CLIMATE CAUSES LARGE-SCALE SPATIAL SYNCHRONY IN POPULATION FLUCTUATIONS OF A TEMPERATE HERBIVORE

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Abstract. Theoretical analyses have shown that the spatial scaling of environmental autocorrelation, strength of density regulation, and the dispersal of individuals determine the scaling of synchrony in population fluctuations. By modeling the separate effects of density regulation, environmental stochasticity, and demographic stochasticity, we estimate the spatial scaling of the component that is due to environmental stochasticity in the population dynamics of roe deer (Capreolus capreolus) in Norway.

The estimated spatial scaling of the environmental noise was ~200 km. An examination of how different weather variables influenced the scaling indicated that snow depth was the major weather variable affecting the scaling of synchrony in population fluctuations, and was negatively related to population growth rates in 97.4% of the 151 populations included in the study. A large-scale climatic phenomenon, the North Atlantic Oscillation, was positively related to population growth rates in 94.7% of the populations but did not significantly affect the pattern of synchrony among populations.

We used newly developed theoretical results of the contribution of environmental noise and dispersal to the spatial scale of synchrony to show that the spatial scaling estimated in this study could not be explained by dispersal. This suggests that common environmental noise operating mainly during the winter is able to synchronize population fluctuations of roe deer over large distances.

Key words: Capreolus capreolus; density regulation; environmental stochasticity; North Atlantic Oscillation; roe deer; snow depth; spatial synchrony; stochastic population dynamics.

INTRODUCTION

Population dynamics of ungulates are determined by a combination of stochastic and density-dependent factors (Sæther 1997, Grenfell et al. 1998, Aanes et al. 2000, 2002, Sæther et al. 2002). In temperate areas, high population density during winter can result in increased mortality or a reduction in fecundity rate. Similar demographic effects can also be caused by climatic variation. Several studies have documented strong effects of climatic variability during both summer and winter (see review in Sæther 1997). In northern environments, low temperatures combined with precipitation during the neonatal period in early summer could cause neonatal mortality due to hypothermia (Linnell et al. 1998). Similarly, summer rainfall and temperature may affect the quantity and/or quality of food plants (Sæther 1985, Post and Stenseth 1999). This, in turn, is important for body growth of calves, and later can potentially affect the age at maturity (Sæther and Haagenrud 1983). Variability in climate during winter may also influence ungulate population dynamics through effects on mortality, productivity, and body growth (Sæther et al. 1996, Mysterud et al. 2000, 2001). Temporal variation in climate may therefore also act as a synchronizing agent of population fluctuations over large distances (Ranta et al. 1998, 1999, Bjørnstad et al. 1999a, Lande et al. 1999). The presence of such a Moran effect (Moran 1953) has been indicated in several species (Ranta et al. 1995, 1997, 1998, Sutcliffe et al. 1996, Paradis et al. 1999).

Population synchrony, measured as the correlation of temporal fluctuations in the size of local populations, usually decreases with geographic distance between localities (Bjørnstad et al. 1999a, Koenig 1999, Lindberg et al. 2000). An important characteristic of this function is the spatial scaling that gives the distance from zero in which the temporal fluctuation in population size is over a certain level. The scale of a distribution or function can be measured in different ways (Lande et al. 2003); a commonly used measure is the distance over which a function decays to $e^{-1} \approx 0.37$ of its maximum value (Roughgarden 1977). However, for non-exponential functions, the standard deviation of the scaled autocorrelation function is a preferable measure of the width of the distribution (Lande et al. 1999). By using...
the standard deviation as a measure of scale, a simple general formula for the spatial scale of population synchrony in terms of the spatial scales of dispersal and environmental autocorrelation in a homogenous model can be obtained (Lande et al. 1999, 2003).

Interpretation of spatial autocorrelation functions is complicated by the fact that synchrony in population fluctuations is affected by dispersal (Kendall et al. 2000, Ripa 2000) and the strength of density regulation in addition to environmental autocorrelation (Lande et al. 1999, Engen et al. 2002a, b). Disentangling the relative contributions of these processes to the scaling of synchrony has therefore been difficult due to lack of proper statistical techniques (Bjørnstad et al. 1999b). For instance, Engen et al. (2002b) showed that estimating spatial autocorrelation functions from data on (log) population sizes or yearly differences in (log) population sizes could produce very different results. The spatial scale of yearly differences in population size often will be practically independent of dispersal and local density regulation and approximately equal to the autocorrelation function for the environmental noise after subtracting the constant long-distance correlation.

