

Effects of climate on population fluctuations of ibex

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Abstract

Predicting the effects of the expected changes in climate on the dynamics of populations require that critical periods for climate-induced changes in population size are identified. Based on time series analyses of 26 Swiss ibex (*Capra ibex*) populations, we show that variation in winter climate affected the annual changes in population size of most of the populations after accounting for the effects of density dependence and demographic stochasticity. In addition, precipitation during early summer also influenced the population fluctuations. This suggests that the major influences of climate on ibex population dynamics operated either through loss of individuals during winter or early summer, or through an effect on fecundity. However, spatial covariation in these climate variables was not able to synchronize the population fluctuations of ibex over larger distances, probably due to large spatial heterogeneity in the effects of single climate variables on different populations. Such spatial variation in the influence of the same climate variable on the local population dynamics suggests that predictions of influences of climate change need to account for local differences in population dynamical responses to climatic conditions.

Keywords: *Capra ibex*, demographic stochasticity, density-dependence, environmental stochasticity, ibex, spatial synchrony, stochastic population dynamics

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Introduction

Population dynamics of ungulates are determined by a combination of stochastic and density-dependent factors (e.g. Sæther, 1997; Gaillard *et al.*, 1998, 2000; Grenfell *et al.*, 1998; Aanes *et al.*, 2000, 2002; Sæther *et al.*, 2002). Climate variation constitutes a major component of the influence of environmental stochasticity on ungulate population fluctuations in temperate areas (Sæther, 1997; Gaillard *et al.*, 1998; Post & Stenseth, 1999; Solberg *et al.*, 1999; Mysterud *et al.*, 2001b). For instance, summer rainfall and temperature may affect the quantity and/or quality of food plants (Sæther, 1985; Post & Stenseth, 1999), which in turn influences age at maturity through an influence on the rate of body growth early in life (Sæther & Haagenrud, 1983). In addition, variability in climate during winter may influence ungulate population dynamics, mainly through an effect on mortality (Sæther *et al.*, 1996; Mysterud

et al., 2001b) or body condition (e.g. Sæther & Gravem, 1988).

These patterns suggest that there are two different mechanisms for how stochastic fluctuations in the environment may influence fluctuations in population size that both are important to consider for understanding the influence of climate variation on changes in size of ungulate populations. According to the ‘tap-hypothesis’ (Sæther *et al.*, 2004b), climate variation will operate through an effect on recruitment, closely related to an influence of weather during the breeding season on the fecundity rates. In contrast, the ‘tub-hypothesis’ suggests that climate-induced changes in population size from one year to the next is mainly determined by the number of individuals that manage to survive harsh weather conditions during the nonbreeding season. Determining the critical periods affecting the population dynamics is a first step in predicting the consequences of the climate change on population dynamics (Hallett *et al.*, 2004; Sæther *et al.*, 2004b).

Temporal variation in climate may synchronize population fluctuations over large distances (Bjørnstad *et al.*, 1999; Lande *et al.*, 1999; Liebhold *et al.*, 2004),

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and synchrony in population fluctuations caused by spatially correlated temporal variation in climate increases the risk of local and global extinction (Allen *et al.*, 1993; Bolker & Grenfell, 1996; Heino *et al.*, 1997; Palmqvist & Lundberg, 1998; Engen *et al.*, 2002). The presence of such a Moran-effect (Moran, 1953; Royama, 1992) has been indicated in several species (Ranta *et al.*, 1995; Grenfell *et al.*, 1998; Paradis *et al.*, 1999; Benton *et al.*, 2001, 2002; Grøtan *et al.*, 2005). However, the theoretical prediction of Moran (1953) stating that correlations in population fluctuations equals the correlation in environmental noise is based on log-linear density regulation and equal effects of the environmental covariates in all populations. Both the form of density regulation (Myrsterud *et al.*, 2000; Sæther *et al.*, 2003; Williams *et al.*, 2003) and the effects of environmental covariates could vary spatially (Myrsterud *et al.*, 2000; Sæther *et al.*, 2003; Both *et al.*, 2004). Theoretical analyses have shown that spatial variation in the strength of density regulation (Greenman & Benton, 2001; Engen & Sæther, 2005) and in the effects of environmental covariates (Engen & Sæther, 2005) result in shorter spatial scales of synchrony than suggested by the Moran theorem. Thus, spatial variation in density regulation and influence of environmental covariates are important to consider when examining the effects climate variables on the spatial synchrony of population fluctuations.

