

## STOCHASTIC POPULATION DYNAMICS OF AN INTRODUCED SWISS POPULATION OF THE IBEX

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**Abstract.** Using a long-term data set on the fluctuations of a reintroduced Swiss population of ibex we estimated the parameters in a stochastic population model with theta-logistic density regulation, and how the environmental stochasticity was related to different climate variables. Our aim was to examine quantitatively the relative effects of variation in parameters describing the expected dynamics and the environmental stochasticity as well as the uncertainties in them for the development of reliable population projections. The specific growth rate  $r_1$  was 0.14. Density regulation mainly happened close to the carrying capacity  $K$ , indicating that the commonly used assumption in population ecology of loglinear density regulation is not always valid. Annual variation in the point estimates of the environmental stochasticity was correlated with winter climate. Uncertainties in parameter estimates were high, especially in the estimates of density regulation and  $r_1$ . In order to examine the dynamical consequences of the estimates as well as the uncertainties in them, we constructed Population Prediction Intervals (PPI). A PPI is the stochastic interval that includes the unknown population size with probability  $(1 - \alpha)$ . Analyses of factors affecting the width of the PPI showed that the form of the density regulation as well as uncertainties in model parameters should be estimated when making projections of future fluctuations of introduced populations.

**Key words:** *Capra ibex; climate variation; density regulation; environmental stochasticity; ibex; stochastic population dynamics; Switzerland.*

### 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, 2002a, Coulson et al. 2000, 2001). In temperate areas, high population sizes during winter result in increased mortality or reduction in fecundity rates. Similar demographic effects can also happen from climatic variation. Several studies (see review in Sæther 1997) have documented strong effects of climatic variability from both summer and winter. Summer rainfall and temperature affects the quantity and/or quality of the food plants (Post and Stenseth 1999). This, in turn, is important for body growth of calves, later affecting the age of maturity (Sæther and Haagenrud 1983). Variability in climate during winter may also have a large impact on ungulate population dynamics (Sæther et al. 1996, Post and Stenseth 1998, Mysterud et al. 2000, 2001), and is likely to be particularly important for arctic and alpine species (Aanes et al. 2000, Gonzales and Crampe 2001, Solberg et al. 2001).

Thus the mechanisms for how variation in environmental conditions and population density affect the demography of ungulates are reasonably well understood. In this paper we will examine quantitatively the relative impact of density-dependent and stochastic factors on fluctuations in population size. Traditionally, two approaches have been used to examine this question. One approach has been to build complex age-structured models (Caswell 2001, Lande et al. 2002), often including both density dependence as well as stochasticity in the different demographic variables. A problem with such models is that they require reliable estimates of a large number of parameters, which often makes it difficult to obtain robust conclusions from the analyses. Another approach has been to fit autoregressive models to the data (Royama 1992), and use ecological models to interpret the results from the statistical analysis (Stenseth et al. 1998, 1999). A common assumption in these analyses is that the density dependence is assumed to be linear at the log scale (Royama 1992, Stenseth et al. 1996). Here we examine the validity of the assumption by estimating the parameters in the theta-logistic model of density regulation (Gilpin and Ayala 1973, Gilpin et al. 1976, Sæther et al. 2002, Lande

et al. 2003). This enables us to estimate the form of density regulation (Sæther et al. 2000). Theoretical analyses have shown that only small variations in the density regulation function may strongly alter the population dynamics (May 1976). Thus, understanding of the factors affecting the fluctuations of a population requires a proper characterization of how the population growth rate varies with population size.

Management decisions often require population projections. For instance, calculating probability of extinction (i.e., when the population size of a sexually reproducing species reaches  $N = 1$  within a given period) is the main focus for population viability analysis (Beissinger and Westphal 1998). Such predictions of future population fluctuations are often difficult for two reasons. (1) Stochastic factors may strongly influence the population dynamics. Demographic stochasticity (random independent events of individual birth and death) and environmental stochasticity (random variation in birth and death rates affecting all individuals in a group in a similar way) may have a profound impact on the mean population size (May 1973, Turelli 1977, Leigh 1981, Ives and Vincent 1998, Lande 1998, Lande et al. 2003). (2) Short time series make estimates of essential population parameters uncertain or even biased (Taylor 1995, Sæther et al. 1998, 2000, Sæther and Engen 2002). Thus the effects of stochastic factors as well as uncertainties in population estimates are important to estimate and model when developing reliable population projections.