Using a stochastic modeling framework that includes the temporal as well as the spatial components (Lande et al. 2003), Engen et al. (2005) developed models that allow for separating out the effect of spatial autocorrelation in the environment. Including demographic stochasticity as well as differences in the strength of density regulation, each time series of population fluctuations is fitted to a stochastic model that also includes environmental covariates (e.g., climatic variables). Thus, accounting for the expected change in population size conditioned on the population size the previous year, the residual variance component is the variance unexplained by covariates and demographic stochasticity. The spatial autocorrelation of these residual variance components from different locations, not necessarily covering the same time span, can then be estimated using classical multinormal theory (Engen et al. 2005). This enables us to estimate the contribution of separate covariates or combinations of covariates to the spatial scaling of synchrony in population dynamics.

In this study we relate fluctuations in estimated growth rates of roe deer (Capreolus capreolus) populations to variations in local and regional climate variables. We then analyze how different environmental variables contribute to the spatial scaling of the synchrony in the population fluctuations.

Roe deer in Fennoscandia (Norway, Sweden, and Finland) occupy a fluctuating environment largely characterized by short growing seasons, cold winters, and high snow accumulation. This applies especially to Norway, where the climatic conditions throughout winter are highly variable from year to year due to an oceanic influence on climate. A few degrees change in mean temperature through winter could potentially constitute a large difference in snow accumulation through a shift from rain to snow (Mysterud et al. 2001). Heavy foot loading, small body size, and low brisket height are among factors that present challenges to roe deer in these northern environments (Holand et al. 1998). Roe deer brisket height is 50–60 cm and snow depths in many regions of Fennoscandia can exceed 1 m (Cederlund and Liberg 1995). In areas with gradients in snow cover, the roe deer actively seeks the most preferable areas, such as valley bottoms, during the winter season. In addition, in many areas it is also a common management measure to provide extra food for roe deer during winter at artificial feeding sites (Holand et al. 1998). However, this does not prevent roe deer populations from suffering high mortality due to starvation and predation in years with high snowfall (Borg 1970, 1991, Cederlund and Lindström 1983). In early summer, low temperatures and high levels of precipitation can cause newborn calves to freeze to death due to hypothermia (Linnell et al. 1998). Thus, we expect that the harsh climatic conditions the roe deer faces throughout Norway should have significant impacts on the temporal and spatial population dynamics.

**METHODS**

**Population data**

From a remnant population of ~100 individuals in southern Sweden in the middle of the 19th century, roe deer have spread out to cover most of the forested parts of Sweden and Norway and a smaller part of Finland (Cederlund and Liberg 1995). Following the expansion northward, hunting was opened wherever the populations were considered viable. The hunting quotas are not age or sex specific, but hunting statistics indicate that the harvest is skewed toward adult males.

Hunting statistics at the municipality level were obtained from Statistics Norway and were available from the mid 1950s to the present. The hunting quotas were also partly available. Averaged over all years and municipalities, only 27.9% ± 18.9% (mean ± 1 sd) of the actual hunting quota was harvested. Only in 2.4% of the cases was more than 70% of the hunting quota harvested. Accordingly, we expect that the numbers of harvested roe deer, to a large degree, reflect changes in actual population size rather than being artifacts of quota size.

Three data sets were available for testing this critical assumption. First, we compared annual variation in the number of roe deer killed in car accidents (provided by Statistics Norway) with the harvest data during the years 1987–2000. The correlations between road kills and harvest data were generally high (Table 1). Second, we compared food-site sightings from several municipalities in the counties of Hedmark and Østfold in southern Norway (Fig. 1) with harvest data from the same municipalities during the years 1994–1998. The
TABLE 1. Correlation coefficients between the number of county road kills of roe deer (N) during the years 1987–2000 (n = 14 years) and the number of roe deer harvested in different counties of Norway.

