise in isolated populations described by the same linear model will induce a correlation in fluctuating population sizes equal to the correlation in local environmental noise. However, Lande, Engen & Sæther (1999) showed, using a homogeneous continuous model, that the correlation between population sizes will increase by increasing migration. A clear prediction that appeared from these analyses was that the effect of migration on the scale of population synchrony decreased with increasing density regulation. Thus, whether regional variation in population dynamics will result in large-scale synchrony in population fluctuations will depend on the deterministic components as well as the stochastic influences on the population dynamics.

The white stork *Ciconia ciconia* lives in close relationship with humans in agricultural areas. In combination with a conspicuous breeding habit (Creutz 1985), this makes it possible to obtain relatively precise population estimates. Population sizes of white storks declined during the nineteenth century over larger parts of its breeding areas in western Europe (Rheinwald, Ogden, & Schulz 1989); however, this decrease seems now to be reversed in many countries (Barbraud, Barbraud & Barbraud 1999; Schulz 1999; Doligez 2004; Schaub, Pradel & Lebreton 2004). Such declines have, however, rarely been recorded in eastern Europe, probably due to less intensified agricultural practices.

Here we will estimate the strength of density dependence and the stochastic influences on different white stork populations, using methods described in Lande, Engen & Sæther (2003). We will then assess how different local and regional climate variables such as the NAO (Hurrell 1995) affect local population fluctuations of white storks in Poland and Slovakia where most individuals winter in Central or Southern Africa (Creutz 1985). The white stork is suitable for such analyses because adult survival is correlated by temporal variation in rainfall in the wintering areas (Kanyamibwa *et al.* 1990; Kanyamibwa, Bairlein & Schierer 1993; Schaub, Kania & Köppen 2005). Because the females usually do not start breeding before they are 3 years or older (Bairlein & Zink 1979; Creutz 1985; Bairlein 1991), we can examine whether climate variation in the wintering areas can affect annual variation in population change, as expected from the 'tube hypothesis' of (Sæther *et al.* 2004b). Finally, following Engen *et al.* (in press) we will estimate the spatial synchrony in population fluctuations and how environmental variables that affect local population dynamics influence the spatial scale of that synchrony.

Materials and methods

STUDY AREAS

The study sites are located (Fig. 1) throughout the Republic of Poland, the Slovak Republic and the Czech Republic

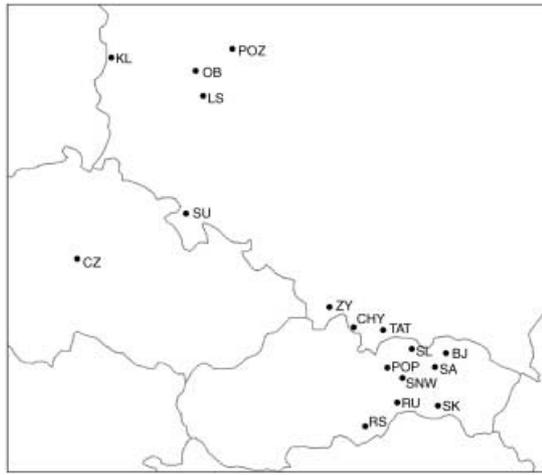


Fig. 1. Location of the study populations in eastern Europe. For location of the French population, see Barbraud *et al.* (1999).

(Hladik 1989). In addition, we used individual-based demographic data from a population in Charente-Maritime in western France that was re-established in 1978 (Barbraud *et al.* 1999). Because the French birds have different wintering areas than the birds from the study areas in eastern Europe (Creutz 1985; Barbraud unpublished data), we did not include the population in France within our comparative analyses.

DATA

Data on individual variation in fitness was only available from the population in western France in which a large proportion of the nestlings were ringed each year (Barbraud *et al.* 1999). Because of their conspicuous breeding habit by extensive use of artificial nesting sites, a large proportion of all individuals breeding in the area could be checked for rings by use of spotting scopes.

The white stork builds large, perennial nests that are most commonly located close to human settlements, and therefore are relatively easy to find and to observe during the breeding period (e.g. Creutz 1985). The size of the local populations was estimated by standard methods used during the International Census of White Storks (Creutz 1985). For further details on methods, see Tryjanowski & Kuzniak (2002), Ptaszyk *et al.* (2003), Tryjanowski, Sparks & Profus (2005a) and Tryjanowski *et al.* (2005b).

POPULATION MODELS

Two different population models were used. For those populations in which there was no significant negative relationship between relative changes in population size N from year t to $t + 1$ $\Delta N / N$ on N , we assumed that population sizes were kept so far below K that density regulation was impossible to estimate. Hence, a population model without density regulation was adopted so that

$$E(\Delta N | N_t) = rN_t \tag{eqn 1a}$$

and

$$\text{var}(N_{t+1} | N_t) = \sigma_d^2 N_t + \sigma_e^2 N_t^2, \tag{eqn 1b}$$

where r is the specific population growth rate, σ_d^2 is the demographic variance and σ_e^2 is the environmental variance. The first order approximation of the mean and variance in $\Delta X = X_{t+1} - X_t = \ln N_{t+1} - \ln N_t$, is then

$$E(\Delta X | X_t) = r - \frac{1}{2}\sigma_e^2 - \frac{1}{2}e^{-X_t}\sigma_d^2 \tag{eqn 2a}$$

and

$$\text{var}(\Delta X | X_t) = \sigma_d^2 e^{-X_t} + \sigma_e^2 \tag{eqn 2b}$$

In those cases in which density regulation was present we fitted the theta-logistic model of density regulation (Gilpin & Ayala 1973). We assume that the logarithm of change in population size $\Delta X = \ln(N + \Delta N) - \ln(N)$ takes the form

$$\ln \lambda(N) = \bar{r}[1 - (N/K)^\theta] \tag{eqn 3}$$

where $\lambda(N) = (N + \Delta N)/N$ is the population growth rate in the absence of stochasticity, K is the carrying capacity, \bar{r} the mean specific growth rate at $N = 0$, and θ describes the form of density regulation. Following Sæther *et al.* (2002a), eqn 3 may alternatively be written as $\ln \lambda = r_1(1 - (N^\theta - 1)/(K^\theta - 1))$, where $r_1 = \bar{r}(1 - K^{-\theta})$ is the specific growth rate when $N = 1$. At $N = K$ with $\lambda(K) = 1$ the strength of density dependence is $\gamma(K) = \bar{r}\theta$ (Sæther *et al.* 2000). Thus, strong density dependence and short return times to equilibrium at K (May 1981) occurs when the specific population growth rate is high and/or for large values of θ . We also see that when $\theta = 0$ (Gompertz density regulation) $\gamma(K) = r_1/\ln K$ and when $\theta = 1$ (logistic density regulation) $\gamma(K) = \bar{r}$ (Sæther *et al.* 2002a; Sæther, Engen & Matthysen 2002b). The moments of the stationary distribution of population size N for the theta-logistic model are

$$E N^m = \frac{K^m \Gamma\left(\frac{\alpha + m}{\theta}\right)}{\left(\frac{\alpha + 1}{\theta}\right)^{m\theta} \Gamma\left(\frac{\alpha}{\theta}\right)}, m = 1, 2, \dots, \tag{eqn 4}$$

where $\alpha = (2r_1/\sigma_e^2)(1 - K^{-\theta})$ and Γ denotes the gamma function (Diserud & Engen 2000).