Here, we will use time series of the fluctuations in size of 26 reintroduced populations of ibex (*Capra ibex*) in Switzerland (Table 1). Such time series provide data for periods even when only a few individuals are present, which allows estimation of the specific growth rate at small population sizes (Komers & Curman, 2000). In this study, we relate fluctuations in estimated growth rates of ibex populations to variations in local and regional climate variables in order to determine the most critical season that affects population fluctuations of the ibex. We then estimate the degree of spatial synchrony in population fluctuations and how the most important environmental variables contribute to the spatial scaling in the synchrony of the population fluctuations. We use a stochastic modelling framework that includes temporal as well as spatial components (Lande *et al.*, 2003; Engen *et al.*, 2005). Each time series of population fluctuations is fitted to a stochastic model that in addition to demographic stochasticity and strength of density dependence also includes the local effects of environmental covariates (e.g. climatic variables). Thus, the residual variance component is the residual population size after accounting for density dependence, environmental covariates and demographic stochasticity. The spatial autocorrelation of these residual variance components from different loca-

tions 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 synchrony in the population fluctuations.

Materials and methods

Study populations

The ibex was almost driven to extinction by overexploitation at the beginning of the 19th century when only <100 individuals were left in the Gran Paradiso Mountains in the Italian Alps (Nievergelt, 1966; Meile *et al.*, 2003). Reintroductions have repopulated the ibex over almost its entire original range of distribution in the Alps (Stüwe & Nievergelt, 1991; Filli, 2002; Meile *et al.*, 2003).

We study the fluctuations of 26 Swiss ibex populations (Table 1) that was founded as part of the reintroduction programme (Stüwe & Nievergelt, 1991). For location of the study populations, see Sæther *et al.* (2007c). The reintroductions occurred over several years. In our analyses, we only included time series for the years after the end of the reintroductions.

The ibex show exclusive use of areas above timberline throughout the year (Nievergelt, 1966). In spring, new vegetation growth occurs first in areas close to the timberline, and both sexes of Ibex concentrate in these restricted areas in April and May (Wiersema, 1984; Abderhalden, 2005), allowing for easy observation during their search for newly developed vegetation. The populations were censused once a year in April or May by experienced rangers (Bächler, 1935; Nievergelt, 1966; Ruhlé *et al.*, 1994; Tschirky, 2004). Thus, the number of ibex counted each year is assumed to represent the number of ibex present before calving in June–July (Bon *et al.*, 2001). These observations are generally considered to be accurate compared with other ungulate population counts (Filli, 2002; Sæther *et al.*, 2002).

Population model

Some of the populations were harvested during autumn. Consequently, this has to be incorporated in the population models. First, we adopted a population model without density regulation so that the expected change in population ΔN from 1 year to another is

$$E(\Delta N|N_t, H_t) = r(N_t - H_t) \quad (1)$$

and

$$\text{var}(\Delta N|N_t, H_t) = \sigma_a^2(N_t - H_t) + \sigma_e^2(N_t - H_t)^2, \quad (2)$$

where N_t is the population size in the spring in year t , H_t is the number animals recorded to be harvested during

Table 1 The selected models based on the AICc-criterion in the various populations