<table>
<thead>
<tr>
<th>County</th>
<th>N</th>
<th>Δ log N</th>
</tr>
</thead>
<tbody>
<tr>
<td>Østfold</td>
<td>0.64*</td>
<td>0.65*</td>
</tr>
<tr>
<td>Akershus</td>
<td>0.73**</td>
<td>0.75***</td>
</tr>
<tr>
<td>Hedmark</td>
<td>0.55*</td>
<td>0.82***</td>
</tr>
<tr>
<td>Oppland</td>
<td>0.96***</td>
<td>0.83***</td>
</tr>
<tr>
<td>Buskerud</td>
<td>0.89***</td>
<td>0.68***</td>
</tr>
<tr>
<td>Vestfold</td>
<td>0.76**</td>
<td>0.57</td>
</tr>
<tr>
<td>Telemark</td>
<td>0.78**</td>
<td>0.77***</td>
</tr>
<tr>
<td>Aust-Agder</td>
<td>0.83***</td>
<td>0.5</td>
</tr>
<tr>
<td>Vest-Agder</td>
<td>0.91***</td>
<td>0.90***</td>
</tr>
<tr>
<td>Rogaland</td>
<td>0.90***</td>
<td>−0.06</td>
</tr>
<tr>
<td>Møre og Romsdal</td>
<td>0.77**</td>
<td>0.61*</td>
</tr>
<tr>
<td>Sør-Trøndelag</td>
<td>0.73**</td>
<td>0.65*</td>
</tr>
<tr>
<td>Nord-Trøndelag</td>
<td>0.08</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Notes: Data are provided by Statistics Norway. Δ log N represents the correlation between the annual differences in log numbers of roe deer killed and the difference in the number of shot animals. The latter was done to remove the common trend in some of the time series. *P < 0.05; **P < 0.01; ***P < 0.001.

feeding sites were established by local people to offer additional winter forage for the local roe deer population. Extensive use of census lines during periods with snow cover revealed that all tracks from roe deer were found <700 m away from known artificial feeding sites, indicating that most animals are confined to the surroundings of such feeding sites. The correlation between annual variation in the mean number of sightings at the food site and the number of roe deer shot in the same area was 0.94 (P < 0.05, n = 5 years). Third, we reconstructed fluctuations in the size of the population at the island of Yttersøya, Levanger, Central Norway, using Virtual Population Analysis and following the methods of Solberg et al. (1999). The reconstruction was based on 2998 sex- and age-determined individuals during the period 1984–2003 (V. Grøtan, E. J. Solberg, B.-E. Søther, and E. Lund, unpublished data). Red foxes (Vulpes vulpes) and other large predators are absent on the island, which reduces the impact of causes of mortality other than hunting on the roe deer population. A close correlation was found between estimated population size and the number of animals harvested on the island (correlation coefficient = 0.86, P < 0.001, n = 19 years). Thus, this supports the assumption that variation in the number of shot animals is a reliable population index for the roe deer.

Harvest data were available from 265 municipalities. We selected time series from municipalities with more than 30 years of harvest data. To reduce the effect of demographic stochasticity, only time series in which the carrying capacity (in the harvest) was estimated to be >30 were included in the analysis, resulting in a set of 151 time series from different municipalities in the counties of Nord-Trøndelag, Sør-Trøndelag, Møre og Romsdal, Hedmark, Buskerud, Østfold, Akershus, Vestfold, Telemark, Aust-Agder, Vest-Agder, and Rogaland (Fig. 1).

Most of the study area is situated within the boreal vegetation zone, except for the very southern part that also embraces parts of the nemoral vegetation zone.

Fig. 1. The location of the municipalities included in the study (shaded). The municipalities are mainly located in a southern and northern part, separated by a mountainous area with less suitable habitat for roe deer. However, there could be some dispersal between the southern and northern part due to valleys connecting the two areas.
For further descriptions of the study area, see Sæther and Heim (1993), Sæther et al. (1996), Solberg et al. (1997), and Hjeljord and Histol (1999).