A large number of studies of ungulates have documented a strong effect on several demographic variables of variation in climate conditions during summer (reviews in Sæther 1997, Solberg et al. 1999, and Gaillard et al. 2000) as well as during winter (Post and Stenseth 1999, Aanes et al. 2000, 2002a, Solberg et al. 2001). However, the quantitative effects on the population dynamics of this variation have been more difficult to estimate, mainly due to difficulties in separating out the stochastic variation from the expected dynamics. Here we will use climate variables in different seasons as covariates in the environmental component (Engen et al. 1998) and estimate its influence by jointly estimating the unknown coefficients and the strength of density dependence from time series data.

The concept of Population Prediction Interval (PPI), introduced into population viability analysis by Dennis et al. (1991), may be useful when deriving predictions for future population fluctuations. Following Sæther et al. (2000) and Engen and Sæther (2000), a PPI is defined as the stochastic interval that includes the unknown population size with probability  $(1 - \alpha)$ , where  $\alpha$  is the probability that the variable we want to predict is not contained in the stochastic interval. This approach enables us to examine how stochastic effects on the dynamics as well as uncertainties in parameter estimates affect future population sizes. Thus we predict whether a given interval of population sizes will

be reached in a predetermined time interval. For large stochastic effects on the dynamics or uncertain population estimates, the PPI soon becomes large (Sæther et al. 2000, Engen et al. 2001, Sæther and Engen 2002).

The ibex *Capra ibex* went extinct in Switzerland as in most other parts of the Alps at the beginning of the 19th century (Tschudi 1890). In 1920 ibex was reintroduced into the Swiss National Park. During the 20th century this introduction led to the establishment of a viable population. Such successful releases of individuals into areas where a species was previously extirpated or has been strongly reduced in numbers often occur in ungulates (Saltz and Rubenstein 1995, Wolf et al. 1996, 1998, Spalton et al. 1999, Komers and Curman 2000). In addition to being an important conservation tool, such reintroductions provide an excellent opportunity to examine ecological processes that are often difficult to record in more natural systems (Sarrazin and Barbault 1996).

Here we will use the fluctuations in the size of one population of ibex to examine how well we can predict the future dynamics of an introduced population by estimating the parameters of the theta-logistic model. We will analyze how the environmental stochasticity relates to annual variation in respective summer and winter climate. Finally, we will relate the width of the PPI to uncertainty in the different estimates (e.g.,  $\theta$  and  $r_1$ ) as well as variation in the environmental stochasticity.

#### POPULATION MODEL

We estimate the type of density dependence using the theta-logistic model of Gilpin and Ayala (1973). If we write  $X = \ln N$ , where  $N$  is the population size, and let  $\Delta X = \ln(N + \Delta N) - \ln N$ , we then have

$$E(\Delta X) = r[1 - (N/K)^\theta] \quad (1)$$

where  $E$  represents expected values and  $\theta$  describes the theta-logistic type of density regulation,  $r$  is the specific growth rate when  $N = 0$ , and  $K$  is the carrying capacity (Sæther et al. 2000). Eq. 1 may be written in the form

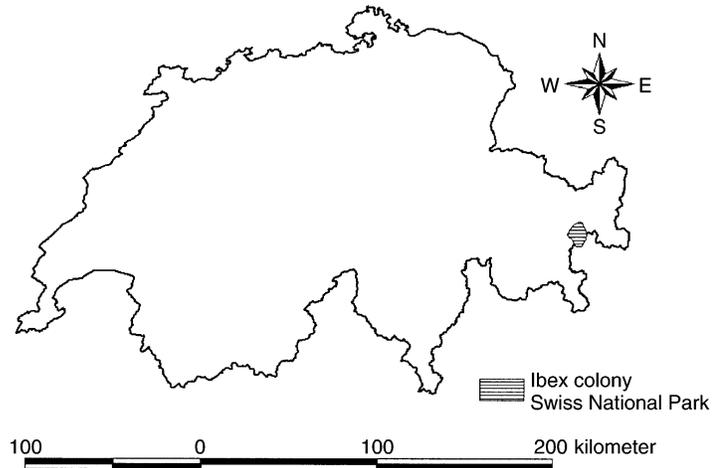
$$E(\Delta X) = r_1 \left[ 1 - \frac{N^\theta - 1}{K^\theta - 1} \right] \quad (2)$$