To examine the effects of climate on the population fluctuations we rewrite our population models (eqns 1 and 3) on the form

$$X_{t+1} = E(X_{t+1} | X_t) + U_d \sigma_d / \sqrt{N_t} + U_e \sigma_e \tag{eqn 5}$$

where E denotes the expectation, U_d and U_e are independent variables with zero mean and unit variance and no temporal autocorrelation. We can use eqn 5 to examine how different climate variables affect fluctuations in population size by modelling climate variable y_t as random effect (Sæther *et al.* 2004b), writing

$$U_e \sigma_e = \sum \beta_i y_{i,t} + U\sigma, \quad \text{eqn 6}$$

where U is another standardized variable, β_i is the regression coefficient for the effects of climate variable number i , and σ^2 is the component of the environmental variance that cannot be explained by fluctuations in the covariates. This leads to the relation

$$\sigma_e^2 = \text{var}(\sum \beta_i y_{i,t}) + \sigma^2, \quad \text{eqn 7}$$

so that the covariates together explain a fraction

$$\psi = \text{var}(\sum \beta_i y_{i,t}) / [\text{var}(\sum \beta_i y_{i,t}) + \sigma^2] \quad \text{eqn 8}$$

of the total environmental variance in the noise.

Several climate variables were included in the analyses. The NAO is a regional climate phenomenon that refers to variation in sea-level pressure differences between the Arctic and subtropical Atlantic (Hurrell 1995; Hurrell *et al.* 2003). We used the NAO index for the winter (December–March) period that is based on the difference of normalized sea-level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland (<http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html>). We also used monthly means of temperature and precipitation at local weather stations (obtained from the National Oceanic and Atmospheric Administration at <http://www.noaa.gov>) for the period February–September to describe the weather in the breeding areas. To characterize the weather in the wintering areas we computed the monthly standardized Sahel rainfall index from 14 stations located between latitudes 8°S–20°N and longitudes 20°W–10°E obtained from <http://jisao.washington.edu/data/sahel>. In addition, we also included precipitation anomalies for Africa (http://wlf.ncdc.noaa.gov/oa/climate/research/ghcn/ghcngrid_prpc.html), which was computed for each square in a 5 × 5 degree grid within the wintering areas of white storks from eastern Europe for the period November–February (Creutz 1985; Berthold *et al.* 2002, 2001a,b).

Following Engen *et al.* (2005a), the analyses of spatial synchrony in population dynamics were based on studying the residuals obtained from fitting the population models (eqn 1 or eqn 3) to time-series observations in location z ,

$$R_t(z) = X_{t+1}(z) - E[X_{t+1}(z) | X_t(z), Y_t] \approx \sigma(z)U_t(z) + \sigma_d(z)U_{d,t}(z) / \sqrt{N_t(z)} \quad \text{eqn 9}$$

We used the normal approximation and chose a parametric form for the spatial autocorrelation of the U

$$\rho(z) = \text{corr}[U(w), U(w+z)] = \rho_\infty + (\rho_0 - \rho_\infty)h(z), \quad \text{eqn 10}$$

where $h(z)$ decreases from 1 to 0 as z increases from 0 to infinity. One likely positive definite autocorrelation function is the exponential form $h(z) = e^{-z/l}$. Here we applied, following Lande *et al.* (1999), the standard deviation l of the scaled form of this function as a measure

of spatial scaling defined for the residuals. Simulation studies have shown that this procedure gives robust estimators for the spatial synchrony of population fluctuations (Lillegård, Engen & Sæther 2005).

ESTIMATION OF PARAMETERS

Individual-based demographic data were only available for the population in western France. Following Engen *et al.* 2005b, we calculated the demographic variance σ_d^2 from the projection matrix (Caswell 2001) based on the contributions (B_{it}, I_{it}) for the different age-classes i in year t , where B_{it} is the number of offspring produced of a female of age i in year t , and $I_{it} = 1$ if a mother of age i survives between year t and $t + 1$ or $I_{it} = 0$ if she dies. We separated these contributions into components that are generated by demographic stochasticity in each vital rate.

For those populations in which we assumed exponential population growth (eqn 2), our estimates are those derived from the likelihood function obtained by assuming that X_{t+1} given X_t is normally distributed. Writing x_t for the observed log abundances in year t , the log likelihood function

$$\ln L(r, \sigma_e^2) = - \frac{1}{2} \sum_{t=1}^{n-1} \left[\ln v_t + \frac{\left(x_{t+1} - \left(x_t + r - \frac{1}{2}v_t \right) \right)^2}{v_t} \right], \quad \text{eqn 11}$$

where $v_t = \sigma_e^2 + \sigma_d^2 e^{-x_t}$. The likelihood function for the stochastic growth rate $s = r - \frac{1}{2}v_t$ was maximized numerically with respect to the two unknown parameters r and σ_e^2 .

For those populations in which there was density dependence, we estimated the parameters in the theta-logistic model (eqn 3) by means of least square techniques (see Sæther *et al.* 2000, and Sæther *et al.* 2002a for procedures).

Unfortunately, reliable estimates of r_1 are difficult to obtain and are often also biased because it is often necessary to interpolate the population fluctuations over large ranges of nonobserved values of N (Aanes *et al.* 2002). In this study, an estimate of r_1 was only obtained for the population in western France that was followed from re-establishment up to reaching carrying capacity (Barbraud *et al.* 1999). This estimate was used when estimating θ and σ_e^2 for the density-regulated populations in eastern Europe.