**Population Model**

Writing \( N_t \) for the population size at a given location, the dynamics are modeled by

\[
N_{t+1} = N_t + rN_t - \beta N_t^2
\]

where \( r \) is the specific density-independent growth rate varying stochastically between years, and \( \beta N_t^2 \) defines the logistic form of density regulation and

\[
\text{var}(r) = \sigma_r^2 + \frac{\sigma_r^2}{N_t}
\]

where \( \sigma_r^2 \) and \( \sigma_a^2 \) are the environmental and demographic variance, respectively (May 1973, 1974, Turelli 1977, Engen et al. 1998, Lande et al. 2003). For small and moderate population fluctuations, a simple first-order approximation gives the model

\[
E(\ln N_{t+1} \mid N_t) = \ln N_t + r - \frac{1}{2} \sigma_r^2 + \frac{1}{2N_t} \sigma_a^2 - \beta N_t
\]

\[
\text{var}(\ln N_{t+1} \mid N_t) = \sigma_r^2 + \frac{\sigma_a^2}{N_t}
\]

(Lande et al. 2003). Setting \( \ln N_t = \ln x_t \) this model can be rewritten as

\[
X_{t+1} = E(X_{t+1} \mid X_t) + U_a \sigma_a \sqrt{N_t} + U_r \sigma_r
\]

where \( U_a \) and \( U_r \) are independent variables with zero mean and unit variance. Because our main goal is to examine the contribution of the environmental noise terms at different locations, we introduce environmental covariances as random effects by writing

\[
U_a \sigma_a = \sum \alpha_i y_{i,t} + U_a \sigma
\]

where \( y_{i,t} \) is a given random covariate \( i \) at time \( t \), \( \alpha_i \) is the effect of the covariate, \( U_a \) is a normalized variable, and \( \sigma \) is the component of the environmental variance that cannot be explained by fluctuations in the covariates. This leads to the relation

\[
\sigma_r^2 = \text{var} \left( \sum \alpha_i y_{i,t} \right) + \sigma_a^2
\]

where the covariates explain a proportion of the total environmental variance,

\[
p = \frac{\text{var} \left( \sum \alpha_i y_{i,t} \right)}{\text{var} \left( \sum \alpha_i y_{i,t} \right) + \sigma_a^2}
\]

**Estimation of Parameters**

**Demographic variance**

The total contribution of a female \( i \) in year \( t \) (\( R_i \)) is the number of female offspring she gives birth to during this year that survive for at least one year plus 1 if the female herself survives to the next year. The demographic variance was estimated (Sæther et al. 1998) as the weighted mean across years as follows:

\[
\hat{\sigma}_a^2(t) = (1 - a)^{-1} \sum (R_i - \bar{R})^2
\]

where \( \bar{R} \) is the mean contribution of the individuals and \( a \) is the number of recorded contributions in year \( t \). Data on individual variation in the fitness contributions to the following generations (Lande et al. 2003) were obtained from 35 radio-collared females at the island Storosna in central Norway (Andersen and Linnell 1998, Gaillard et al. 1998).

A problem for our analysis of population synchrony was that we possessed data only on the number of hunted individuals and not on the actual numbers of individuals present. Thus, the latter had to be approximated in order to estimate the effect of demographic stochasticity that is density dependent (Lande et al. 2003). We assumed that 20–30% of the total numbers present in populations are harvested annually. Assuming a linear relationship between hunting statistics and population abundance, we multiplied the numbers of harvested individuals by 4 to get an estimate of abundance in the populations.

**Population parameters**

Assuming that \( X_{t+1} = \ln N_{t+1} \) is normally distributed when conditioned on \( N_t \), and writing \( f(x; \mu, \sigma^2) \) for the normal probability distribution with mean \( \mu \) and variance \( \sigma^2 \), the log likelihood function takes the form

\[
\ln L = \sum \ln f(X_{t+1}; m(N_t, Y_t), \nu(N_t))
\]

where \( Y_t \) denotes the vector of covariates, \( \nu(N) = \sigma^2 + \frac{\sigma_r^2}{N_t} \), and the mean is the appropriate modification of Eq. 2.

\[
m(N_t; Y_t) = \ln N_t + r - \frac{1}{2} \sigma_r^2 - \beta N_t + \sum \alpha_i y_{i,t}
\]

The sum in Eq. 9 is taken over those years for which the population size in the previous year is known. This means that if there are time gaps in the data of more than one year, we ignore the information contained in the population change over this gap, which in any case will be rather small. Then, assuming known demographic variance, all other unknown parameters are estimated by numerical maximization of the log likelihood, and uncertainties are evaluated by parametric bootstrapping (Efron and Tibshirani 1993) involving simulating the time series using the initial value of the data and the estimated parameters.