Locality	Model	σ_{res}^2	σ_e^2	p	$\Delta AICc$
Albris (DD)	$T09_{t+1}^{**} - T03_{t+1}^{***} - S04_{t+1}$	0.022	0.033	0.33	2.041
Alpstein (DI)	$T02_{t+1} - 04_{t+1}^{***} - P02_{t+1} - 04_{t+1}^{***} - S11_{t-1} - 01_{t+1}^{***}$	0.004	0.009	0.55	0.011
Augstmatthorn-Brienzerrothorn (DD)	$-T04_{t+1}^{***} - P06_{t-1} - 08_{t-1}^{***} + P07_t^{***}$	0.000	0.002	0.88	3.017
Bire-Oeschinen (DI)	$-T06_t^{***} + S12_{t-1} - S04_{t+1}^{***}$	0.002	0.009	0.78	1.913
Blatten (DI)	–	–	< 0.001	–	0.181
Calanda (DI)	$T05_{t-1} - 07_{t-1}^{***} + P03_{t-1} - 05_{t-1}^{***} - P06_{t-1} - 08_{t-1}^{***}$	0.021	0.058	0.64	1.23
Falknis (DD)	$-T05_t^{***} + P11_{t-1} - 01_t^{***} + S03_t^{***}$	0.008	0.020	0.59	0.581
Fergen-Seetal (DD)	$P12_{t-1} - 02_t^{***} - S03_t^{**} + NAO_{t+1}^{**}$	0.000	0.004	1.00	0.176
Flüela (DI)	$T08_{t-1} - T10_{t-1}^{***} - T06_t^{**} - T08_{t-1} - 10_t^{***}$	0.013	0.028	0.54	0.276
Foosstock (DI)	$-T08_{t-1}^{***} + P11_t^{***} + S02_t^{***}$	0.004	0.034	0.87	0.735
Gastern (DD)	$-P08_{t-1}^{**} - P09_{t-1}^{**} - S01_{t+1} - 03_{t+1}^{***}$	0.003	0.011	0.70	0.171
Gross-Lohner (DD)	$T02^{***} + T09^{***} + S01_{t-1} - 03^{***}$	0.005	0.014	0.65	0.550
Hochwang (DD)	$-T01_{t+1}^{***} - P11_t^{***} + P03_{t+1}^{***}$	0.003	0.015	0.78	2.033
Julier (DD)	$-P06_{t-1} - 08_{t-1}^{***} - T07_t^{***} + P06_t - 08_t^{***}$	0.002	0.006	0.61	3.184
Justistal (DD)	$-T10_{t-1} - 12_t + T01_{t+1}^{**} - P06_{t-1}^{***}$	0.000	0.000	1.00	1.376
Kärpf (DD)	$-T03_{t+1} + P01_{t-1} - 03_t^{***} - S04_t^{***}$	0.004	0.028	0.85	0.182
Macun (DD)	$-P05_{t-1} - 07_t^{***} - S01_{t-1} - 03_t^{***} - NAO_{t+1}^{***}$	0.001	0.009	0.92	1.473
Mont Pleureur (DD)	$P11_{t-1}^{**} - P07_t^{**} - P11_t^{***}$	0.012	0.016	0.24	0.090
Oberalp-Tödi (DD)	$T07_{t-1}^{**} - T09_{t-1}^{***} + P06_{t-1}^{***}$	0.007	0.015	0.53	0.128
Olden (DI)	$T05_{t-1}^{***} - P06_{t-1} - 08_{t-1}^{***} + P08_t^{***}$	0.000	0.021	1.00	0.194
Rothorn (DI)	$P05_{t-1}^{***} + P06_{t-1} - 08_{t-1}^{***} - S04_t^{***}$	0.012	0.030	0.59	2.552
Schwarzmoöch (DI)	$P03_{t+1} + S03_{t+1}^{**} + NAO_t^{***}$	0.002	0.007	0.68	0.222
SNP (DD)	$-T05_t^{***} + T04_{t+1}^{***} + P04_t^{***}$	0.008	0.014	0.42	0.071
Terza-Sesvenna (DD)	$-P07_{t-1} - 09_{t-1}^{***} + P07_t - 09_t^{***} - S12_{t-1} - 02_{t+1}^{***}$	0.004	0.023	0.82	1.349
Umbrail (DD)	$T07_{t-1} - 09_{t-1}^{***} + P05_{t-1}^{***} + P06_t^{***}$	0.006	0.044	0.85	0.865
Wetterhorn1 (DI)	$P03_{t-1} - P03_{t+1}^{*} - S04_{t+1}^{***}$	0.000	0.002	1.00	0.039

DD and DI indicates whether the fluctuations in population size at a given locality were modelled using a density dependent [Eqn (1)] or a density independent model [Eqn (5)], respectively. T indicates temperature, P is precipitation and S is snow cover. The months are numbered from January (1) to December (12). Subscripts indicates the year before census ($t-1$), the year of census (t) and the year after census ($t+1$) respectively.

Significant effects of covariates are indicated by $*$ ($\alpha < 0.05$), $**$ ($\alpha < 0.01$) and $***$ ($\alpha < 0.001$). σ_e^2 is the environmental variance in population growth rates and σ_{res}^2 is the residual variance in growth rates estimated by fitting the selected models [Eqn (11)]. p is the fraction of σ_e^2 explained by the covariates [Eqn (12)] in the selected models. $\Delta AICc$ is the difference in the AICc-value between the second best and the best model.

autumn in year t , r is the specific population growth rate, and σ_e^2 and σ_d^2 are the environmental and demographic variance, respectively. The first-order approximation of the mean and variance in $\Delta X = \ln N_{t+1} - \ln(N_t - H_t)$ is then

$$E(\Delta X|N_t, H_t) = r - \frac{\sigma_e^2}{2} - \frac{\sigma_d^2}{2(N_t - H_t)} \quad (3)$$

and

$$\text{var}(\Delta X|N_t, H_t) = \sigma_e^2 + \sigma_d^2/(N_t - H_t). \quad (4)$$

In populations for which the regression of annual relative changes in log population size $\ln[N_{t+1}/(N_t - H_t)]$ on $(N_t - H_t)$ was significant, we used a density dependent model. Earlier analyses of the population dynamics of ibex (Sæther *et al.*, 2002) using the θ -logistic model (Lande *et al.*, 2003) shows that the logistic model of density regulation (May, 1981) could be a reasonable

approximation to the density-dependent component of the population dynamics of the ibex. Thus, in those cases in which density regulation was present we fitted the logistic model of density regulation. Writing N_t for the population size at a given location, the dynamics are modelled by

$$E(\Delta N|N_t, H_t) = r_t(N_t, H_t) - \beta(N_t - H_t)^2, \quad (5)$$

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

$$\text{var}(r_t) = \sigma_e^2 + \sigma_d^2/(N_t - H_t). \quad (6)$$

For small and moderate population fluctuations a simple first-order approximation (Lande *et al.*, 2003)

gives the model

$$E(\Delta X|N_t, H_t) = \bar{r} - \frac{\sigma_e^2}{2} - \frac{\sigma_d^2}{2(N_t - H_t)} - \beta(N_t - H_t) \quad (7)$$

and

$$\text{var}(\Delta X|N_t, H_t) = \sigma_e^2 + \sigma_d^2/(N_t - H_t). \quad (8)$$

