CLIMATE FORCING AND DENSITY DEPENDENCE IN A MOUNTAIN UNGULATE POPULATION

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Abstract. Population models in ecology are rarely validated by comparing their predictions to long-term observations of changes in population size. We have used a variety of analytical tools to examine a 45-year time series of annual censuses of Alpine ibex (*Capra ibex*) in the Gran Paradiso National Park in northwestern Italy. This ibex population grew from about 3300 to almost 5000 individuals in the 1980s during a decade of anomalously mild winters, and then began to decline in the 1990s. By 1997, the population size had returned to previous levels. Adult survival apparently increased and adult sex ratio may have changed to slightly favor males during the increase in population density. Yearly changes in total population were correlated with seasonal average snow depth and population density over the 39 years for which climate data were available. Our results show that the ibex population size was limited by both density dependence and deep snow. A model based on these factors fit to the first 19 years of data was used to forecast subsequent changes in total population based on initial population size and yearly snow depth. The model was able to predict the increase and subsequent decline in total population size over the final 20 years of the study but failed to reproduce population levels after the eruption. Our results suggest that the 1980s episode of population growth was primarily driven by increased adult survival, rather than increased recruitment.

Key words: climate changes and population fluctuations; density dependence; ibex, Alpine; Italy, Gran Paradiso National Park; model validation; population dynamics; time series, population data.

INTRODUCTION

Species that live in arctic or alpine environments can be particularly sensitive to changes in climate (Post et al. 1999) and may thus face an increased extinction risk (Derocher and Stirling 1995, 1998). It is therefore essential to test the ability of population models not only to explain historic patterns of population fluctuations, but also to predict future changes (Forchhammer et al. 1998*a*), based on climate projections. Reviews of studies based on long-term monitoring of marked individuals in ungulate populations suggest that juveniles are the age class most likely to be affected by both extrinsic and density-dependent processes, while the survival of adult females is generally unaffected by changes in density or in environmental conditions (Gaillard et al. 1998, 2000). Severe winter weather is generally thought to affect juvenile survival by increasing the probability of starvation, through a combination of greater thermoregulatory costs and decreased forage availability because of deep snow (Goodson et al. 1991, Forchhammer et al. 1998*b*, Loison and Langvatn 1998, Portier et al. 1998). A rather

consistent result of ungulate studies is that high population density increases the age of primiparity, so that fewer age classes of females contribute to recruitment (Fowler 1987, Jorgenson et al. 1993, Langvatn et al. 1996, Gaillard et al. 1998, 2000, Swihart et al. 1998). One goal of our research is to determine whether changes in ibex population size were due to variations in recruitment, as might be expected from these previous works, or to changes in adult survival.

The processes that control animal abundance are of fundamental interest to ecologists. Recently, several studies of ungulates have suggested that an interaction of year-to-year changes in weather and density-dependent changes in survival and reproduction may explain changes in population density in environments where large predators are very rare or absent (Langvatn et al. 1996, Sæther 1997, Forchhammer et al. 1998*b*, Post and Stenseth 1999). Other studies suggest that even in the presence of healthy predator populations or human harvests, climate and density may play an important role in ungulate population dynamics (Post and Stenseth 1998, Coulson et al. 2000). Studies of feral sheep populations that show strong density-dependent fluctuations have suggested that changes in climate may synchronize the dynamics of populations on separate islands in the same geographical area (Grenfell et al. 1998). Despite the wealth of information that has ac-

cumulated, however, tests of the predictive power of specific models using time-series data on population size are rare: researchers have mostly used climatic variables to explain historic variation in population size or in specific vital rates (Solberg et al. 1999, Coulson et al. 2000). The scarcity of attempts to predict population changes stems partly from the rarity of studies that have accumulated the many years of demographic data required by this exercise. For example, the ability of population-viability analysis models to predict population dynamics over several years is subject to considerable debate (Brook et al. 2000, Coulson et al. 2001b). Here we take advantage of the unusual opportunity of having a 45-year time series of Alpine ibex (*Capra ibex*) counts to test the ability of a simple model based on snow depth and population density to predict changes in total ibex abundance. We first estimate the independent effects of snowfall and density on year-to-year changes in population size for Alpine ibex in the Gran Paradiso National Park, Italy. Having demonstrated that both of these factors affect the population dynamics, we then develop a simple model incorporating both factors. We assess the long-term predictive power of this model using an out-of-sample prediction test: the model parameters are determined using only the first 19 years of data, then the model predictions for the following 20 years of population change are compared with actual changes in ibex abundance. Numerous techniques have been proposed for statistical detection of density dependence, but these all have potential pitfalls that constrain their usefulness (Pollard et al. 1987, Holyoak 1993, Wolda and Dennis 1993, Dennis and Taper 1994, Fox and Ridsdill-Smith 1995). To compensate for differences in the strengths and weaknesses of these various techniques, in this paper we have used multiple statistical tests for density dependence. In addition, we have shown the generalization of these tests to the detection of population dependence on extrinsic environmental factors such as climatic conditions.