To reduce the number of parameters we assumed a logistic model ($\theta = 1$) for the density-regulated populations when estimating the effects of climatic covariates and spatial synchrony in the fluctuations of eastern European populations. Following Engen *et al.* (2005a), the complete likelihood function for the spatial scaling of the residual variation after accounting for density dependence, demographic stochasticity and different climate variables at each locality, defined by eqns 9 and

10, was maximized numerically to give estimates for ρ_0, ρ_{∞} , and l . The sampling properties of the estimates are found by parametric bootstrapping (Efron & Tibshirani 1993). The residuals are simulated from the appropriate multinormal model defined by the autocorrelation function and the distance matrix. The multinormal likelihood function can be calculated numerically using a lower triangular linear transformation, the Choleski decomposition (Riply 1987), which can also be used to give the stochastic simulations required for performing the bootstrapping (see Engen *et al.* 2005a, and Lillegård *et al.* 2005). The significance of a change in the estimates due to inclusion of covariates was estimated by examining whether 0 was included in the appropriate lower and upper quantiles of the distribution for the differences between the two bootstrap distributions (Efron & Tibshirani 1993).

Results

The pattern in the annual fluctuations in the population size differed among the white stork populations (Fig. 2). The trajectory of the French population was characterized by an establishment period followed by some years with rapid growth. During the recent years the population has fluctuated around some equilibrium size. The populations in eastern Europe in which density dependence seems to be present were characterized by relatively small annual fluctuations (Fig. 2).

The stochastic components of the white stork population in western France was $\hat{\sigma}_d^2 = 0.098$ and $\hat{\sigma}_e^2 = 0.035$. The specific growth rate at $N = 1$ was $\hat{r}_1 = 0.189$. An extremely strong density regulation occurred around $K(\hat{\theta} = 11.52)$, although this estimate was uncertain,

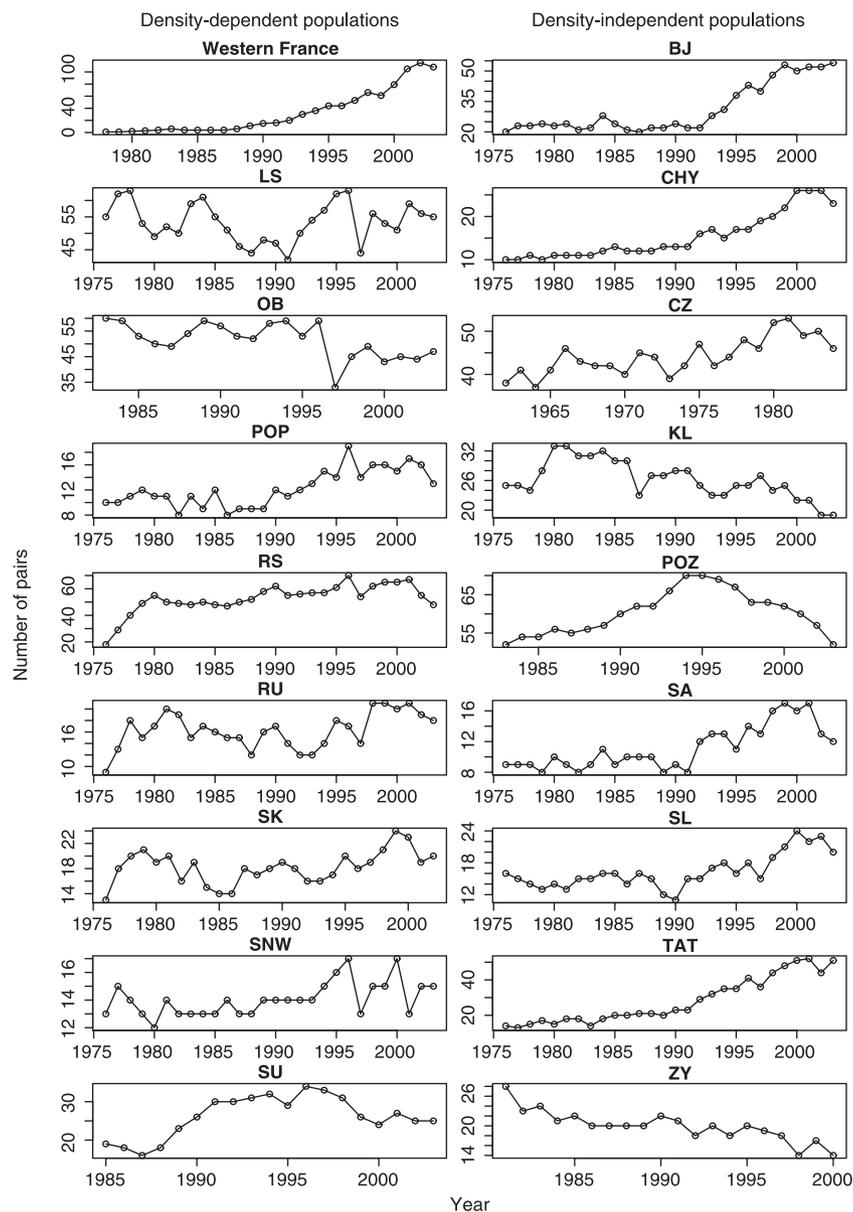


Fig. 2. Annual fluctuations in the size of the study populations. For locations of the eastern European populations, see Fig. 1.

Table 1. The estimates of the parameters for each population (for locations, see Fig. 1) either assuming a theta-logistic model of density regulation (eqn 3) or the exponential growth model (eqn 1). The figures in the brackets denote the 95% confidence interval. We assume a demographic variance $\sigma_d^2 = 0.098$ and for the populations in which a theta-logistic model was fitted, a constant specific growth rate at $N = 1$ $r_1 = 0.188$. θ is the form of density regulation, r is the deterministic specific growth rate for the exponential growth model, K is the carrying capacity, σ_e^2 the environmental variance, γ is the strength of density regulation at K and CV is the coefficient of variation in the quasi-stationary distribution σ_N/K with initial population size K

| Locality | r | K | θ | γ | σ_e^2 | CV |
|-----------------------------------|-------------------------|------------|------------------|----------|----------------------------|------|
| Exponential growth | | | | | | |
| BJ | 0.042 [0.020, 0.064] | | | | 0.00782 [0.00255, 0.01381] | |
| CHY | 0.033 [0.014, 0.054] | | | | 0.00131 [0.00000, 0.00556] | |
| CZ | 0.011 [-0.007, 0.029] | | | | 0.00437 [0.00064, 0.00827] | |
| KL | -0.007 [-0.028, 0.016] | | | | 0.00530 [0.00061, 0.01079] | |
| POZ | 0.000 [-0.011, 0.011] | | | | 0.00000 [0.00000, 0.00116] | |
| SA | 0.018 [-0.011, 0.049] | | | | 0.01479 [0.00212, 0.02825] | |
| SL | 0.013 [-0.010, 0.040] | | | | 0.00922 [0.00225, 0.01778] | |
| TAT | 0.054 [0.030, 0.082] | | | | 0.01055 [0.00348, 0.01847] | |
| ZY | -0.033 [-0.061, -0.004] | | | | 0.00787 [0.00042, 0.01711] | |
| Theta-logistic density regulation | | | | | | |
| LS | | 54 [51–57] | 3.22 [1.87–5.55] | 0.61 | 0.00725 [0.00290–0.01310] | 0.09 |
| OB | | 55 [53–57] | 3.93 [2.27–6.60] | 0.74 | 0.00278 [0.00030–0.00650] | 0.06 |
| POP | | 13 [10–15] | 1.58 [0.59–4.20] | 0.30 | 0.02055 [0.00641–0.03920] | 0.22 |
| RS | | 57 [54–61] | 3.01 [1.65–5.91] | 0.57 | 0.00499 [0.00150–0.00980] | 0.08 |
| RU | | 17 [15–19] | 2.56 [1.35–5.29] | 0.48 | 0.01450 [0.00430–0.02850] | 0.15 |
| SK | | 19 [17–21] | 2.51 [1.41–5.15] | 0.47 | 0.00853 [0.00171–0.00800] | 0.12 |
| SNW | | 14 [14–15] | 4.05 [2.57–6.40] | 0.76 | 0.00000 | 0.07 |
| SU | | 28 [15–23] | 1.18 [0.27–4.84] | 0.23 | 0.00528 | 0.15 |