Setting $\ln N_t = X_t$, both models can be rewritten on the general form

$$X_{t+1} = E(X_{t+1}|N_t, H_t) + U_d \sigma_d / \sqrt{N_t - H_t} + U_e \sigma_e, \quad (9)$$

where U_d and U_e are independent variables with zero mean and unit variance and no temporal autocorrelation. Equation (9) can now be used to examine how different environmental variables affect fluctuations in population size. By introducing a climate variable y as a random effect (Sæther *et al.*, 2004b; Engen *et al.*, 2005) we can write

$$U_e \sigma_e = \sum \alpha_i y_{i,t} + U \sigma_{res}, \quad (10)$$

where α_i is the regression coefficient for the effects of climate variable i varying with time t , U is a standardized variable and σ_{res}^2 is the component of the environmental variance that can not be explained by fluctuations in the covariates. This leads to the relation

$$\sigma_e^2 = \text{var}(\sum \alpha_i y_{i,t}) + \sigma_{res}^2, \quad (11)$$

where the covariates explain a fraction

$$p = \text{var}(\sum \alpha_i y_{i,t}) / [\text{var}(\sum \alpha_i y_{i,t}) + \sigma_{res}^2] \quad (12)$$

of the total environmental variance.

Estimation of parameters

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

$$\ln L = \sum \ln f[X_{t+1}; m(N_t, H_t, Y_t), v(N_t)], \quad (13)$$

where Y_t denotes the vector of covariates, $v(N_t) = \sigma^2 + \sigma_d^2/(N_t - H_t)$, and the mean $m(N_t, H_t, Y_t)$ is the appropriate modification of Eqns (3) and (7). The sum in Eqn (13) is taken over those years for which the population size in the previous year is known. Then, assuming a known demographic variance of $\hat{\sigma}_d^2 = 0.267$ (Sæther *et al.*, 2007c), all other unknown parameters were estimated by numerical maximization of the log likelihood (see Engen *et al.*, 2005 for more detailed procedures), and uncertainties were evaluated by parametric bootstrapping (Efron & Tibshirani, 1993; Lillegård *et al.*, 2005) involving simulating the time

series using the initial value of the data and the estimated parameters.

Spatial synchrony. Following Engen *et al.* (2005), the analyses of spatial synchrony in the population dynamics were based on studying the residuals obtained by fitting the population models [Eqns (3), (7), (13)] to time series observations in location z ,

$$R_{t+1}(z) = X_{t+1}(z) - \hat{E}[X_{t+1}(z)|N_t(z), H_t(z), Y_t] \\ \approx \sigma(z)U(z) + \sigma_d(z)U_d(z)/\sqrt{N_t(z) - H_t(z)}, \quad (14)$$

where \hat{E} denotes the estimated expected value. We used the normal approximation and chose a parametric form for the spatial autocorrelation of the U

$$\rho(z) = \text{corr}[U(w), U(w+z)] \\ = \rho_\infty + (\rho_0 - \rho_\infty)h(z), \quad (15)$$

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 (for further details, see Engen *et al.*, 2005). Simulation studies have shown that this procedure gives robust estimators for the spatial synchrony of population fluctuations (Lillegård *et al.*, 2005).

The significance of a change in the estimates of parameters describing spatial synchrony (ρ_0 , ρ_∞ and l) due to inclusion of covariates was evaluated by examining whether 0 was between the appropriate lower and upper quantiles of the distribution for the differences between the two bootstrap distributions (Efron & Tibshirani, 1993).

Climate data

Monthly data on precipitation, snow and temperature from several weather stations throughout Switzerland were obtained from the Swiss Meteorological Institute (MeteoSwiss). We used monthly and 3-monthly averages in the analyses. As effects of fluctuations in weather could be lagged due to an influence on body condition of females (e.g. Solberg *et al.*, 1999), we included weather during May year $t-1$ through April year t in addition to weather during May year t through April year $t+1$.