METHODS

Study area and population

The Gran Paradiso National Park (GPNP) was established in 1922 in northwestern Italy (45°25′ N, 7°34′ E), in part to protect the only surviving population of Alpine ibex. The park is bounded on the west by the Parc National de la Vanoise in France. The GPNP is composed entirely of mountainous terrain and is sparsely populated by humans. Alpine pastures, moraines, cliffs, glaciers, and rock account for 59% of its 720-km² area. Ibex use elevations ranging from ~800 m above sea level to beyond the upper limit of vegetation at ~3200 m. There is no hunting of ibex either inside or outside the park in either Italy or France, and human activities in general are severely limited inside the GPNP. Although there have been a few sightings

of both lynx (*Lynx lynx*) and wolf (*Canis lupus*) in recent years, large predators have been absent for most of the past 100 years. There were no reported sightings of wolves during the period of this study, and the first lynx sighting was in 1995. Predation is believed to be a negligible factor in the dynamics of this ibex population, as most ibex die of senescence, starvation, or disease (Bassano et al. 1992). The GPNP has been the source of ibex for many reintroductions in the Alps. Yearly removals for transplants never exceeded 1% of the park's ibex, and were 0–0.5% in most years, and are thus assumed to have had a negligible impact on the population. The only other wild mountain ungulate in the park is the chamois (*Rupicapra rupicapra*).

Adult ibex are highly sexually dimorphic. Males weigh ~95–100 kg, about twice as much as females (Giacometti et al. 1997). Like most sexually dimorphic ungulates, ibex are sexually segregated outside the rut, with males four years of age and older in bachelor groups and females, juveniles, and subadult males in nursery groups (Gross et al. 1995). Females may produce their first kid at two years of age, although age of primiparity may be delayed in high-density populations, as in most other ungulates (Gaillard et al. 2000). Twins are almost never observed in the GPNP, but have been documented in captivity (Stüwe and Grodinsky 1987). Ibex are unique among ungulates studied thus far in that the survival of prime-aged adult males does not appear to be lower than that of adult females. Adults of both sexes up to about 10 years of age have been shown to enjoy 95–99% annual survival (Toïgo et al. 1997).

Data

In this study we attempt to model the variability of the total number of animals counted in the autumn census at GPNP from 1956 to 2000. The GPNP census data and methodological details appear in Appendix A. Daily meteorological observations of minimum and maximum temperature, precipitation, and snow depth were available for most of the study period from two stations within the GPNP. Data for the Serrù station, at an elevation of 2240 m, were available from 1962. Observations at Teleccio Lake, elevation 1866 m, were available from 1959. The daily meteorological observations at these two stations were aggregated into seasonal quantities to provide indicators of each year's climate. We also computed the number of days in each winter when the snowpack was deeper than one of two level values, set at the mean winter snow depth for each station (level 1) and at the mean plus one standard deviation (level 2).

Population models

Our aim in this work is to construct simple models for the changes in total ibex population (the number of animals aggregated across gender and age classes). The variable of canonical interest is the relative change in

total population size. If the number of individuals in the total population is designated by ''n,'' then the relative change is $y = 1/n \; dn/dt = d(\ln n)/dt = dx/dt$, where, following convention, we define x as $\ln n$. For N discrete observations, this becomes

$$y_i = x_{i+1} - x_i = \ln\left(\frac{n_{i+1}}{n_i}\right) \qquad (1)$$

where the index $i = (1, 2, \ldots, N - 1)$. We wish to determine whether y is affected by climate or density (Bulmer 1975, Vickery and Nudds 1984, Pollard et al. 1987, Wolda and Dennis 1993, Dennis and Taper 1994). Several simple models of density dependence have been proposed, and here we only consider two basic formulations. The stochastic Gompertz model takes the form

$$n_{i+1} = n_i \exp(a + b \ln n_i + \sigma\varepsilon_i) \qquad (2)$$

in which ε_i and σ represent the stochastic contribution from noise and unmodeled processes. Taking the natural log of Eq. 2 and recalling the definitions (Eq. 1) we have

$$y_i = a + bx_i + \sigma\varepsilon_i. \qquad (3)$$

In contrast, the stochastic Ricker model assumes an exponential density dependence:

$$n_{i+1} = n_i \exp(a + bn_i + \sigma\varepsilon_i) \qquad (4)$$

$$y_i = a + bn_i + \sigma\varepsilon_i. \qquad (5)$$

In both the Gompertz and Ricker growth models a population is said to be density-dependent if b is significantly different from zero, as would be expected in the presence of competition for limited resources. Populations with no limiting factors may be expected to grow according to the stochastic growth equation,

$$y_i = a + \sigma\varepsilon_i \qquad (6)$$

which describes perturbed exponential growth. In the following sections we explore models that account not only for the effects of density, but also for the effects of climate on the population growth.