**Spatial synchrony**

The spatial analysis is based on studying the residuals obtained from fitting the model to time series observations at each location \( z \).

\[
R_{t+1}(z) = X_{t+1}(z) - E[X_{t+1}(z) | X(z), Y(z)]
\]

\[
= \sigma(z)U(z) + \sigma_d(z)U_d(z) / \sqrt{N(z)}
\]
where $\hat{E}$ denotes the estimated expected value. We use the normal approximation and choose a parametric model for the spatial autocorrelation of the form

$$
\rho(z) = \text{corr}[U(w), U(w + z)] = \rho_u + (\rho_0 - \rho_u)h(z)
$$

(12)

where $h(z)$ decreases from 1 to 0 as $z$ increases from 0 to infinity. We use the positive definite autocorrelation function of the Gaussian form:

$$
h(z) = e^{-\frac{z^2}{2\theta^2}}.
$$

Using the same type of spatial autocorrelation function for the population sizes, Lande et al. (1999) and Engen et al. (2002, 2004, 2005) applied the standard deviation of the function $h(z)$ scaled to become a distribution as a measure of spatial scaling of population synchrony. Hence, the parameter $l$ in these functions is actually the measure of spatial scaling defined for the residuals. The parameters $\rho_0$ and $\rho_u$ are the correlation at zero and infinite distance, respectively.

Data from different locations are often available over different, but partly overlapping, time periods. However, for each year we do have a set of residuals with zero means, estimated standard errors, and correlations defined by Eqs. 11 and 12. For a given set of parameters ($\rho_0$, $\rho_u$, $l$) defining the spatial synchrony, we have a complete description of a multivariate normal distribution each year, but possibly with different sets of locations at different years due to missing values. The complete likelihood function is found by multiplying the functions for each year, or actually, adding the log likelihood contributions for each year. Finally, this function is maximized numerically to give estimates for ($\rho_0$, $\rho_u$, $l$). The sampling properties of the estimates are found by parametric bootstrapping (Efron and 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 (Ripley 1987). The same representation also gives a fast method for the stochastic simulations required to perform the bootstrapping (see Engen et al., 2005).

Using a model on a log scale that allows large population fluctuations, Engen et al. (2005) showed that the autocorrelations for the residuals, $l_{\text{res}}$, in a similar model without demographic variance, could be approximated as

$$
l_{\text{res}}^2 \approx l_e^2 + M \quad \text{for } \gamma < 1.15
$$

(13)

where $l_e$ is the scaling of the environmental noise, $M$ is the product of the variance in dispersal distance in any given direction and the dispersal rate, and $\gamma$ is the strength of the local density regulation (Lande et al. 1999). Expressed by the mean yearly dispersal distance, $d$, this is approximately

$$
l_{\text{res}}^2 \approx l_e^2 + 0.64d^2.
$$

(14)

**Significance testing**

To compare models, we must test whether the parameters differ among models. A significant difference among models can be estimated by examining whether 0 is included in the appropriate lower and upper quantiles of the distribution of differences between the two bootstrap distributions.

**Climate variables**

The North Atlantic Oscillation (NAO) is a global climate phenomenon (Visbeck et al. 2001) and is expressed by an index based on the difference in normalized sea level pressures between Lisbon, Portugal, and Stykkisholmur, Iceland, from 1864 through 2002 for the winter period (see Climate and Global Dynamics: Climate Analysis Section, Climate Indices, available online). A high positive NAO index is generally associated with relatively warm winters with much precipitation in northern Atlantic coastal Europe, whereas low values of the index tend to result in cold winters with low levels of precipitation (Hurrell and VanLoon 1997).