In addition we obtained the NAO Index from <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>. This index is the winter (December–March) index of the North Atlantic Oscillation (NAO) based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur, Reykjavik, Iceland. The North Atlantic Oscillation is a regional climate phenomenon

that refers to variation in sea level pressure differences between the Arctic and sub-tropical Atlantic (Hurrell *et al.*, 2003), and has been shown to be correlated annual changes in the population size of many species (Mysterud *et al.*, 2001b; Stenseth *et al.*, 2003; Hallett *et al.*, 2004). We included NAO in year t (covering the period from December year $t-1$ through March year t) and NAO in year $t+1$ (covering the period from December year t through March year $t+1$).

As the relative contributions of winter and summer conditions are of interest, we divided the climatic variables into summer variables (the period from May through October) and winter variables (the period from November through April). NAO was regarded as a winter variable. The 3-months averages were categorized based on the majority of months belonging to either summer or winter period.

Model selection

We used information-theoretic approaches (Burnham & Anderson, 2002) to select the most parsimonious model in each population. We used the corrected AIC (AICc) in which there is a penalty equation for low sample size compared with the number of parameters included in the model (Burnham & Anderson, 2002).

Results

In 10 populations (Table 1) there were no significant negative relationship between relative changes in populations size $\ln[N_{t+1}/(N_t-H_t)]$ and (N_t-H_t) , so the dynamics of these populations were modelled using a model without density regulation [Eqn (1)].

The mean of the estimated environmental variance in populations (Table 1) was $\hat{\sigma}_e^2 = 0.017 \pm 0.014$ (mean \pm SD) with maximum $\hat{\sigma}_e^2 = 0.058$ in Calanda. There was no significant difference ($t = 0.675$, $df = 25$, $P > 0.1$) in $\hat{\sigma}_e^2$ among populations with (mean = 0.018) and without (mean = 0.014) density-dependent dynamics (Table 1).

The climate variable that on average explained the largest proportion of the environmental variance in the population fluctuations was snow depth during April year $t+1$ (Fig. 1, $\hat{\rho} = 0.079$). In 19 of the populations the population growth rate r decreased with increasing snow depth (significant at $\alpha < 0.05$ in Albris, Alpstein, Bire Oeschinen, Gastern, Kärpf and SNP), whereas in seven of the populations there was a positive (significant in Flüela and Jüststal) relationship. A similar negative effect of snow depth was also found during November in year t ($\hat{\rho} = 0.056$) in 17 populations (significant in Albris and Calanda). The population growth of 20 population was negatively related to precipitation

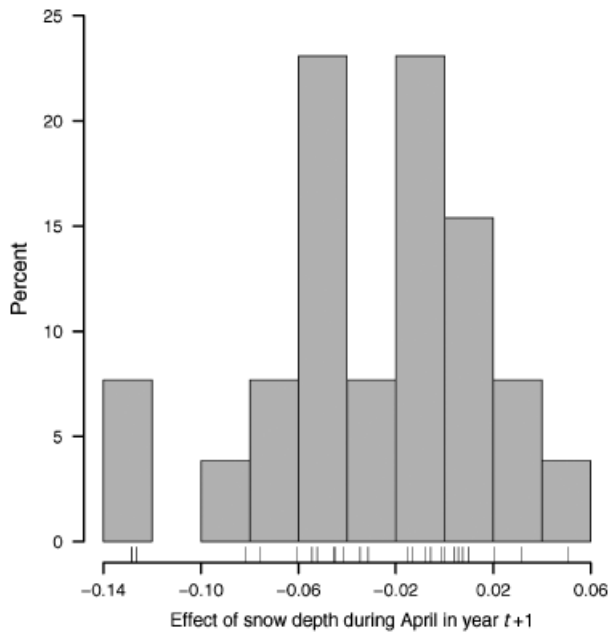


Fig. 1 Distribution of the estimated effect of snow depth during April in year $t+1$ in the 26 populations on changes in the size of 26 Swiss ibex populations.

during the period from November in year t to January in year $t+1$ ($\hat{\rho} = 0.056$) (significant in Albris, Bire Oeschinen, Mont Pleureur and Schwarzmoöch). Thus, the three climatic variables that explained the largest average proportion of the environmental variance were all variables that described environmental conditions during winter in year $t+1$. This suggests a climate-induced influence on juvenile survival. In addition, a positive relationship between temperature during the period from February to April in year t ($\hat{\rho} = 0.045$) and the population growth rates in 16 populations (significant in Flüela, Oberalp-Tödi and Terza-Sesvenna) suggest that winter conditions affecting reproduction or reproductive performance the following breeding season may contribute to fluctuations in the size of ibex populations.