Tests for density dependence

Much effort has been devoted to developing statistical methods to detect density dependence in natural mammal populations for which the available time series are limited in duration, corrupted by observational errors, and subject to external influences. We chose three representative methods to detect density dependence. We test whether the null hypothesis that the b parameter of Eqs. 3 or 5 is zero against a two-sided alternative. The observed value of b is examined to determine how likely it is that it may have been generated by a stochastic process represented by the null model (Eq. 6). The probability distribution function (PDF) of the test statistic under the null hypothesis is estimated by resampling methods such as the parametric bootstrap, jackknife, and random shuffle.

Bulmer's first and second tests (Bulmer 1975), which assume a Gompertz growth model, attempt to detect excessive correlation between y and x. The two test statistics, R and R^*, are measures of this correlation, and their associated confidence intervals are given by functional fits to the empirically determined PDF of the null model (Bulmer 1975). The two test statistics differ in how the compromise between detection and consideration of observational error is set; R is the more powerful of the two tests, but R^* is preferable when there are considerable errors in the data (Bulmer 1975). The Bulmer technique has been criticized as being ineffective when there is a trend present in the data (Slade 1977, Vickery and Nudds 1984). However, despite more than two decades of research to find more robust methods, Bulmer's tests are still valued for their simplicity (Fox and Ridsdill-Smith 1995).

The randomization technique of Pollard et al. (1987) attempts to address the deficiencies of Bulmer's tests. In their work the test statistic was the likelihood ratio between the stochastic Gompertz density-dependent model (Eq. 3) and a stochastic density-independent model (Eq. 6). Confidence limits were established by generating a large number of surrogate data sets and computing the test statistic for each. The surrogate data were generated by shuffling the x values in (Eq. 3), whereas the y values remained in their original order. This action destroys any serial correlation between x and y. Pollard et al. (1987) performed their test by instead shuffling the y values and generating the x series from that shuffled series, but this modification allows us to test multivariate models of density dependence. The number of possible reorderings of x is $(n - 1)!$, which for $n = 44$ is greater than 10^{46}. The chance that two reordered sets in 100 000 are identical is correspondingly small, therefore we do not attempt to assure uniqueness of the shuffled sets.

The technique of Dennis and Taper (Wolda and Dennis 1993, Dennis and Taper 1994) has been used to test the stochastic Ricker model expressed by (Eq. 5). The test statistic was again the likelihood ratio between the density-dependent and density-independent models. The method used a ''parametric'' bootstrap to establish the empirical distribution of the likelihood ratio by explicitly evaluating the null model. In this case, the null model, the stochastic growth equation (Eq. 6), is fitted to the observed population changes by computing the maximum-likelihood value of the growth parameter a_n. The variance of the null model residuals, σ_n^2, is then computed. Each surrogate data set is generated by starting at the observed initial population level, and allowing the population to grow stochastically via Eq. 6 using the values of a_n and σ_n and independent Gaussian deviates produced by a random number generator. The confidence interval method proposed by Dennis and Taper (1994) can be applied to other proposed forms of density dependence, such as the Gompertz model.

Whereas both methods can be used to estimate the PDF of the test statistic of a density-independent population, the shuffling technique is more parsimonious than the parametric bootstrap since it makes no assumption about the explicit form of the null model. Since the random shuffling technique uses the actual data, the distribution of each surrogate data set is guaranteed to have the same one-point statistical moments as the original one. These properties are not necessarily preserved for surrogate data sets generated by a parametric bootstrap.

We have evaluated the Gompertz and Ricker models using both techniques for determining confidence limits. In addition, we present results in which the test statistic is not a likelihood ratio, but rather is the value of the b parameter. Use of a model parameter as the test statistic presents an additional concern, because the maximum-likelihood methods used to determine the model parameter values are only valid to the extent that the data are distributed normally about their modeled values. This means that the significance levels reported for such tests are only valid if the model residuals are Gaussian. For this work we proceeded heuristically by exploring significance levels and rejecting models for which the residuals were not acceptably Gaussian.