where  $r_1 = r/(1 - K^{-\theta})$  is the specific growth rate at the smallest possible population size (excluding extinction) at  $N = 1$ . We obtain a stochastic model with the same form of density regulation writing

$$\Delta X = r_1(t) - r_1 \frac{N^\theta - 1}{K^\theta - 1} \quad (3)$$

where  $r_1(t)$  is the specific growth rate in Eq. 2, now fluctuating between years with mean  $r_1$ , the stochastic growth rate, and variance  $\sigma_{r_1}^2$ . When  $\theta$  approaches zero, the limit of Eq. 3 takes the form  $\Delta X = r_1(t) - r_1(\ln N / \ln K) = r_1(t) - (r_1 / \ln K)X$ . This is the well-known loglinear model often used in ecological modeling

FIG. 1. The location of the ibex in the Swiss National Park in southeastern Switzerland.



(Royama 1992). For large  $\theta$  ( $\theta \gg 1$ ), density regulation first starts to act for population sizes closer to  $K$ . When  $\theta = 1$ , we get the logistic model (Sæther et al. 1996).

In general, the strength of the density regulation (Sæther et al. 2000) is minus the slope of the per capita growth rate at the carrying capacity ( $d/dX E(\Delta X|N = K)$ ), that is

$$\gamma = r_1\theta/(1 - K^{-\theta}) = r\theta. \quad (4)$$

Thus, density regulation increases with the growth rate  $r_1$  and  $\theta$ . For a logistic model ( $\theta = 1$ ), the strength of density regulation is equivalent to the specific growth rate,  $\gamma = r_1$ .

STUDY AREAS

The study was conducted in the Swiss National Park located in southeastern Switzerland (Fig. 1), and ranges in altitude from 1500 to 3170 m above sea level. The tree line is at  $\sim 2200$  m and the forest is dominated by Swiss stone-pine *Pinus cembra* and Larch *Larix decidua*. Above tree line alpine grasslands and bare rock dominate. The climate is dry, with  $<1000$  mm precipitation in areas below 2000 m. The growing period above the tree line is  $<80$  d, on average.

A total of 34 animals (12 males and 22 females) were introduced at three different places within the Swiss National Park. Most of the animals (26) were yearlings; 5 and 2 individuals were two and three years old, respectively, whereas 1 female was approximately six years old. The first introductions occurred in 1920 with the release of 7 animals (4 males, 3 females) in the area Piz Terza. During the period from 1923 to 1926 8 animals (2 males and 6 females) were introduced in Val Cluozza. Finally, in 1933 and 1934 19 animals (6 males, 13 females) were released in the Val Tantermozza area (Bächler 1935, Zimmerli 1949, Burckhardt 1961, Nievergelt 1966).

METHODS

Population censuses

The ibex show exclusive use of areas above timberline throughout the year (Nievergelt 1966). In spring,

the ibex follow the onset of new vegetation growth, occurring first in the areas close to the timberline. In April and May both sexes concentrate in these restricted areas (Wiersema 1984), where they can be easily observed.

The population was censused once a year in April or May by experienced rangers who have made these censuses for decades (Fig. 2). The area was divided into blocks that were censused by rangers operating in groups of two to four persons. In order to standardize observation conditions only periods with maximum sightability were used. If animals were observed close to borders between blocks, great emphasis was put on noting details of the individuals (e.g., horn characteristics) and exact location to ensure that no animals were counted twice. Thus the effort invested in avoiding double counts as well as the open landscape suggest that these estimates are relatively precise compared to most other ungulate population counts (see also Filli 2001).

When encountering animals, the sex and age (i.e., calf, yearling born the previous year, or adult) of the individuals were determined. The proportion of calves

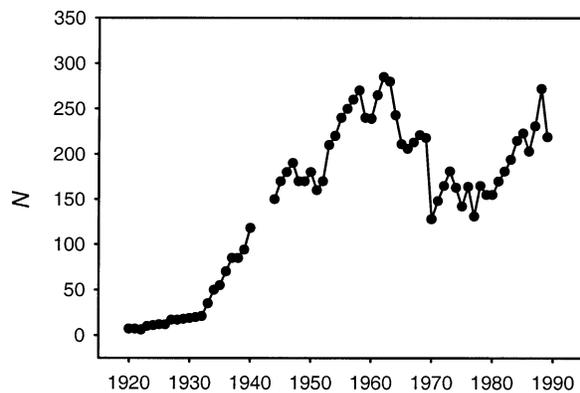


FIG. 2. Annual variation in population size of the ibex population in the Swiss National Park.

in the population was used as an estimate of the fecundity.