Our next step was to allow a range of one to three covariates to enter the model and perform model selection according to the AICc-criterion (Table 1). In all populations, except for the population in Blatten, the most parsimonious model included three covariates. Generally, the models explained a large fraction of the environmental variance (Table 1). In some populations the best model had quite weak support as other competing models had very similar AICc values (Table 1). However, the models with very similar AICc values generally included two of the covariates in the best model, in addition to a third covariate that was very similar (e.g. precipitation in the period June–August instead of precipitation in July) to the third covariate in

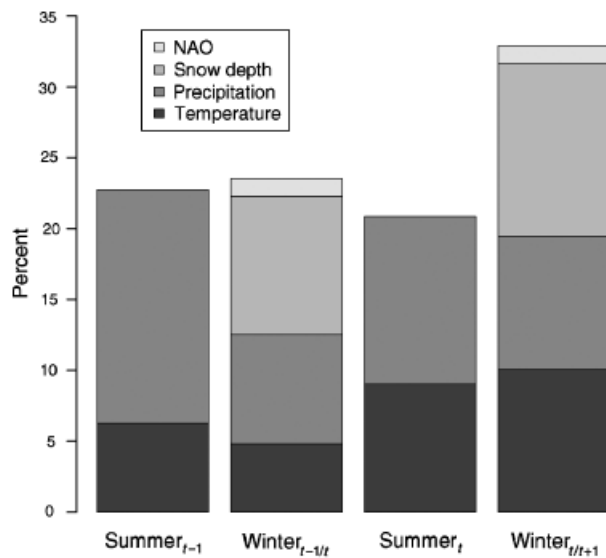


Fig. 2 Frequency of inclusion of climate variables at different time of the year in the most parsimonious models that explained the local dynamics of 26 ibex populations. For each population, models with a difference in AICc-value < 2 were included. The number of occurrences of a covariate in the included models were counted and weighted by the number of models in each population, giving equal weight of each population in the overall calculation of the relative contributions of the different time periods.

the best model. Summer year $t-1$, winter year $t-1/t$ and summer year t , which are all variables likely to affect female fecundity and early juvenile survival, were present in approximately 23%, 23% and 21% of the models, respectively. Climate variables during the winter period in year $t+1$ were present in approximately 33% of the models (Fig. 2), again indicating effects of winter weather on juvenile and possibly adult survival during the nonbreeding season. Precipitation was more important during summer than during winter as precipitation was present in 16% and 12% of the models during summer in year $t-1$ and year t , respectively, whereas precipitation was present in 8% and 9% of the models during winter in year $t-1/t$ and year $t/t+1$, respectively. Temperature was present in 6%, 5%, 9% and 10% of the models in summer year $t-1$, winter year $t-1/t$, summer year t and winter year $t/t+1$, respectively. This indicates that temperature acts more strongly as a direct effect than as a delayed effect on ibex population fluctuations. Finally, snow in winter year $t-1/t$ and year $t/t+1$ were present in 10% and 12% of models, respectively. In contrast, NAO was only included in 1% of the models and hence was a poor predictor of fluctuations in the size of ibex populations.

The spatial synchrony in the population dynamics of Swiss ibex was small after accounting for the effects of

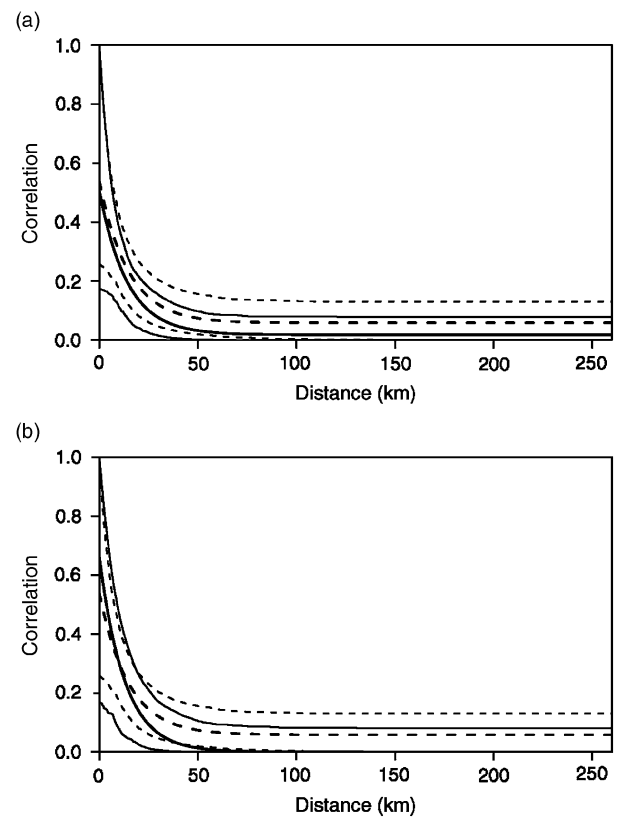


Fig. 3 The estimated correlation functions based on fitting local models with (a) snow cover during April year $t+1$ and (b) covariates selected by the AICc criterion (Table 1). The estimated correlation function obtained by fitting local models without including any covariates is indicated by stippled lines. The maximum likelihood estimates are indicated with thick lines and 2.5% and 97.5% quantiles are indicated by thinner lines.

density dependence and demographic stochasticity (Fig. 3). The spatial scaling was significant larger than 0 but was only $\hat{l} = 14.7$ km [CI: 4.6, 44.5]. There was no significant common environmental noise in the population fluctuations $\hat{\rho}_\infty = 0.058$ [0, 0.130] (Fig. 3). Even at short distances the correlation in residual population size was rather small ($\hat{\rho}_0 = 0.537$ [0.258, 1]). The spatial correlation function of the residuals obtained after including single climate variables or variables selected by the AICc criterion (Table 1) in the local dynamics had only small effects on the estimated spatial correlation function.