Model evaluation

Our stochastic formulations, e.g., Eq. 3, and the standard least-squares methods used to obtain the maximum-likelihood parameter values for them, assume that the residuals are independent samples of a normally distributed random variable with constant variance, σ^2, as expressed by the term "$\sigma\varepsilon_i$." This stochastic process is intended to represent both observational error and processes that are omitted or misrepresented by the model. As a result, one way of identifying a model that fails to resolve critical processes is to examine its residuals for systematic variance. Model parameters obtained using least-squares methods are by definition those that minimize the variance of the residuals, but they cannot be considered maximum-likelihood parameters if the residuals fail to meet the aforementioned criteria.

We applied five tests to the model residuals. The first two compared the skewness and kurtosis of the residuals following the t test technique outlined by Sokal and Rohlf (1995: Section 7.9). Following Tong (1990), the autocorrelation function (ACF) of the residuals was examined to test the assumption of residual independence. Periodic oscillations or lagged dependencies that are not addressed by a model may appear as significant peaks in the autocorrelation function. Since the ACF members beyond lag 0 of a white-noise sequence should themselves be Gaussian I.I.D. (independent, identically distributed), Tong recommends that no more than 5% of those elements should exceed the level of $\pm\ 1.96/\sqrt{N}$, where N is the number of data points in the ACF.

Another test that Tong recommends is the computation of the Lin-Mudholkar (LM) normality statistic (Lin and Mudholkar 1980), which is based on the principle that the mean and variance of a Gaussian distribution are independent. For normally distributed residuals, the LM statistic is itself expected to be normally distributed with mean of zero and unit variance, and its significance can therefore be obtained from the normal cumulative distribution function (CDF) with those parameters.

Another common technique for assessing goodness of fit is to examine the departures of the empirical cumulative distribution function from the CDF of the normal distribution of which the residuals are assumed to be samples (e.g., Stephens 1974). We chose to use a variant of the Kolmogorov-Smirnov test proposed by Lilliefors (1967) for cases in which the mean and variance of the residuals are not known in advance.

With the exception of the examination of the ACF, which is an informal procedure, all of these measures of normality were tested against two-sided alternatives at the $\alpha = 0.05$ level.

The time series of residuals, r, is related to the observed population changes, y, and the modeled population changes, m, as $y_i = m_i + r_i$, so the variance of y can be computed as

$$\text{var}(y) = \text{var}(m) + \text{var}(r) + 2\text{cov}(m, r). \quad (7)$$

This expresses the apportioning of variance of y among the deterministic variance, $\text{var}(m)$, the variance of the residuals, $\text{var}(r) = \sigma^2$, and the model-residual covariance, $\text{cov}(m, r)$. This covariance term tends to zero in the limit of an infinitely long series of independent residuals, and for models whose residuals are acceptably Gaussian it becomes negligibly small. A convenient way to quantify model performance is to compute the proportion of observed variance which it explains

$$R^2 = \frac{\text{var}(m)}{\text{var}(y)}. \quad (8)$$

This multiple R^2 can be used to compare the explanatory power of different models, but it does not provide an unbiased means of comparing models having different numbers of free parameters. We instead use the Akaike Information Criterion (AIC), an unbiased estimator of the expected log likelihood, l, of a given model, corrected for the number of free parameters, p, in the model: $\text{AIC} = -2l + 2p$ (Sakamoto et al. 1986). Akaike (1974) suggests that when comparing two models, the one with the lower AIC should be selected.

RESULTS

Changes in ibex population and in snow depth

During the first 28 years of the study period the total number of ibex seen in the autumn census counts averaged about 3400 individuals and ranged from ~2600 to ~4000 ibex with no visually apparent trend. Although oscillations with periodicities of about three and eight years appear to be present (von Hardenberg et al. 2000), the time series is too short to make a determi-
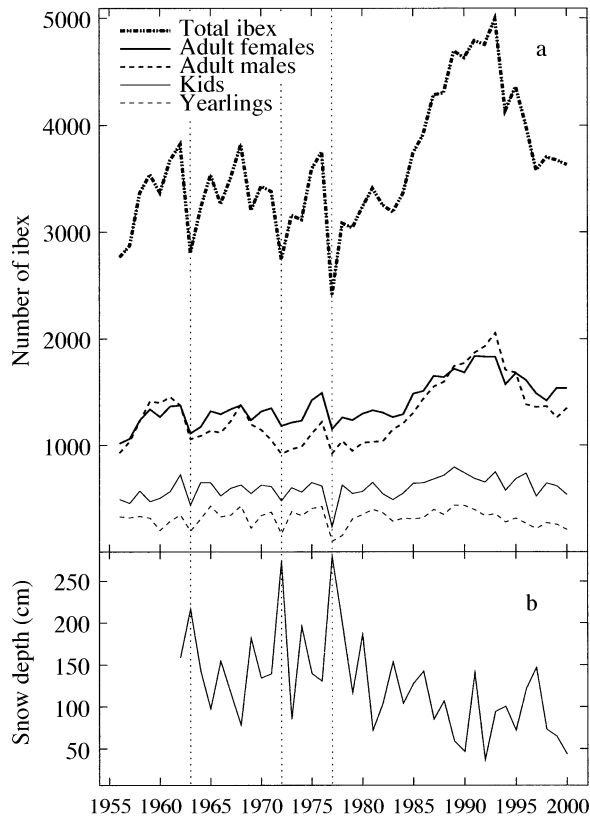
FIG. 1. Alpine ibex population classes and average winter snow depth. (a) Total population of Alpine ibex and sizes of the individual population classes counted during the autumn census in the Gran Paradiso National Park, Italy. (b) Average winter snow depth at Serrù station. Vertical dotted lines indicate the three winters with the highest average snow depth (1962–1963, 1971–1972, and 1976–1977).