*Climate data*

Monthly data on precipitation and temperature were provided by the Swiss Meteorological Institute (MeteoSchweiz) from the Buffalora station, situated ~13 km from the study area.

*Estimates of population parameters*

Because data on individual variation in reproductive success are not available for calculating the demographic variance (see Sæther et al. 1998), we approximate  $\sigma_e^2(N)$  by a constant environmental variance  $\sigma_e^2$  (May 1973, Keiding 1975, Turelli 1977, Leigh 1981, Lande 1993, 1998, Engen et al. 1998). We estimate the parameters in Eq. 1 using only observed time steps of one year by means of least square techniques. Writing  $\alpha = r_1$ ,  $\beta = -r_1/[h(\ln(K); \theta)]$ , and  $v = h(X; \theta)$ , where  $h(\ln K; \theta) = (e^{\theta \ln K} - 1)/\theta$ , we find that  $Z$  is normal with mean  $\alpha + \beta v$  and constant variance, which is a simple linear regression that can be solved for a given  $\theta$ . The population parameters  $r_1$  and  $K$  are then estimated by  $\hat{r}_1 = \hat{\alpha}$  and  $\hat{K} = (1 - \hat{r}_1/\beta)^{1/\theta}$  for  $\theta \neq 0$  and  $e^{-\hat{r}_1/\hat{\beta}}$  for  $\theta = 0$ . The sum of squares  $1/(n - 2) \sum (Z_i - \hat{\alpha}u_i - \hat{\beta}v_i)^2$ , where  $n$  is the number of time steps, is an approximately unbiased estimator for  $\sigma_e^2$ . This estimator  $\hat{\sigma}_e^2(\theta)$  is finally minimized numerically with respect to  $\theta$  to get  $\hat{\theta}$ .

Unfortunately, reliable estimates of  $r_1$  are difficult to obtain and are often also biased (Taylor 1995, Aanes et al. 2002b). We used parametric bootstrapping to estimate the expected error in the estimate of  $r_1$  (Efron and Tibshirani 1993). The biases in the estimate of  $r_1$  were obtained simulating repeated data sets using the obtained estimates ( $\hat{r}_1, \hat{K}, \hat{\sigma}_e^2, \hat{\theta}$ ). Writing  $\bar{r}_1$  for the mean of the estimates of  $r_1$  obtained from the bootstrap replications, the bias is estimated as  $\bar{r}_1 - \hat{r}_1$ . Using this difference to correct the original estimates we obtained the corrected estimate  $2\hat{r}_1 - \bar{r}_1$  (Efron and Tibshirani 1993). Finally, we ran simulations to ensure that this correction did not substantially increase the variance of the estimate. The estimations for the other parameters turned out to be approximately unbiased so those bootstrap replicates were directly used to assess the uncertainty in the estimates.

We analyzed the effects of the climate factors on the population fluctuations by using them as covariates in the environmental component (see Engen et al. 1998). We first analyzed the monthly values of the different climate variables, and then repeated the analyses for the mean of all possible 2-, 3-, and 4-mo periods. A period of 3 mo explained the highest proportion of the variance in the point estimates of the environmental variance.

We also used the prewar data before 1940, assuming no density dependence, to compute the mean growth

TABLE 1. Effects of uncertainty in the form of density regulation on the estimates of the parameters as well as the width of the Population Prediction Interval for the ibex population in the Swiss National Park.

Parameter	$\theta_{25}$	$\theta_{\dagger}$	$\theta_{75}$
$\hat{r}_1^{\ddagger}$	0.15	0.14	0.11
$\hat{K}^{\S}$	210	212	220
$\hat{\sigma}_e^2^{\parallel}$	0.021	0.021	0.021
$q_{0.05}^{\ulcorner}$	118	124	129
$q_{0.50}^{\ulcorner}$	198	200	207
$q_{0.95}^{\ulcorner}$	313	302	295

$\dagger$  The estimate of the density regulation;  $\theta_{25}$  and  $\theta_{75}$  denote the lower and upper quartiles of the bootstrap distribution of  $\theta$ , respectively (see Fig. 3a).

$\ddagger$  The estimate of the specific growth rate when  $N = 1$ .

$\S$  The estimate of the carrying capacity (i.e., when the expected change in population size is zero).

$\parallel$  The estimate of the environmental stochasticity.