with bootstrap replicates almost uniformly distributed over the interval $4 < \theta < 100$.

The mean of the estimates of θ in the density-regulated populations in eastern Europe (Fig. 1) was $\hat{\theta} = 2.76$ (Table 1), ranging from 1.18 to 4.05. This shows that maximum density regulation in white stork populations occurs close to K . Accordingly, the mean time for return to equilibrium $1/\gamma$ was short (2.52 years), indicating strong density dependence. A consequence of this is that the presence of density dependence in the population dynamics will be difficult to identify if the population size is below K .

For populations with positive growth rates, and assuming exponential growth, the estimates of the specific population growth rate ranged from 0.0107 to 0.0539 (Fig. 2, Table 1), with a mean annual population growth rate of 2.84%.

The influence of environmental stochasticity on white stork population dynamics in eastern Europe was small with a mean environmental variance σ_e^2 of 0.0075 (Table 1). For instance, in two populations with no density-dependent effects (CHY and POZ) and in one population with strong density dependence (SNW) $\hat{\sigma}_e^2$ was very close to zero. No significant ($P > 0.1$) difference was found between the two types of density-dependent models in the mean values of σ_e^2 .

As a consequence of a combination of strong density dependence and small environmental stochasticity, the variance of the quasi-stationary distribution of N σ_N^2 (eqn 4) was small. This shows that a characteristic of white stork population dynamics is small fluctuations around K (Fig. 2, Table 1).

After accounting for the effects of density dependence, variation in climate at the breeding sites as well as in the wintering areas influenced the residual variation in population size in several of the populations. Changes in population size were positively related to winter NAO in 13 of the 17 populations. Assuming that the signs of the regression coefficient are binomially distributed with probability $p = 0.5$ if there are no systematic climatic influences, there was a higher number of positive β than expected just by chance [$P = 0.049$], $\beta > 0$ was significant ($P < 0.05$) in seven populations (BJ, OB, POP, POZ, RS, SU and TAT). NAO strongly affects local winter weather over large areas of the northern hemisphere (Hurrell 1995; Hurrell *et al.* 2003). Accordingly, in 15 of the populations [$P = 0.0023$], a positive regression coefficient β (see eqn 6) was found for temperature during February [$\beta > 0$ significant ($P < 0.05$) in the localities POP, RS, RU and SNW]. In 12 of 17 populations β was larger than 0 [$P = 0.144$] also for precipitation during this month [although $\beta > 0$ significant ($P < 0.05$) in only the localities RS and TAT], i.e. relatively large populations were found after mild and wet Februaries. Furthermore, the weather during the final stage of the breeding season affected the population size the following years. For instance, the population change from t to $t + 1$ was positively related to the mean temperature during June and July in year t in 15 of 17 populations [$\beta > 0$ significant ($P < 0.05$) in the localities CZ, POP, RS and SU]. Similarly, temperature during May–June explained the highest average proportion of the variation in population size for any of the weather variables during the breeding period $\bar{p} = 0.23$, $\beta > 0$ significant

($P < 0.05$) in the localities BJ, CZ, POP, RU, SK and SNW]. All together, a significant effect of temperature for some interval during the period May–July was found in 52% of the populations.

Weather in the wintering areas of the white stork in Africa also influenced the population dynamics. In 14 of 17 [$P = 0.013$] populations changes in population size was positively related to the index for rainfall in the Sahel region during January or February [although $\beta > 0$ was significant ($P < 0.05$) in only two of the localities (SK and ZY)]. Similarly, population changes were also correlated to Sahel rainfall during October in 13 populations [$P = 0.049$] in which β was significantly ($P < 0.05$) larger than 0 in 4 populations (LS, POP, RS and SU). However, the largest average effect was found for the Sahel rainfall during December ($\bar{\psi} = 0.26$). In six populations (BJ, LS, OB, POP, RS and RU) this was related to a significant ($P < 0.05$) negative effect of rainfall on fluctuations in population size.

There was also large temporal and spatial variation within the wintering areas in the autocorrelation between rainfall and annual changes in population size (Fig. 3). Using gridded (5×5 degrees) anomalies (see Methods), we found positive effects of rainfall during November

and February in Sudan and Ethiopia (Fig. 2a,d). Furthermore, rainfall in Kenya and in eastern Tanzania during the period November–January also has a positive effect on the growth rates of most populations (Fig. 3a–c). In contrast, rainfall in Zambia, Botswana and South Africa especially during November (Fig. 3a) was related to a decrease in population size. Finally, rainfall in Mozambique in the period December–February also affected the population fluctuations of the white stork (Fig. 3b–d), with a negative effect of rainfall during December and February, but with a positive relationship between change in population size and rainfall during January.