nation of the significance of those cycles. From 1982 to 1990 the ibex counts increased steadily and peaked at almost 5000 individuals in 1993. The population then began to decline, and by 1997 it had returned to levels characteristic of those before this event. Changes in different sex–age classes generally paralleled each other over time (Fig. 1), although in later years the proportion of yearlings appeared to decline.

There is a clear univariate correlation ($r = -0.48$) between year-to-year changes in population size and average winter snow depth at the Serrù station (Fig. 2a). A plot of population change vs. density (Fig. 2b) suggests that there was a stronger dependence on density in years with deep snow. In particular, three deep-snow winters between 1962 and 1977 were associated with population declines of more than 15%, and the steady increase from 1982 to 1993 (Fig. 1) occurred during a period in which the average winter snow depth was lower than in the previous period ($P < 0.001$, Wilcoxon rank sum test): between 1962 and 1982 the average snow depth was 152 ± 58 cm, whereas between 1983 and 1999 it was 92 ± 36 cm (mean ± 1 SE). These observations suggest a climatic amplification of density dependence, an effect that is investigated in the following sections. One possible way that this amplification may manifest itself is by a threshold effect, in which the parameter b of (Eq. 3 or Eq. 5) would take on two different values, one in mild winters and one in harsh winters.

Modeling density dependence and the effects of snow depth

We first attempted to detect density dependence without the effects of climate using the stochastic Gompertz and Ricker models discussed in *Population models*, above. To detect direct density dependence—i.e., a non-zero value of the parameter b in Eq. 3 or Eq. 5—we employed the Bulmer test, the randomization test, and the parametric bootstrap.
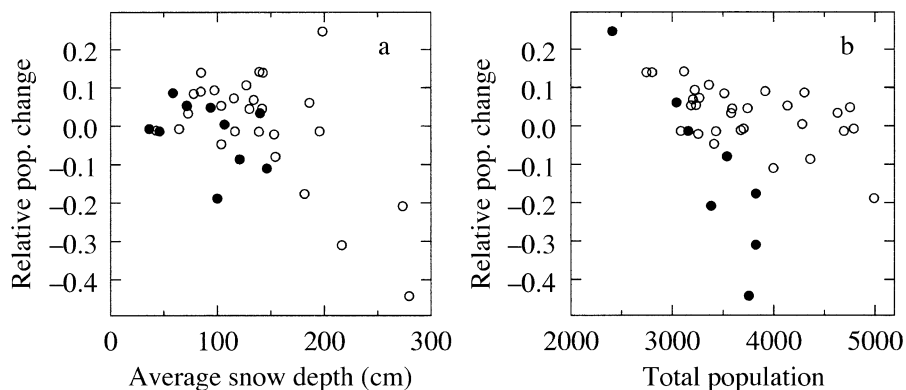

FIG. 2. Relative change in ibex population size, y of Eq. 1, as a function of snow depth and total population. (a) Relative change in population plotted against average winter snow depth at Serrù station. Solid circles represent years for which the total ibex population, N, was large (greater than half a standard deviation above mean). (b) Relative population change plotted against population size. Solid circles indicate that the annual mean winter snow depth at Serrù is more than half a standard deviation above the average.

TABLE 1. Results of Bulmer's first (R) and second (R^*) tests (Bulmer 1975) for ibex total population changes in the Gran Paradiso National Park (northwest Italy) between 1956 and 1997.

Test statistic	Value	First percentile	Fifth percentile	Density dependence
R	2.105	1.316	1.824	not detected
R^*	−0.103	−0.333	−0.243	not detected

Notes: The R test is more powerful, but the R^* test is more conservative in the face of errors in the observations. Also given are the estimated first and fifth percentiles of the density-independent distribution.