$\ulcorner$  The lower boundaries of different population prediction intervals (5%, 50%, and 95%) for a period of 200 yr.

rate  $\mu = \overline{\Delta X}$  and variance  $\sigma^2 = \text{var}(\Delta X)$  (Dennis et al. 1991).

*Population Prediction Interval (PPI)*

The Population Prediction Interval (PPI) was evaluated at each point by stochastic simulations (Efron and Tibshirani 1993), using each bootstrap replicate of the parameter value. The upper  $(1 - \alpha)$  interval at time  $t$  ranges from the corresponding quantile obtained from the simulations. Although this method is not exact, Sæther et al. (2000) and Engen et al. (2001) showed by stochastic simulations of a specified model that the coverage probability is normally very close to the theoretical probabilities.

RESULTS

The estimate of the specific growth rate in the population was  $\hat{r}_1 = 0.14 \pm 0.03$  (mean  $\pm 1$  SD) (Table 1, Fig. 3a). A similar estimate was also found for a Brownian motion model for the prewar period ( $\hat{\mu} = 0.14$ ). Uncertainties in the estimate of  $\theta$  had only a small influence on the estimate of  $r_1$  (Table 1).

The density regulation was estimated to  $\hat{\theta} = 1.54$  (Fig. 3b). This indicates operation of strong density regulation around  $\hat{K} = 212 \pm 22$  (mean  $\pm 1$  SD) (Table 1, Fig. 3c). The distribution of the bootstrap replicates (Fig. 3b) showed, however, large uncertainties in the estimates of  $\theta$  ( $\pm 1$  SD = 1.31). For instance, the difference between the lower and upper quartiles of the bootstrap distribution was 1.52, ranging from 1.29 to 2.81. Even with these large uncertainties,  $\theta = 0$  was located outside the 95% confidence interval, suggesting that the assumption of a loglinear density regulation was not justified for this population. The strength of density regulation at  $K$  was relatively weak ( $\hat{\gamma} = 0.23$ ). In contrast, less uncertainty was found in the estimates of this parameter (Fig. 3e) than in  $\theta$ .

The estimate of the environmental stochasticity was  $\hat{\sigma}_e^2 = 0.021 \pm 0.004$  (mean  $\pm 1$  SD) (Table 1), whereas