Thus, these analyses show that population fluctuations of the white stork were explained by weather at different parts of the year. Consequently, seasonal variation was also found in the relative contribution of temperature and precipitation to the environmental stochasticity. Of the climatic variables in the breeding areas, temperature in May–June the preceding year ($\bar{\psi} = 0.23$), summer (June–August) precipitation ($\bar{\psi} = 0.22$) and temperature during February ($\bar{\psi} = 0.19$) explained on average the highest proportion of the variance in σ_e^2 . This was similar to the average proportion

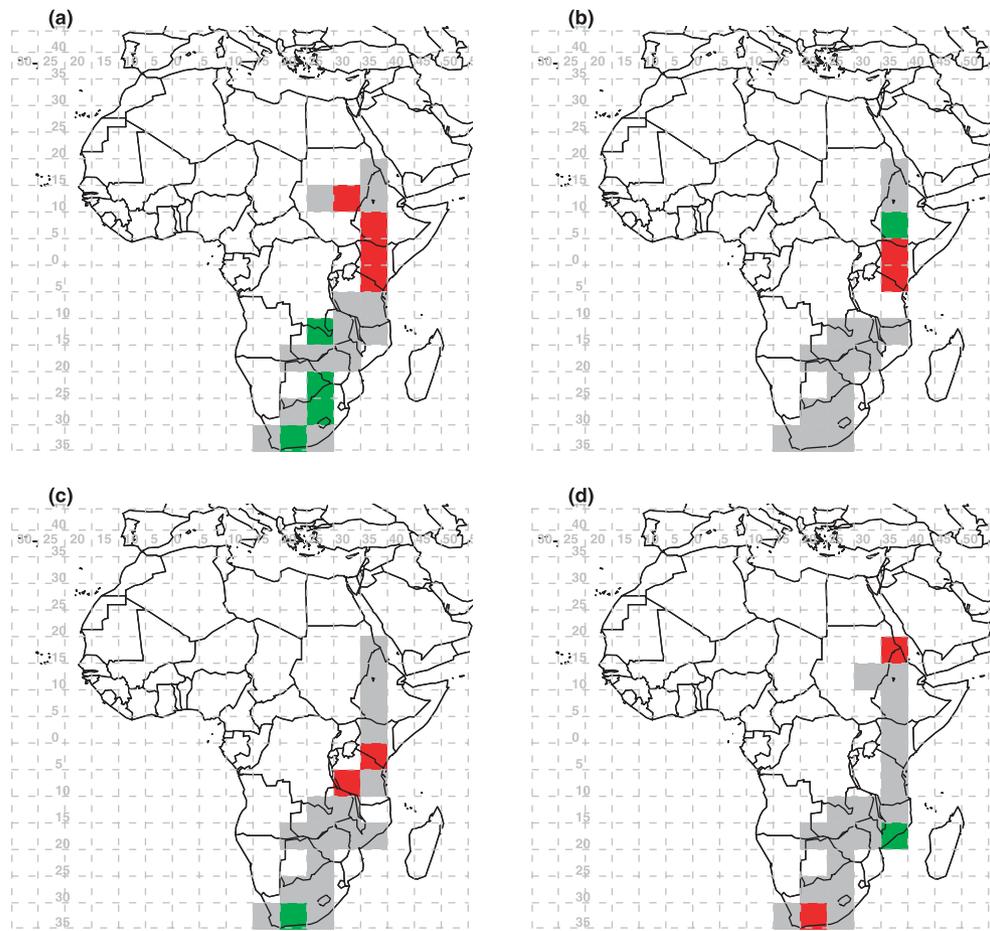


Fig. 3. The influence of variation in rainfall during November (a), December (b), January (c) and February (d) in different parts of Africa on the fluctuations in the size of eastern European white stork populations. Grids in which $\beta > 0$ in 12 or more populations are indicated with red colour, whereas grids in which $\beta < 0$ in 12 or more populations are indicated with green. The grey areas denote grids included in the analyses.

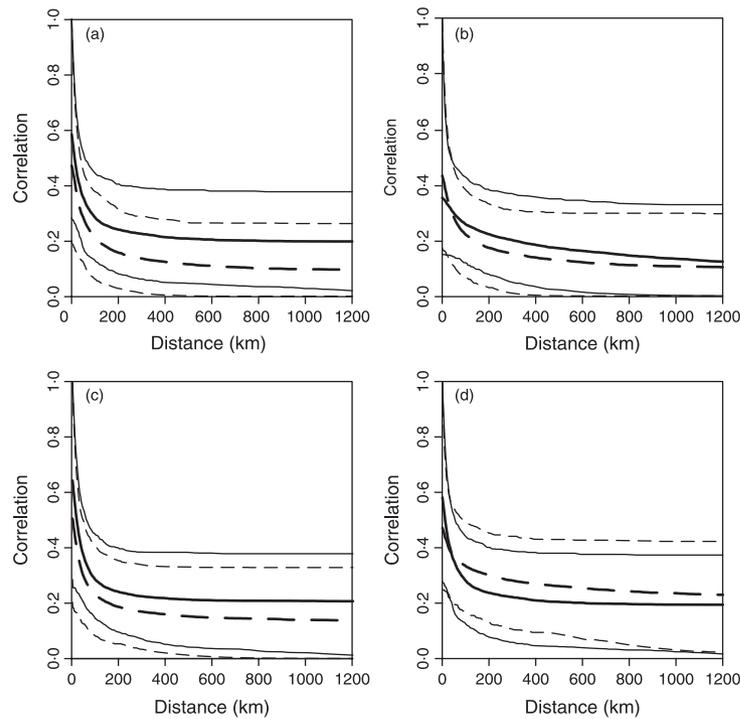


Fig. 4. The effects on spatial synchrony in residual size of eastern European white stork populations after accounting for demographic stochasticity and density dependence of including: (a) NAO; (b) local temperature during May and June during the breeding season in year $t - 1$; (c) Sahel rainfall during December; and (d) precipitation anomalies in the grid 25–30°S 20–25°E (see Fig. 3) during February. The solid line is the estimate based on including no climatic covariate. The dotted line shows the estimated spatial autocorrelation of residual variation in population size after including the covariate in the local models. Thick line denotes the 50% quantile and thin lines the 2.5% and 97.5% quantile, respectively.

explained by regional climate phenomena such the NAO ($\bar{\psi} = 0.19$) and Sahel rainfall ($\bar{\psi} = 0.23$ and $\bar{\psi} = 0.21$ for October and March, respectively). However, this is a slightly smaller proportion than explained by rainfall anomalies in 5×5 degrees grids in the wintering areas in Africa. In fact, for the grid located in Mozambique (Fig. 3) $\bar{\psi} = 0.28$ for rainfall in February, for the grid at the border area between Tanzania and Mozambique $\bar{\psi} = 0.26$ for rainfall during December and for the grid at the border between Tanzania and Zambia $\bar{\psi} = 0.26$ for rainfall during January.

After accounting for the local effects of density dependence and demographic stochasticity, the spatial correlation in the residual variation in population size decreased with distance (Fig. 4). The spatial scale was $\hat{l} = 67$ km that was significantly ($P < 0.05$) larger than 0. The correlation at zero distance ($\hat{\rho}_0 = 0.518$) was not significantly different from 1 ($P > 0.1$), whereas the correlation in the noise at infinite distance ($\hat{\rho}_\infty = 0.214$) was not significantly different from 0 ($P > 0.1$).