These three tests were performed on our data set of 44 year-to-year differences. The Bulmer tests do not suggest density dependence in this population, since the R and R^* values are above the estimated first and fifth percentiles (Table 1). The parametric bootstrap and shuffle results are inconclusive, however. Of the eight permutations of the tests, two indicate density dependence at the $\alpha = 0.05$ level (Table 2).

While these results confirm that density plays a role in the dynamics of this ibex population, analysis of the model residuals (See *Model evaluation*, above) reveals that density, whether in the form of Eq. 3 or Eq. 5, is not by itself a sufficient explanation of the observed population changes. The results of the residuals analysis for the stochastic Gompertz model (Eq. 3) are shown in Table 2 and in Appendix B. Neither model explains more than 18% of the variance in observed population changes, and some of the residuals in y are suspiciously large. While only 2.3% of the ACF (autocorrelation function) elements (1 of 44, excluding the zero-lag correlation) exceed the level of ± 0.3, an extreme value of the ACF at three-year's lag, and the systematically high values at 14–20 years' lag indicate that there may be deterministic variations that are incompletely treated by this model. The residuals also

do not pass the skewness, kurtosis, and LM (Lin-Mudholkar) tests for normality. Together, these results indicate that the residuals are neither Gaussian nor uncorrelated, and we therefore conclude that density dependence alone does not satisfactorily explain the observed population changes.

Delayed density dependence.—We also explored the possibility that population changes depend on time-delayed dynamics. Density variables with lags l from 1 to 10 years were tested with adapted versions of Eqs. 3 and 5. The P values for this test reveal that delayed density dependence is at best a second-order effect. The three- and eight-year cycles found in earlier spectral analyses of this population (Bassano et al. 1992, von Hardenberg et al. 2000) are suggested by these results. Perhaps most importantly, the one-year lagged results are among the least significant, suggesting that the high autocorrelation of residuals at one-year's lag (Appendix B) is probably not due to delayed density dependence.

Climate effects.—To ascertain whether climate variations affect the abundance of Alpine ibex, we tested the dependence of relative population change on climate without the effects of density dependence. Because counts were conducted in autumn, total population changes are compared with climate from the previous summers and winters. For instance, the change in population between 1969 and 1970 is compared with climate in the winter of 1969–1970 and the summer of 1970 (Appendix C).

The winter total precipitation and all the snow-depth variables have significant negative correlations with changes in total ibex population. This relationship can be clearly seen in Fig. 1. At both stations the winter precipitation variables are significantly correlated with year-to-year changes in total ibex population. Since these variables are not independent, however, we choose only one of them for further analysis. Building on the observation of Nievergelt (1966) that ibex avoid

TABLE 2. Significance of density-dependence tests for year-to-year changes in total autumn ibex counts based on a distribution of 100,000 surrogate data sets.

Model	Test statistic†	P value‡ Bootstrap	P value‡ Shuffle	R^2§	AIC‖	Skewness (P)	Kurtosis (P)	LM (P)	LKS (P)	ACF (%)
Gompertz, Eq. 3	LR	0.0614	0.1055#	0.175	−62.1	<0.0001	<0.0001	0.0004	0.2827	2.3
	b	0.0579	*0.0047*							
	LR	0.1345††	0.2486	0.15	−60.7	<0.0001	<0.0001	0.0039	0.1676	2.3
Ricker, Eq. 5	b	0.2010	*0.0131*							

 † "LR" indicates that the test statistic is a likelihood ratio of the conditional probabilities of the test model and the null model (Pollard et al. 1987, Dennis and Taper 1994), and b is the model density-dependence parameter.
 ‡ The two-sided probability of incorrectly concluding that the population is density dependent.
 § R^2 is the proportion of variance in the observed population changes that is explained by the model.
 ‖ Aikaike Information Criterion value.
 ¶ The results of the skewness, kurtosis, Lin-Mudholkar (LM), and Lilliefors Kolmogorov-Smirnov (LKS) normality tests are given as P values against a two-sided alternative hypothesis of nonnormality, so a significant result ($\alpha = 0.05$) indicates that the residuals are not plausibly Gaussian. In the last column, the percentage of residual autocorrelation function (ACF) members above the expected level is listed (see *Methods: Model evaluation*).
 # Two-sided test of Pollard et al. (1987).
 †† Two-sided test of Dennis and Taper (1994).

slopes with deep snow depth, we reason that the snow-depth variables are likely to be more directly relevant to population dynamics than is total precipitation. Although the number of days with above-average snow depth has a slightly more significant correlation with changes in ibex population, we have chosen annual average snow depth for further analysis. This quantity is simpler to compute, and does not depend on the definition of the climatological mean snow depth at a station. The interdependence of all the climate variables and the resulting power of average snow depth to represent climatic conditions was also confirmed by an exploratory principal-components analysis of all the environmental indicators (not shown). Although both spring and summer total precipitation are negatively correlated with changes in the ibex population, we did not further explore the roles of these variables.