Discussion

We have demonstrated that climate, especially during late winter, is able to explain a significant proportion of the annual changes in the size of Swiss ibex populations (Table 1, Figs 1 and 2). However, there was interpopula-

tion variation even over short distance in the effects of the same climate variable on the local dynamics (Table 1, Fig. 1). As a consequence, spatial synchrony in the population fluctuations was small (Fig. 3).

The environmental stochasticity in the population dynamics of ibex was small ($\sigma_e^2 < 0.058$ in all populations). In fact, our estimates of the environmental variance are slightly too large because of the effects of sampling error. We have previously shown by using MCMC techniques (Clark & Bjørnstad, 2004) that the median coefficient of variation in population estimates due to sampling error is 5.1% (Sæther *et al.*, 2007c), and based on the relative magnitude of sampling variance and environmental variance found in that study we could expect that on average approximately 40% of the estimated environmental variance in this study is due to sampling variance rather than environmental variance. Thus, estimated environmental stochasticity in ibex population dynamics are similar or smaller than the levels found in many long-lived vertebrates (Sæther *et al.*, 2004b, 2005, 2007b; Lande *et al.*, 2006; Engen *et al.*, 2007). Accordingly, the ibex have high rates of adult survival (Toigo *et al.*, 1997, 2002, 2007; Loison *et al.*, 2002) and has the life history characteristics of a capital breeder (Festa-Bianchet *et al.*, 1998; Andersen *et al.*, 2000; Toigo *et al.*, 2002). This implies that it relies heavily on body reserves for raising offspring and trading off allocation in reproduction in favour of adult survival (Festa-Bianchet & Jorgenson, 1998; Gaillard & Yoccoz, 2003). Fitness components whose variation has greatest impact on the population growth rate have been suggested to be buffered against temporal fluctuations in the environment (Sæther & Bakke, 2000; Gaillard & Yoccoz, 2003; Sæther *et al.*, 2004a). The small estimates of environmental stochasticity in this study show that such a life history strategy can also translated into small temporal variability in population fluctuations. Furthermore, the estimated environmental variance did not differ between the populations that were categorized as density dependent vs. density independent (see 'Results'). This suggests that the ibex is well adapted to buffer climate-induced environmental variability (Toigo *et al.*, 2007).

Determining the critical periods affecting the population dynamics is of large interest as this could help gaining a better understanding of the relative influences of recruitment and adult survival (Sæther, 1997; Gaillard *et al.*, 1998, 2000) and to what extent the population dynamics are affected by environmental conditions during the breeding season (the 'tap-hypothesis') vs. the nonbreeding season (the 'tub-hypothesis'). In this study, we divided the covariates into four periods, two periods that is expected to affect female fecundity (summer in year $t-1$ and winter year $t-1/t$), one period expected to be closely linked to breeding conditions and early juvenile survival (summer year t) and finally a period linked to both juvenile and adult

survival (winter year $t/t+1$). The most important period of environmental influences affecting the population dynamics were winter year $t/t+1$. As the temporal variation in prime age adult survival of ibex seems small (Toigo *et al.*, 1997; Loison *et al.*, 2002; Sæther *et al.*, 2004b), the major effect of winter climate is likely to be on juvenile survival, thus supporting the 'tub-hypothesis'. However, climate effects during the summer was also important for the ibex population dynamics, and is likely to affect neonatal mortality or the rate of body growth of young females that in turn can affect the proportion of younger females giving birth the following year (Gaillard *et al.*, 2000; Toigo *et al.*, 2002). Thus, climate-induced effects on the recruitment, supporting the 'tap-hypothesis', could also be important in many ibex populations (Jacobson *et al.*, 2004).