Weather affected the spatial synchrony of the population fluctuations (Fig. 4). After accounting for the effects on the local dynamics of regional weather phenomena such as the NAO (Fig. 4a) or Sahel rainfall (Fig. 4c), the spatial correlation in the residual variation in population fluctuations at given distance generally decreased, showing that these regional climate variables synchronized the population dynamics of white storks in eastern Europe. A similar effect was also found for

temperature during May–June in year $t - 1$ at the breeding grounds (Fig. 4b). In contrast, weather in some parts of the wintering areas (Fig. 4d) generally increased the residual variation in population sizes. This shows that climate variation may also act desynchronizing on the population fluctuations of white storks.

Discussion

This study shows that a characteristic of white stork population dynamics is strong density dependence (Table 1, Fig. 2) and relatively small environmental stochasticity (Table 1) that are influenced by climatic conditions during the breeding season as well as in the wintering areas in Africa (Fig. 3). Local climate in the breeding areas acted mainly by synchronizing the spatial variation in residual population fluctuations after accounting for density dependence and demographic stochasticity in the local dynamics (Fig. 4).

These analyses are based on several simplifying assumptions.

1. Obtaining unbiased estimates of the specific growth rate r_1 are extremely difficult for populations fluctuating around the carrying capacity (Aanes *et al.* 2002; Lande *et al.* 2002). We therefore assumed that the specific growth rate r_1 for the population in western France also was typical for all our eastern European populations. Although this estimate lies within the range that is estimated for several other bird species, it is considerably higher

than the estimates of r from the populations in which there was no evidence for density dependence (Fig. 2, Table 1). A biased r will affect the estimates of θ through a negative sampling covariance and often results in very uncertain estimates of θ (Sæther *et al.* 2000). Hence, if we have overestimated r_1 , our estimates of θ (Table 1) are too small, indicating even stronger density regulation around K . However, the estimates of γ are less influenced by biases in r_1 (Engen *et al.* unpublished data).

2. No data were available from any eastern European population on individual variation in fitness that are necessary for obtaining estimates of demographic variance σ_d^2 . Thus, we used the estimate $\hat{\sigma}_d^2 = 0.098$ of the French population that lay within the lower range of variation recorded for species with similar life-history characteristics of the white stork (Sæther *et al.* 2004a). If we have underestimated σ_d^2 , our estimates of σ_e^2 (Table 1) are likely to represent overestimates (Engen, Sæther & Møller 2001).

3. In our analyses we have ignored age-structure effects that are known (Caswell 2001; Lande *et al.* 2002) to induce autocorrelations in time series of population fluctuations in such long-lived species such as the white stork (Kanyambwa *et al.* 1993, 1990). Thus, our estimates of σ_e^2 (Table 1) also include a component that is due to fluctuations in the age structure and thus represent an overestimate of the effects of environmental stochasticity on population dynamics. Because our estimates (Table 1) of θ or γ are larger (Sæther *et al.* 2000, 2002a; Lande *et al.* 2002; Sæther & Engen 2002) and our estimates of σ_e^2 are smaller (Sæther *et al.* 2000, 2004a) than in many other bird populations, this only supports the conclusion that population dynamics of the white stork are characterized by strong density regulation with relatively small environmentally induced fluctuations around K .

The strong density regulation recorded in white stork populations may be related to their social organization. White storks often defend a territory during the breeding season that is used for foraging (Creutz 1985). Thus, at high densities access to suitable breeding territories with either sufficient food or suitable breeding sites may be limited. Such a regulation of populations through territorial behaviour is common in birds (Newton 1998) and has previously been suggested to occur also in white storks (Tryjanowski & Kuzniak 2002). In fact, in the French population, the number of interactions between breeding pairs increased with increasing population size, particularly at sites with the highest densities. These interactions ranged from displays in flight to fights and could eventually result in destruction of clutches or small chicks (Barbraud unpublished data). Alternatively, density regulation may also operate through limited availability of food resources at the wintering grounds in Africa (Bairlein 1991) or at the breeding grounds. Accordingly, in many altricial bird species density dependence primarily operates during the nonbreeding season (Sæther *et al.* 2004b).

Several studies have shown that the demography of the white stork is influenced by weather both in the

wintering areas (Kanyambwa *et al.* 1990, 1993) and at the breeding grounds (Zink 1967; Jovani & Tella 2004). This study demonstrates that these climate-mediated changes in demography affect annual variation in size of most of the populations, mainly due to a combined effect of local summer and winter weather as well as the rainfall at the winter grounds (Fig. 3). Large population sizes were found after large rainfall especially in eastern Africa (Fig. 3a–c), probably reflecting higher survival in those years (Kanyambwa *et al.* 1990, 1993; Schaub *et al.* 2005). A combination of satellite telemetry studies and ringing recoveries have shown that those areas are important wintering areas for eastern European white storks (Berthold *et al.* 2001a, 2001b). Furthermore, large effects on the change in population size were found in Sudan, Ethiopia and Kenya for rainfall during December–January (Fig. 3a–c), which coincides with a period of high accumulation of body mass after the end of autumn migration. However, rainfall, particularly in southern Africa, could also have negative effects on population fluctuations of most white stork populations in eastern Europe (Fig. 3). Such spatial heterogeneity in the effects of the same climate variable on the population dynamics have also been recorded in other bird species as well (Sæther *et al.* 2003, 2004b).

Because most white storks do not start breeding before they are 3 or 4 years of age (Bairlein & Zink 1979; Creutz 1985; Bairlein 1991), the effects on summer weather on next year's population size cannot be directly related to variation in fledgling production. This suggests that the influence of summer climate on population dynamics operates through a climate-mediated effect on the cost of reproduction. Alternatively, summer weather may also affect the gain of body resources among the nonbreeding birds that in turn affect their survival or their probability of obtaining a territory the following spring. Accordingly, large seasonal variation is found in the body mass of white storks (Berthold *et al.* 2001a). Finally, there was also a tendency for larger population sizes following high temperatures in February. This effect was surprising because most white storks arrived at our study sites from the end of March (Ptaszyk *et al.* 2003; Tryjanowski *et al.* 2004). Because arrival occurs later and breeding success is poorer in cold years (Zink 1967; Tryjanowski *et al.* 2004), we suggest that February temperatures affect the phenological development and that more new recruits will be able to establish themselves as breeders in years with a warm February. One reason for this may be that warm pre-breeding seasons increase resource availability or improve foraging efficiency for the white storks. Whatever mechanisms, our results indicate that the population dynamics of white storks in eastern Europe are likely to be sensitive to changes in climate both in Africa and Europe.

Climate-induced changes in population size of small passerine temperate birds often occur through an effect of weather during the nonbreeding season and thus support the 'tube hypothesis' of Sæther *et al.* (2004b). Such an effect was also present in white stork population

dynamics (Table 1). In addition, some evidence suggests that summer weather may affect recruitment the following breeding season, as expected from a 'tap effect' of climate. Such an effect of recruitment driven changes in population size seems to be typical for the population dynamics of many precocial birds.