We also tested for lagged climate dependence, with the same procedures used for lagged density dependence (*Delayed density dependence*, above). Significant positive correlations with relative changes in ibex population were detected in all four winter precipitation variables at lags of both one and four years.

Lagged exogenous variables may act as a proxy for population density if extreme climatic conditions in one year hamper population growth, setting the stage for greater population growth in later years due to reduced competition. In analyses that include both climate and density dependence (next section), one- and four-year lagged snow depth is no more of an improvement to the population growth models than is unlagged snow depth. We thus conclude that lagged climate forcing does not make a significant contribution to the population dynamics. For explaining changes in ibex population, a model with snow-depth dependence alone,

$$y_i = a + cv_i + \sigma\varepsilon_i \qquad (9)$$

is a significant improvement over a simple random walk. This model displays normally distributed residuals for data at either meteorological station, with no significant peaks in the ACF (Appendix B). However, it only explains between 16% and 25% of the observed population-change variance.

Interaction of climate and density.—Although snow depth plays a strong role in the dynamics of the Alpine ibex population, it leaves much of the deterministic variability in ibex abundance unexplained. Bootstrap and jackknife significance tests indicate that some mechanism for including both snow and density is warranted. We therefore analyzed models including density, snow depth, and a term representing the interaction of these two quantities (either $v_i n_i$ or $v_i x_i$). These complete models are as follows:

$$y_i = a + bn_i + cv_i + ev_i n_i + \sigma\varepsilon_i \qquad (10)$$

$$y_i = a + bx_i + cv_i + ev_i x_i + \sigma\varepsilon_i. \qquad (11)$$

Other "subset" models formed by dropping individual terms from the complete models were also tested (permutations listed in Table 3 and Appendix D). However, as suggested by Fig. 2, the dynamics of this population might be well represented by a two-state system, or threshold model. In a threshold model there are two different sets of parameter values, one set for years with low snow depth and one set for years with high snow depth. Thus we also investigated a suite of threshold models, for which b, c, or e take on different values in different years (the a and σ do not depend on snow depth). The threshold value chosen is that of Fig. 2, namely the mean snow depth plus 1/2 the sample standard error, about 154 cm. The details of model performance clearly depend on the choice of threshold value. We conducted a limited sensitivity study on this matter, and this particular value yielded the best performance in that study. The complete list of climate–density models is given in Table 3 and in Appendix D.

Models fit to Serrù climate data consistently outperform the same models fit to Teleccio data, possibly because the Serrù station is at a higher altitude and thus reflects more accurately the snow depth in ibex habitat. Only results for the Serrú climate data are presented here.

Four threshold models using Serrù data (Eqs. D.11–D.14 in Appendix D) stand out from the others. They account for about three-quarters of the input variance, and their residuals pass the battery of normality tests (Table 3, Appendix B). These candidate models were retained for further analysis.

Testing model predictive ability

A powerful test of a model's performance is whether it can predict population changes in a later period when its parameter values are determined only from data limited to an earlier period ("out-of-sample" prediction). Model predictions of *y* are perturbed with random fluctuations ε as in Eq. 10, with standard deviation σ determined from the residuals of the trained model fit. Since this is a stochastic prediction, this procedure is carried over an ensemble of 1000 trials to get stable statistics on the prediction.

We tested how well the candidate threshold models (Eqs. D.11–D.14 in Appendix D) predicted the population variability during the evaluation period of 1981–2000 with parameter values determined from the training period 1961–1980. We present two measures of out-of-sample performance: a bias parameter and a confidence-interval width. The bias parameter is the average over the evaluation period and over the ensemble trials of the deviations of the model predictions from observations:

$$\beta = \frac{1}{1000} \sum_{j=1}^{1000} \left[\frac{1}{19} \sum_{i=1}^{19} (\hat{n}_i^j - n_i) \right] \qquad (12)$$

where *j* is the index of the ensemble trial, and $\hat{n}_i^j$ is the *j*th ensemble prediction of n_i. The confidence-interval width is the mean over the evaluation period of the

TABLE 3. Performance of complete list of climate- and density-dependent models.