Monthly means of precipitation, snow, and temperature from weather stations located in different areas of Norway were obtained from the Norwegian Meteorological Institute. In cases in which we did not have a weather station situated within the municipality borders, we used the nearest weather station situated in another municipality. We used monthly snow cover data from October to May, precipitation data from May to August, and temperature data from October to August. In addition, we computed all possible sets of two- and three-month averaged values.

**Results**

The estimate of demographic variance was $\hat{\sigma}^2_d = 0.745$. We first used this estimate to fit local models without any covariates included (Eqs. 2 and 3). Fig. 2a shows the estimates of carrying capacity $K = 500 \pm 461$ (all values are presented as mean $\pm$ SD) in the municipalities, ranging from 122 to 3144. The stochastic specific growth rates (Fig. 2b) showed large variation among municipalities: $\hat{f} = 0.189 \pm 0.189$. In the logistic model, the strength of density regulation is equal to $r$ (May 1981). Thus, differences in the estimated $r$ imply differences in the strength of density regulation around the carrying capacity among municipalities. However, the uncertainties in these estimates are large. Finally, the average estimate of environmental variance in populations (Fig. 2c) was $\hat{\sigma}^2_e = 0.211 \pm 0.159$.

To examine the spatial pattern in the synchrony in population fluctuations, we fitted a spatial autocorrelation model of the Gaussian form (Fig. 3a). Parametric bootstrap distributions for the set of parameters ($\rho_0$, $\rho_u$, $l$) defining the spatial synchrony are shown in

<http://www.cgd.ucar.edu/cas/catalog/climind/>
Fig. 2. The distribution of municipality-specific estimates of (a) the carrying capacity $\hat{K}$, (b) the stochastic population growth rates $\hat{r}$, and (c) the environmental variance $\hat{\sigma}_e^2$ of Norwegian roe deer.

Fig. 3. The correlation in population fluctuations of Norwegian roe deer in relation to distance for (a) a model with North Atlantic Oscillation as covariate, (b) for a model with snow depth during the period from October to December as covariate, and (c) for a model with differences in log harvest quotas as covariate. For the sake of comparison, the model without any covariates is included as dashed lines in the figures. The thin lines are the 5% and 95% quantiles.

Fig. 4. The estimated scale of the local component of synchrony was $l = 191 \pm 10$ km. Furthermore, the estimate of the correlation in population fluctuations at zero distance was $\hat{\rho}_0 = 0.487 \pm 0.011$, which was significantly less than 1 as the 95% quantile of the bootstrap distribution of $\hat{\rho}_0$ was 0.503. Finally, the correlation at infinite distance was estimated to $\hat{\rho}_\infty = 0.175 \pm 0.029$, which was significantly larger than 0 (5% quantile of the bootstrap distribution was 0.114). This shows a common environmental influence on the population dynamics of the roe deer operating over large distances.
The North Atlantic Oscillation Index was positively related to population growth rates in 94.7% of the municipalities ($\alpha = 0.078$, $SD = 0.053$, range $-0.037$ to $0.246$, $P(\alpha > 0) < 0.05$ in 29.8% of municipalities). However, the NAO index only explained a small fraction ($\hat{\rho} = 0.068$, $SD = 0.064$, range $0.0-0.266$) of the total environmental variance. Fitting the spatial autocorrelation model (Fig. 3a) resulted in an estimate of $\hat{\rho}_0 = 0.471 \pm 0.011$. The estimate of the scaling was $l = 191 \pm 10$ km, $\hat{\rho}_t = 0.155 \pm 0.029$ was significantly larger than 0 as the 5% quantile of the bootstrap distribution was 0.104. Although the inclusion of NAO as a covariate did reduce the estimate of the correlation at all distances, none of the estimated parameters in this model was significantly different from the estimates obtained in the model without any covariates.

No covariate related to summer climatic conditions was able to explain variations in the environmental variance component to any significant degree, as the fraction of the environmental variance explained by these covariates never exceeded 0.04.