Although local fluctuations of eastern European white stork populations were influenced by variation in climate variables that were correlated over large areas, the spatial scaling of the residual variation in population size after accounting for density dependence was far shorter (Fig. 4) than recorded in small temperate passerines (Sæther *et al.* in prep.) and for the continental great cormorant *Phalacrocorax carbo sinensis* in central Europe (Engen *et al.* 2005a). One reason for this difference is the strong density dependence in the population dynamics of the white stork (Table 1) and continental great cormorant (Engen *et al.* 2005a) that is expected to decrease the spatial scaling of the synchrony in population fluctuations (Lande *et al.* 1999). However, climate variation was still able to affect the synchronizing of the population dynamics in eastern Europe (Fig. 4). Most climate variables acted by synchronizing the population dynamics (Fig. 4a–c). A desynchronizing effect of weather in southern Africa was also present (Fig. 4d). This is in accordance with theoretical results showing that large spatial heterogeneity in the effects of environmental variables on local dynamics can reduce the spatial synchrony even though the environmental variable is autocorrelated over large areas (Engen & Sæther 2005). However, all these effects were far from significant.

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References

- Aanes, S., Engen, S., Sæther, B.-E., Willebrand, T. & Marcström, V. (2002) Sustainable harvesting strategies of Willow Ptarmigan in a fluctuating environment. *Ecological Applications*, **12**, 281–290.
- Bairlein, F. (1991) Population studies of White Storks (*Ciconia ciconia*) in Europe. In: *Bird Population Studies* (eds C. Perrins, J.-D. Lebreton & G.J.M. Hirons), pp. 207–229. Oxford University Press, Oxford.
- Bairlein, F. & Zink, G. (1979) Der Bestand des Weissstorchs *Ciconia ciconia*. Südwestdeutschland: eine Analyse der Bestandsentwicklung. *Journal für Ornithologie*, **120**, 1–11.

- Barbraud, C., Barbraud, J.C. & Barbraud, M. (1999) Population dynamics of the White Stork *Ciconia ciconia* in western France. *Ibis*, **141**, 469–479.
- Berthold, P., van den Bossche, W., Fiedler, W., Gorney, E., Kaatz, M., Lesheim, Y., Nowak, E. & Querner, U. (2001a) Der Zug des Weissstorchs (*Ciconia ciconia*): eine besondere Zugform auf Grund neuer Ergebnisse. *Journal für Ornithologie*, **142**, 73–92.
- Berthold, P., van den Bossche, W., Fiedler, W., Kaatz, M., Lesheim, Y., Nowak, E. & Querner, U. (2001b) Detection of a new important staging and wintering area of the White Stork *Ciconia ciconia* by satellite tracking. *Ibis*, **143**, 450–455.
- Berthold, P., Bossche, W.V.D., Jakubiec, Z., Kaatz, C., Kaatz, M. & Querner, U. (2002) Long-term satellite tracking sheds light upon variable migration strategies of White Storks (*Ciconia ciconia*). *Journal für Ornithologie*, **143**, 489–493.
- Brown, J.H., Mehlman, D.W. & Stevens, G.E. (1995) Spatial variation in abundance. *Ecology*, **76**, 2028–2043.
- Caswell, H. (2001) *Matrix Population Models*. Sinauer, Sunderland, MA.
- Cattadori, I.M. & Hudson, P.J. (1999) Temporal dynamics of grouse populations at the southern edge of their distribution. *Ecography*, **22**, 374–383.
- Creutz, G. (1985) *Der Weiss-Storch*. A. Ziemsen Verlag, Wittenberg Lutherstadt.
- Curnutt, J.L., Pimm, S.L. & Maurer, B.A. (1996) Population variability of sparrows in space and time. *Oikos*, **76**, 131–144.
- Diserud, O. & Engen, S. (2000) A general and dynamic species abundance model, embracing the lognormal and the gamma models. *American Naturalist*, **155**, 497–511.
- Doligez, B., Thomson, D.L. & van Noordwijk, A.J. (2004) Using large-scale data analysis to assess life history and behavioural traits: the case of the reintroduced White Stork *Ciconia ciconia* population in the Netherlands. *Animal Biodiversity and Conservation*, **27**, 387–402.
- Efron, B. & Tibshirani, R.J. (1993) *An Introduction to the Bootstrap*. Chapman & Hall, New York.
- Engen, S. & Sæther, B.-E. (2005) Generalizations of the Moran effect explaining spatial synchrony in population fluctuations. *American Naturalist*, **166**, 603–612.
- Engen, S., Sæther, B.-E. & Møller, A.P. (2001) Stochastic population dynamics and time to extinction of a declining population of barn swallows. *Journal of Animal Ecology*, **70**, 789–797.
- Engen, S., Lande, R., Sæther, B.-E. & Weimerskirch, H. (2005b) Extinction in relation to demographic and environmental stochasticity in age-structured models. *Mathematical Biosciences*, **195**, 210–227.
- Engen, S., Lande, R., Sæther, B.-E. & Bregnballe, T. (2005a) Estimating the synchrony of fluctuating populations. *Journal of Animal Ecology*, **74**, 601–611.
- Gilpin, M.E. & Ayala, F.J. (1973) Global models of growth and competition. *Proceedings of the National Academy of Sciences, USA*, **70**, 3590–3593.
- Hladik, B. (1989) Bestandsänderungen des Weissstorchs im nordosten des Böhmischemährischen Hügellandes. In: *White Stork. Status and Conservation* (eds G. Rheinwald, J. Ogden & H. Schulz), pp. 77–80. Dachverband Deutscher Avifaunisten, Braunschweig.
- Hurrell, J.W. (1995) Decadal trends in the North-Atlantic Oscillation-regional temperatures and precipitation. *Science*, **269**, 676–679.
- Hurrell, J.W., Kushnir, Y., Ottersen, G. & Visbeck, M. (2003) An overview of the North Atlantic Oscillation. In: *The North Atlantic Oscillation. Climate Significance and Environmental Impact* (eds J.W. Hurrell, Y. Kushnir, G. Ottersen & M. Visbeck), pp. 1–35. American Geophysical Union, Washington, DC.
- Jovani, R. & Tella, J.L. (2004) Age-related environmental sensitivity and weather mediated nestling mortality in white storks *Ciconia ciconia*. *Ecography*, **27**, 611–618.