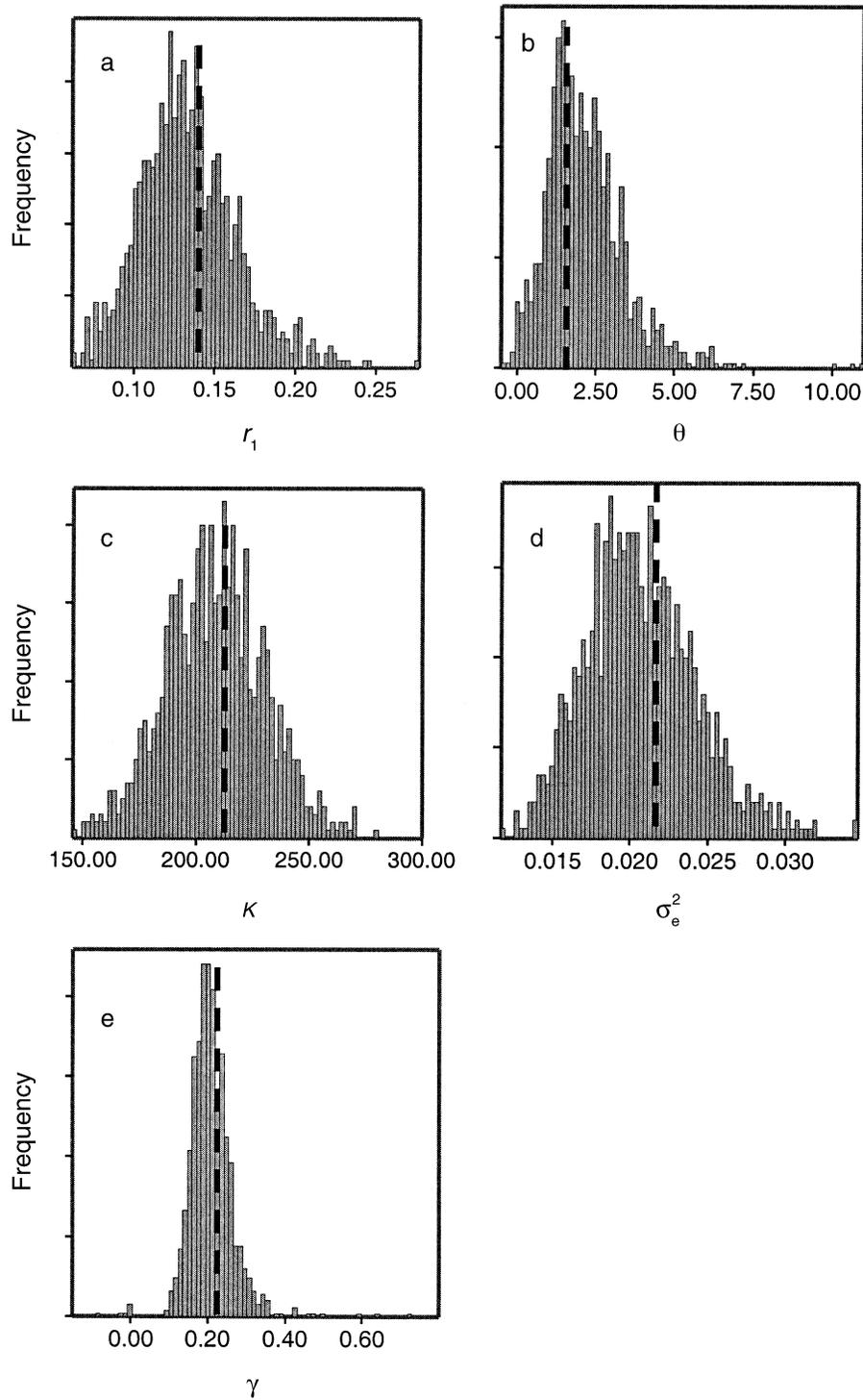


FIG. 3. The distribution of the bootstrap replicates of (a) the specific growth when  $N = 1$ ,  $r_1$ ; (b) the form of the density regulation,  $\theta$ ; (c) the carrying capacity,  $K$ ; (d) the environmental stochasticity,  $\sigma_e^2$ ; and (e) the strength of the density regulation at  $K$ ,  $\gamma$ , of the ibex population in the Swiss National Park.

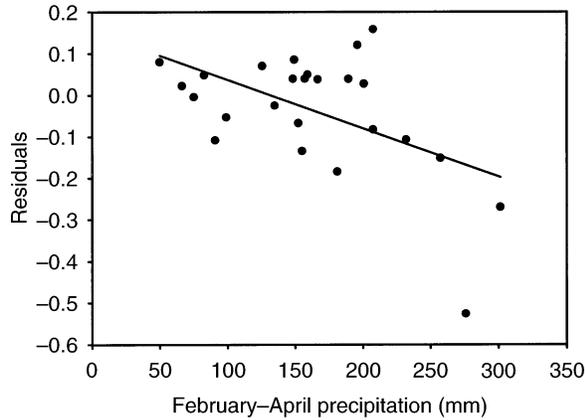


FIG. 4. Annual variation in the residuals from the deterministic model (i.e., the point estimates of the environmental stochasticity,  $\sigma_e^2$ ) of the ibex population in the Swiss National Park in relation to winter (February–April) precipitation. The fitted line is from linear regression.

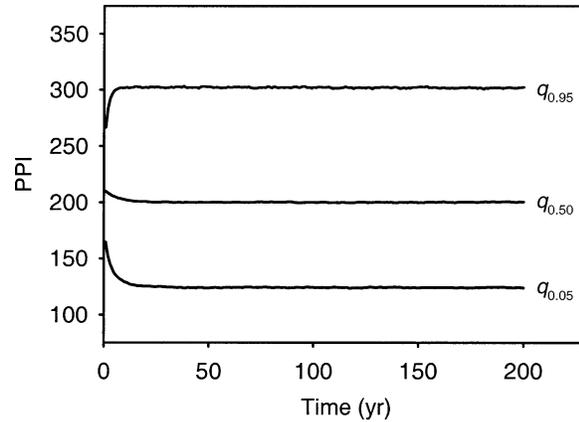


FIG. 5. Population Prediction Intervals (PPI) for the ibex population in the Swiss National Park. The lower boundaries for 5%, 50%, and 95% PPI are represented by  $q_{0.05}$ ,  $q_{0.50}$ , and  $q_{0.95}$ , respectively. For further explanation, see *Methods: Population Prediction Interval (PPI)*.

the estimate of  $\sigma^2$  in the Brownian motion model was somewhat higher ( $\hat{\sigma}^2 = 0.031$ ). A large fraction (83.5%) of the bootstrap replicates of  $\sigma_e^2$  was located between 0.01 and 0.03 (Fig. 3d). Furthermore, the estimate of  $\sigma_e^2$  was independent of the uncertainty in the density regulation (Table 1).