All covariates that included snow depth were able to reduce the residual environmental variance component, in general by more than 10%. The covariate that explained the highest proportion of the environmental variance was snow depth during the period from October to December ($\hat{\rho} = 0.213$, $SD = 0.181$, range $0.0-0.82$; $\alpha = -0.033$, $SD = 0.022$, range $-0.110-0.010$, $P(\alpha < 0) < 0.05$ in 70.2% of municipalities). Large snow depth reduced the population growth rates (negative effects in 97.37% of the municipalities). As expected, snow depth explained a large proportion of the synchrony in population fluctuations (Fig. 3b). Including snow depth reduced the spatial scale of synchrony to $\hat{l} = 162.3 \pm 14$ km, significantly lower than the estimate obtained without including any covariates (Fig. 5a; $P < 0.05$). The estimate of $\hat{\rho}_t = 0.368 \pm 0.016$ was significantly lower than the estimate obtained without including covariates (Figs. 3b and 5b; $P < 0.001$). This shows that variation in snow depth synchronizes population fluctuations of roe deer at relatively short distances. Finally, the estimate of $\hat{\rho}_c = 0.185 \pm 0.029$ was not significantly different from the estimate based on no covariates.

**Discussion**

This study demonstrates synchronous fluctuations in the size of Norwegian roe deer populations over large distances (Figs. 3 and 4). As has been commonly found (Ranta et al. 1998, Koenig 1999), the degree of synchrony decreased with distance. However, a significant common environmental noise term $\rho_c$ was still present (Figs. 3 and 4c).

Snow depth during the period from October to December was the climatic variable explaining most of the observed synchrony in population fluctuations (Figs. 3b and 5b). Snow depth had an almost consistently negative effect on growth rates after accounting...
for density dependence and demographic stochasticity. Such effects have also been found in other temperate ungulates (Sæther et al. 2002). Snow depths at this time of the year seldom reach the levels needed to cause immediate mortality among roe deer. However, unlike many other northern vertebrates, roe deer have meager fat reserves (Holand et al. 1998). Therefore, high snow depths in early winter effectively prolong the period of negative energy balance through an early depletion of the limited fat reserves. This will accordingly increase the negative effects (through either mortality or reduced reproduction) associated with long periods of low temperatures and deep snow cover through the rest of winter.

The inclusion of NAO did not significantly alter the estimates of synchrony (Fig. 3a). Although the regression coefficients in the present study are almost consistently of the same sign, there can be large differences among different localities in how NAO translates into local conditions affecting population dynamics. Mysterud et al. (2001) showed that the relationship between snow depths and NAO differed over short distances, due to local topographical conditions along the west coast of Norway. Sæther et al. (2003) have also shown that the sign of the regression coefficient of change in population size on NAO could differ over relatively short distances. The environmental noise could also have a nonlinear effect on the population dynamics (Grenfell et al. 1998, Mysterud et al. 2001). In such a case, a poor fit of a linear model will reduce the fraction of the residuals being explained by the environmental covariate. Thus, specifying a linear model for the effect of the environmental noise when the true effect, in fact, is nonlinear will therefore underestimate the effect of the covariate on the spatial scaling of synchrony. Hence, we suggest that the estimated effects of the various covariates (Figs. 3 and 5) represent underestimates of those effects in affecting the synchrony in population fluctuations of roe deer in Norway.

Although snow depths in early winter significantly contributed to the spatial scaling of synchrony (Figs. 3b and 5a), all parameters describing the synchrony in population fluctuations in this model were significantly larger than zero. Thus, there are probably also other synchronizing factors present. Likely candidates are unmeasured autocorrelated environmental influences, trophic interactions (Ims and Andreassen 2000), and dispersal, coupled with weak density regulation (Lande et al. 1999, Kendall et al. 2000, Ripa 2000, Engen et al. 2002a, b). During the study period, the abundance of red fox (Vulpes vulpes), which is a main predator of roe deer fawns, has been varying due to an epizootic of sarcoptic mange during the late 1970s and 1980s (Lindström et al. 1994). However, as we did not possess enough reliable data on red fox abundances, we were not able to test whether variation in red fox abundance could affect the spatial scaling of roe deer fluctuations. Furthermore, Engen et al. (2005) have obtained a simple scaling result for relative contribution of the environmental autocorrelation and dispersal to the scaling of the synchrony in population fluctuations (Eq. 14). The squared spatial scaling of residuals equals the sum of the squared spatial scaling of the environmental noise plus the mean individual dispersal distance for one season multiplied by a factor of 0.64. Having estimated the spatial scaling of residuals, it is straightforward to establish the possible influence of dispersal to spatial scaling of synchrony (Fig. 6). In northern boreal forests, a large fraction of yearlings disperse (95%) and dispersal distances are often long; i.e., dis-