- Kanyamibwa, S., Schierer, A., Pradel, R. & Lebreton, J.D. (1990) Changes in adult annual survival rates in a western European population of the White Stork *Ciconia ciconia*. *Ibis*, **132**, 27–35.
- Kanyamibwa, S., Bairlein, F. & Schierer, A. (1993) Comparison of survival rates between populations of White Stork *Ciconia ciconia*. Central Europe. *Ornis Scandinavica*, **24**, 297–302.
- Lack, D. (1966) *Population Studies of Birds*. Oxford University Press, Oxford.
- Lande, R., Engen, S. & Sæther, B.-E. (1999) Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *American Naturalist*, **154**, 271–281.
- Lande, R., Sæther, B.-E., Engen, S., Filli, F., Matthysen, E. & Weimerskirch, H. (2002) Estimating density dependence from population time series using demographic theory and life-history data. *American Naturalist*, **159**, 321–332.
- Lande, R., Engen, S. & Sæther, B.-E. (2003) *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford.
- Lawton, J.H. (1996) Population abundances, geographic ranges and conservation: 1994 Witherby Lecture. *Bird Study*, **43**, 3–19.
- Lillegård, M., Engen, S. & Sæther, B.E. (2005) Bootstrap methods for estimating spatial synchrony of fluctuating populations. *Oikos*, **109**, 342–350.
- May, R.M. (1981) Models for single populations. In: *Theoretical Ecology* (ed. R.M. May), pp. 5–29. Blackwell Scientific Publications, Oxford.
- Moran, P.A.P. (1953) The statistical analysis of the Canadian lynx cycle. II. Synchronization and meteorology. *Australian Journal of Zoology*, **1**, 291–298.
- Newton, I. (1998) *Population Limitation in Birds*. Academic Press, San Diego.
- Ptaszyk, J., Kosicki, J., Sparks, T.H. & Tryjanowski, P. (2003) Changes in arrival pattern of the White Stork *Ciconia ciconia* in western Poland. *Journal für Ornithologie*, **144**, 323–329.
- Rheinwald, G., Ogden, J. & Schulz, H. (1989) *White Stork. Conservation and Status*. Rheinischer Landwirtschafts-Verlag, Bonn.
- Riply, B. (1987) *Stochastic Simulation*. John Wiley and Sons, New York.
- Sæther, B.-E. & Engen, S. (2002) Pattern of variation in avian population growth rates. *Philosophical Transactions of the Royal Society B*, **357**, 1185–1195.
- Sæther, B.-E., Engen, S., Islam, A., McCleery, R. & Perrins, C. (1998) Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. *American Naturalist*, **151**, 441–450.
- Sæther, B.-E., Engen, S., Lande, R., Arcese, P. & Smith, J.N.M. (2000) Estimating the time to extinction in an island population of song sparrows. *Proceedings of the Royal Society London B*, **267**, 621–626.
- Sæther, B.-E., Engen, S. & Matthysen, E. (2002a) Demographic characteristics and population dynamical patterns of solitary birds. *Science*, **295**, 2070–2073.
- Sæther, B.E., Engen, S., Lande, R., Visser, M. & Both, C. (2002b) Density dependence and stochastic variation in a newly established population of a small songbird. *Oikos*, **99**, 331–337.
- Sæther, B.E., Engen, S., Møller, A.P., Matthysen, E., Adriansen, F., Fiedler, W., Leivits, A., Lambrechts, M.M., Visser, M.E., Anker-Nilssen, T., Both, C., Dhondt, A.A., McCleery, R.H., McMeeking, J., Potti, J., Røstad, O.W. & Thomson, D. (2003) Climate variation and regional gradients in population dynamics of two hole-nesting passerines. *Proceedings of the Royal Society London B*, **270**, 2397–2404.
- Sæther, B.E., Engen, S., Møller, A.P., Weimerskirch, H., Visser, M.E., Fiedler, W., Matthysen, E., Lambrechts, M.M., Badyaev, A., Becker, P.H., Brommer, J.E., Bukacinski, D., Bukacinska, M., Christensen, H., Dickinson, J., du Feu, C., Gehlbach, F., Heg, D., Hötter, H., Merilä, J., Nielsen, J.T., Rendell, W., Robertson, R.J., Thomson, D.L., Török, J. & Van Hecke, P. (2004a) Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. *American Naturalist*, **164**, 793–802.
- Sæther, B.E., Sutherland, W.J. & Engen, S. (2004b) Climate influences on a population dynamics. *Advances in Ecological Research*, **35**, 185–209.
- Sæther, B.-E., Engen, S., Møller, A.P., Visser, M.E., Matthysen, E., Fiedler, W., Lambrechts, M.M., Becker, P.H., Brommer, J.E., Dickinson, J., Gehlbach, F., Merilä, J., Rendell, W., Robertson, R.J., Thomson, D. & Török, J. (2005) Time to extinction of bird populations. *Ecology*, **86**, 693–700.
- Schaub, M., Pradel, R. & Lebreton, J.-D. (2004) Is the reintroduced white stork (*Ciconia ciconia*) population in Switzerland self-sustainable? *Biological Conservation*, **119**, 105–114.
- Schaub, M., Kania, W. & Köppen, U. (2005) Variation of primary production during winter induces synchrony in survival rates in migratory white storks *Ciconia ciconia*. *Journal of Animal Ecology*, **74**, 656–666.
- Schulz (1999) White stork on the up? *Proceedings of the International Symposium on the White Stork, Hamburg 1996*. Naturschutzbund Deutschland, Bonn.
- Tryjanowski, P. & Kuzniak, S. (2002) Size and productivity of the White Stork *Ciconia ciconia* population in relation to Common Vole *Microtus arvalis* density. *Ardea*, **90**, 213–217.
- Tryjanowski, P., Sparks, T.H., Ptaszky, J. & Kosicki, J. (2004) Do White storks *Ciconia ciconia* profit from an early return to their breeding grounds? *Bird Study*, **52**, 222–227.
- Tryjanowski, P., Sparks, T. & Profus, P. (2005a) Uphill shifts in the distribution of the white stork *Ciconia ciconia* in southern Poland: the importance of nest quality. *Diversity and Distributions*, **11**, 219–223.
- Tryjanowski, P., Sparks, T.H., Jakubiec, Z., Jerzak, L., Kosicki, J., Kuzniak, S., Profus, P., Ptaszky, J. & Wuczynski, A. (2005b) The relationship between population means and variance in reproductive success differs between local populations of White Stork (*Ciconia ciconia*). *Population Ecology*, **47**, 119–125.
- Williams, C.K., Ives, A.R. & Applegate, R.D. (2003) Population dynamics across geographical ranges: time-series analyses of three small game species. *Ecology*, **84**, 2654–2667.
- Zink, G. (1967) Populationsdynamik des Weissen Storches, *Ciconia ciconia*, in Mitteleuropa. *Proceedings of the International Ornithological Congresses*, **14**, 191–215.

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