Annual variation in the point estimates of  $\sigma_e^2$  (i.e., the residuals from the deterministic model) was significantly correlated to the winter climate for only one of the periods used in the analyses (see *Methods: Estimates of population parameters*). The point estimates of the environmental stochasticity decreased with the amount of precipitation during the period from February to April (Fig. 4, correlation coefficient =  $-0.53$ ,  $df = 24$ ,  $P = 0.007$ ).

The width of the Population Prediction Interval (PPI) remained constant after  $\approx 25$  yr (Fig. 5). The width of the 95% PPI interval for  $t = 200$  yr ranged from 122 to 304 individuals (Table 1, Fig. 5). The width of the PPI was strongly influenced by the environmental stochasticity  $\sigma_e^2$  (Table 2) and the uncertainty in the estimates of  $\theta$  (Table 1). Smaller values than  $\hat{\theta}$  will strongly increase the width of the PPI. Furthermore, for a given value of  $\theta$ , uncertainties in  $K$  and  $r_1$  will also affect the PPI (Table 2).

DISCUSSION

The population trajectory presented in Fig. 2 is the result of the reintroduction of a few individuals. In general, the probability of a successful introduction will depend on the number of introduced individuals (Pimm 1991, Wolf et al. 1998, Komers and Curman 2000). The reasons for establishment of a viable population in our study area from a limited number of released animals may be due to the fact that the area contains favorable habitats for the ibex, and that no or very little illegal offtake occurred during the initial

phase of the introduction. Strict regulation of offtake of animals has shown to be a prerequisite for a successful reintroduction of ungulates (Spalton et al. 1999).

Our estimates of the specific growth rate  $r_1$  in the theta-logistic model (Fig. 3a, Table 1) as well as  $\mu$  in the Brownian motion model show a rapid increase at low densities. Theoretical analyses have shown that the specific growth rate strongly influences the risk of extinction (Lande 1993, 1998). Thus the large specific growth rates are probably the major reason that the reintroduction did not fail because of extinction due to the effects of demographic and environmental stochasticity.

Our estimate of the stochastic growth rate,  $r_1$ , lies within the range reported from other introduced sheep populations (Komers and Curman 2000). However, these estimates of the growth rate at low densities will give biased estimates of the corresponding deterministic growth rate, even when assuming no density dependence, because stochastic effects usually are not accounted for. An estimate of the deterministic population growth rate at low densities is  $r_1 + (1/2)\sigma_e^2 + (1/2)\sigma_d^2/N$  (Lande 1998), where  $\sigma_d^2$  is the demographic variance. From the figures presented in Table 1, and assuming  $\sigma_d^2 = 0$ , this gives 0.15 in the Swiss National Park. Thus the long run growth rate will be high in the

TABLE 2. Effects of uncertainty in different parameters on the width of the Population Prediction Interval for the ibex population in the Swiss National Park.

No uncertainty...	$q_{0.05}$	$q_{0.50}$	$q_{0.95}$
in any parameter	132	204	295
in $\hat{r}_1$	124	200	303
in $\hat{K}$	130	204	296
in $\hat{\sigma}_e^2$	123	200	304

Note: For explanation of symbols, see Table 1.

TABLE 3. Estimates of parameters and Population Prediction Interval (PPI) of the ibex population in the Swiss National Park, assuming linear density regulation either at a logarithmic ( $\theta = 0$ ) or at an absolute ( $\theta = 1$ ) scale.

$\theta$	$\hat{r}_1$	$\hat{K}$	$\hat{\sigma}_c^2$	PPI		
				$q_{0.05}$	$q_{0.50}$	$q_{0.95}$
0	0.25	271	0.022	78	247	1138
1	0.15	210	0.021	115	199	326

Note: For explanation of symbols, see Table 1.

initial phase of establishment of this population, even after accounting for environmental stochasticity. However, demographic stochasticity will reduce  $r_1$  at small population sizes (Lande 1998, Engen et al. 2001, Lande et al. 2003) and must therefore be estimated when making predictions about the expected population growth of small populations of the ibex.