**Fig. 5.** The distribution of bootstrap replicates from the model without any covariates (black) and the model with snow depth in October–December (gray) for (a) the spatial scale of synchrony $l$ and (b) the correlation at short distances $r_0$. 
The demographic variance of the roe deer was higher than estimated for other mammals (Lande et al. 2003, Sæther et al., in press). This may be related to the high fecundity of the roe deer at the island of Storfonna (mean litter size ranging from 2.04 to 2.44 [Andersen and Linnell 2000]), because demographic variance in birds increases with litter size (Sæther et al. 2004). Theoretical analyses have shown (Engen et al. 2005) that the spatial synchrony in population fluctuations decreases with demographic variance and that this effect increases with decreasing average population size. We also know that demographic variance shows large intraindividual variation (Sæther et al. 2004). However, in the present study, variation in the estimates of the demographic variance that was included in the model had only a minor influence on the estimates of the parameters \( r_{i0}, r_{i}, I \) describing the pattern of synchrony in the population fluctuations. One explanation for this may be that many of the populations were so large (Fig. 2a) that the influence of demographic variance on the population dynamics was small.

In this study we have used the number of harvested animals as an index of population abundance. This assumes a linear relationship between population size and the number of harvested animals, and that the errors in the indices are small. The presence of observation errors will, in general, reduce the strength of spatial synchrony because the errors are expected to increase the variances in the estimated population growth rates, but are not expected to alter the covariance between two independently estimated populations (Lande et al. 1999). The expectation of the scaling of the synchrony is unaffected by observation errors, but the uncertainty in the estimates increases with increasing observation error. Thus, we would have expected a higher level of synchrony if we had data without observation errors. On the other hand, if the observation errors are spatially dependent, this could clearly lead to overestimates of synchrony in population dynamics. For example, the practice of assigning harvest quotas could unquestionably lead to autocorrelated observation errors if the harvest quotas are spatially autocorrelated and the harvest quotas limits the number of harvested animals. However, the harvest quotas of roe deer throughout Norway do not seem to limit the harvest (see Methods). To examine whether variation in harvest quotas could explain the observed pattern of synchrony in population fluctuations, we fitted a model with differenced log harvest quotas as covariate (Fig. 3c). This covariate explained approximately \( \rho = 0.196 \) (SD = 0.182, range 0–0.838) of the environmental variance. High growth rates in quotas were related to high population growth rates (\( \alpha = 0.789 \), SD = 0.811, range \(-0.738 \) to 8.525, \( P(\alpha > 0) < 0.05 \) in 35.1% of municipalities). The spatial scaling was estimated to \( l = 206 \pm 15 \) km, which was not significantly different from the estimate of \( l = 204 \pm 14 \) based on including no covariates. It therefore seems unlikely that the observed synchrony in population fluctuations is an artifact of the assignment of hunting quotas.

Several approaches have been used to analyze spatial pattern of population fluctuations (Bjørnstad et al. 1999a, Buonaccorsi et al. 2001, Haydon et al. 2001, Viljugrein et al. 2001). The approach of fitting a model to local time series and correlating the residuals is not new (Sutcliffe et al. 1996). However, the scaling results obtained by Engen et al. 2005) allow for interpretation of the effect of various covariates. Thus, we are now able to show that a particular covariate (e.g., snow depth) affects the spatial scaling of synchrony. Using
the same scaling results, we are also able to estimate the mean individual dispersal distances needed to explain the observed synchrony in residuals. In this study, the spatial scaling is of such an order of magnitude that we can rule out dispersal as a factor explaining the synchrony in residuals. Thus, the theoretical framework provided by Engen et al. (2005) for analyzing the spatial synchrony in population fluctuations seems to extend earlier approaches in terms of determining the causes of synchrony in population fluctuations.

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LITERATURE CITED