A general pattern recorded in the present study was that the most important climate covariates differed among populations (Table 1). For example, there were interpopulation differences even in the direction of the effect of the most important covariate, snow depth in April in year $t+1$ (Fig. 1). Previous analyses have consistently suggested negative effects of snow depth on population growth rates of ibex (Sæther *et al.*, 2002; Jacobson *et al.*, 2004). However, spatial heterogeneity in the effects of the same climatic variable has also been found in studies of other vertebrate species (Sæther, 1985, 2003, 2004b, 2006; Mysterud *et al.*, 2000, 2001b; Both *et al.*, 2004; Crozier & Zabel, 2006). Although the geographical distances among many of the populations in the present study were small, there are probably large differences among populations in terms of habitat characteristics. For instance, small differences in temperature could lead to very different responses in snow cover in landscapes that are as topographical variable as Switzerland. For example, a relatively warm winter could cause rain in some areas and heavy snowfall in other areas, leading to very different environmental conditions between areas that are geographically close (Mysterud *et al.*, 2000). Accordingly, Mysterud *et al.* (2001a) showed that access to a variable topography, measured as different altitude levels and aspects, was positively related to body weight of red deer in the western part of southern Norway. Increasing snow cover could lead to a longer snow melting season causing prolonged access to high-quality forage (Post & Stenseth, 1999; Mysterud *et al.*, 2001b; Petteorelli *et al.*, 2005). If positive effects of access to high quality forage are larger than negative effects of increased snow cover on survival and body condition this could explain why some populations of ibex show delayed positive responses to snow cover (Table 1). However, the direct effect of snow cover (in year $t+1$) could also simply be caused by an influence of remaining snow cover in spring on the ibex counts in some areas.

It has been suggested that it could be difficult to capture the climatic conditions affecting the population dynamics using local climatic measures such as monthly averages of temperature, rainfall and snow (Stenseth *et al.*, 2002, 2003; Hallett *et al.*, 2004), and the NAO may therefore be a better predictor of environmental conditions (Hallett *et al.*, 2004). However, in this study NAO was only selected as a covariate in the populations of Fergen-Seetal, Macun and Schwarzmöch, indicating that local climatic variables were better in describing the environmental conditions than NAO (Table 1). Finally, the effects of climate variables on the population dynamics could also be dependent on how far the population size were from the carrying capacity K (Gaillard *et al.*, 2000; Toigo *et al.*, 2002; Coulson *et al.*, 2004). However, dividing the populations into density-dependent and density-independent dynamics (Table 1) resulted in largely identical patterns of the relative influences of the different time periods.

The growth rates of the ibex populations showed very little evidence of synchronous fluctuations except at very short distances (Fig. 3). This can be explained by the effects of observation errors in the population estimates, which will result in underestimation of the degree of spatial synchrony in the population fluctuations (Lande *et al.*, 1999; Engen *et al.*, 2005). In fact, our estimate of the population correlation at short distances ρ_0 was significantly <1 . An analysis of the data included in this study using MCMC methods allowing for estimation of observation errors (Calder *et al.*, 2003; Clark & Bjørnstad, 2004; Clark, 2007), indicates that the observation errors are small (Sæther *et al.*, 2007c). Simulations indicate that MCMC-methods are able to separate environmental stochasticity from observation error even for short time series and large observation error (Lillegård *et al.*, in press) However, ibex counts in Belledone (France) was found to be quite uncertain (Gaillard *et al.*, 2003). An alternative explanation is that this small population synchrony is a real characteristic of ibex population dynamics, consistent with our findings that the explanative power of the same environmental variable differed even among populations that were located quite close to each other (Table 1, Fig. 1). Both theoretical (Engen & Sæther, 2005) and empirical (Sæther *et al.*, 2007a) analyses have shown that the contributions of covariates to spatial synchrony depends strongly on spatial heterogeneity in the effects of the covariates. Furthermore, the small residual variation in the noise will also be affected by age-structure fluctuations (Lande *et al.*, 2006; Engen *et al.*, 2007) that will further reduce any spatial autocorrelation in the noise term and desynchronize the fluctuations in population size at different localities.

Projecting responses of climatic conditions that are not yet observed in historical data is difficult (Stenseth *et al.*, 2002). A pattern of spatial variation in effects of similar climatic conditions suggests that predictions of the influences of the expected climate change (Easterling *et al.*, 2000; Meehl *et al.*, 2000) at larger spatial scales need to account for local differences in responses to fluctuations in climate. Thus, a proper understanding of the ecological consequences of environmental changes that occur simultaneously over larger areas will require information about the spatial scaling of their effects on the local population dynamics. Unfortunately, the mechanisms that causes varying effects of fluctuations in climate are, except for in a few cases (Mysterud *et al.*, 2000), poorly understood. Variations in responses to climatic perturbations could for example reflect diverse habitats, genetic differences, differences in trophic interactions or different life history strategies. Thus, conserving populations with different responses to climate could be an important management objective (Hilborn *et al.*, 2003; Crozier & Zabel, 2006) given very uncertain consequences of climate change for many species. However, the low level of environmental variance, different responses to fluctuations in climate and the short spatial scaling of the environmental noise in the population fluctuations could indicate that the ibex populations will respond differently to changes in climate and simultaneous extinction of populations over larger areas seems unlikely given at least moderate changes in climate.

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