The high value of  $\theta$  shows that maximum density regulation occurs around  $K$  (Fig. 3b, Table 1). However, the small value of  $\gamma$  (Fig. 3e), indicating that the strength of density regulation around  $K$  is weak, suggests that the population will not be rapidly knocked down when exceeding  $K$ . We expect that the projections of this population will be characterized by relatively long-term fluctuations around  $K$ . These patterns differ from Soay sheep *Ovis aries*, where strong overcompensatory mortality during winter leads to large annual fluctuations in population size (Grenfell et al. 1992, Clutton-Brock et al. 1997, Coulson et al. 2001). This may be related to the larger litter size of this species, often associated with small values of  $\theta$ , resulting in larger fluctuations above  $K$  (Sæther et al. 2002; Sæther and Engen, *in press*).

In general, time series of fluctuations of vertebrate populations are analyzed by assuming linear density regulation either at an absolute ( $\theta = 1$ ) or logarithmic scale ( $\theta = 0$ ) (see Royama 1992). In our population in the Swiss National Park  $\theta = 0$  was outside the 95% confidence interval for  $\hat{\theta}$  (Fig. 3b). Thus the type of density regulation was different from the one expected from the loglinear model of density regulation that is commonly used in analyzing mammalian population fluctuations (Royama 1992). Assuming such a linear form, density regulation would strongly influence the estimated values of  $r_1$  and  $K$  (Table 3). In contrast,  $\hat{\sigma}_c^2$  was independent of  $\hat{\theta}$  (Table 3). As a consequence, the width of the 90% PPI changed dramatically with the change in value of  $\theta$  (Table 3). Thus, we caution against a priori application of a loglinear model in analysis of vertebrate population dynamics (see also Kendall et al. 1999). Such autoregressive coefficients will also be strongly influenced by life history parameters (Coulson et al. 2001, Lande et al. 2002).

Many demographic studies of ungulate species have demonstrated a strong influence of environmental stochasticity, mainly operating through an effect of climate on the fecundity rate or survival in the youngest

age classes (Sæther 1997). The population dynamical consequences of such variation have however been difficult to assess (Coulson et al. 2000, 2001). The estimated value of  $\sigma_c^2$  in the present study (Fig. 3d, Table 1) is likely to increase the deterministic growth rate at low densities of the ibex population in the Swiss National Park by  $\sim 2\%$ . The higher estimate of the variance in the Brownian motion model is probably due to an effect of demographic variance at smaller population sizes, resulting in  $\hat{\sigma}^2$  to give an overestimate of  $\hat{\sigma}_c^2$  (Engen et al. 2001). A similar small effect on the population growth rate of environmental stochasticity on the growth rate has previously been recorded for red deer *Cervus elaphus* on the island of Rhum (Benton et al. 1995). Such a small environmental variance is probably a general characteristic of long-lived species such as the ibex (Toigo et al. 1997) where the effects of fluctuations in the environment are buffered out over several seasons (Pimm 1991). However,  $\sigma_c^2$  strongly influences the range of variation in population size  $N$  (Table 1, Fig. 5). This illustrates the importance of correctly estimating and modeling the stochastic effects when predicting future population fluctuations (cf., Ives and Vincent 1998).

The width of the PPI remained constant after little more than two decades (Fig. 5). Thus populations are then subject to some sort of regulating factors (Turchin 1995). Our analyses show that winter climate affects the population fluctuations of this population (Fig. 4). This is in accordance with other studies from both arctic (e.g., Aanes et al. 2000, 2002a, Solberg et al. 2001) and alpine (e.g., Gonzales and Crampe 2001) areas showing that the winter may be the main bottleneck for the population growth, and that the limiting effect of adverse winters may be so strong that variation in summer weather plays only a lesser role for the population dynamics than in temperate regions. In ibex such an effect may result from spatial limitation because during winter it is dependent on access to areas with little snow cover. The preferred habitat types are sun-exposed places with no snow (Nievergelt 1966), which during winter and spring mainly are found in south-southwestern expositions with slopes between  $30^\circ$  and  $45^\circ$  (Nievergelt 1966, Hofmann and Nievergelt 1972). With increasing precipitation and snow cover during the last part of the winter, higher competition for access to these habitat types is likely, resulting in reduced population growth. Accordingly, when density increases, the ibex aggregate into larger groups, probably because of limited availability to suitable habitats (Toigo 1999). Thus, such a spatial limitation may also explain the strong density regulation at high densities (Fig. 3b).

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