Model†	Terms‡ b	Terms‡ c	Terms‡ e	Dens. form§	No. par.‖	R^2	AIC	Normality tests Skew. (P)	Kurt. (P)	LM (P)	LKS (P)	ACF (%)¶
Regular												
(D.1)	√	√	√	n	4	0.62	**−78.3**	0.39	0.97	0.37	>0.2	0.0
(D.2)	√	√	√	x	4	0.65	**−81.2**	0.46	0.87	0.43	>0.2	0.0
(D.3)		√	√	n	3	0.62	**−80.3**	0.39	0.98	0.37	>0.2	0.0
(D.4)		√	√	x	3	0.65	**−83.2**	0.46	0.87	0.43	>0.2	0.0
(D.5)	√		√	n	3	0.59	−77.3	0.61	0.67	0.57	>0.2	2.6
(D.6)	√		√	x	3	0.59	−77.0	0.92	0.49	0.91	>0.2	2.6
(D.7)	√	√		n	3	0.55	−73.5	0.76	0.79	0.75	>0.2	2.6
(D.8)	√	√		x	3	0.58	−76.4	0.95	0.51	0.94	>0.2	2.6
(D.9)			√	n	2	0.46	−68.5	0.62	0.91	0.59	>0.2	0.0
(D.10)			√	x	2	0.27	−56.8	0.79	0.28	0.79	>0.2	0.0
Threshold												
(D.11)	√	√	√	n	7	0.8	**−97.6**	0.69	0.31	0.62	>0.2	2.6
(D.12)	√	√	√	x	7	0.8	**−97.0**	0.66	0.31	0.58	>0.2	2.6
(D.13)		√	√	n	5	0.75	**−92.5**	0.38	0.96	0.36	>0.2	2.6
(D.14)		√	√	x	5	0.75	**−92.2**	0.49	0.95	0.47	>0.2	0.0
(D.15)	√		√	n	5	0.69	−83.6	0.38	0.45	0.29	>0.2	**5.1**
(D.16)	√		√	x	5	0.67	−81.1	0.55	0.29	0.44	>0.2	**5.1**
(D.17)	√	√		n	5	0.57	−71.2	0.47	1.00	0.47	>0.2	2.6
(D.18)	√	√		x	5	0.65	−78.8	0.48	0.40	0.38	>0.2	**5.1**
(D.19)			√	n	3	0.47	−67.2	0.36	0.61	0.38	>0.2	2.6
(D.20)			√	x	3	0.3	−56.5	0.34	0.03	0.44	>0.2	0.0

Notes: Normality tests, R^2, and AIC are as defined in Table 2. The four best AIC scores in the Regular and Threshold model groups are boldface.

† Model numbers correspond to equation numbers in Appendix D. Models D.1 and D.2 are the complete models given by Eqs. 10 and 11 in the text.

‡ A check mark in the *b*, *c*, or *e* column means that the corresponding term from the complete models, D.1 or D.2 (Eq. 10 or 11), was included.

§ The form of the density variable: n is the total ibex counts and x is log(n).

‖ The number of model parameters.

¶ The percentages in boldface differ significantly from the expected values of zero at $\alpha = 0.05$.

difference between the 95th and 5th percentiles of the 1000-member ensemble (Table 4). While these evaluation criteria can be computed for both *y* and *n*, the differences between models are most evident in *n* space.

Two models, the five-parameter model (D.13) and the seven-parameter (D.11), outperform the other models in this out-of-sample test (Fig. 3). Both of these models do an adequate job of reproducing the mid-1980s population eruption. Due to its better out-of-sample performance, we regard the five-parameter model as more robust than the seven-parameter model. In particular, its parsimony may make it less susceptible to the danger of overfitting.

TABLE 4. Performance of candidate threshold models on the out-of-sample test.

Model	Bias, β	90% CI width
(D.11)	56.1	1040
(D.12)	275	1290
(D.13)	9.7	979
(D.14)	143	1100

Notes: The bias parameter and confidence interval are defined in *Results: Testing model predictive ability*. Both parameters have dimension of number of ibex.

Equilibrium density

The final two candidate models admit equilibrium solutions of no growth for $y_i = 0$. The resulting equilibrium density (ED) for model (D.11) is

$$n_i^* = \begin{cases} \exp\left(-\dfrac{a + c_l v_i}{b_l + e_l v_i}\right) & \text{if } v_i < v_{\text{thresh}} \\ \exp\left(-\dfrac{a + c_h v_i}{b_h + e_h v_i}\right) & \text{if } v_i \geq v_{\text{thresh}} \end{cases} \quad (13)$$

where the *l* and *h* indices represent parameters for low and high snow-depth years, respectively.

Similarly, model D.13 has an ED of

$$n_i^* = \begin{cases} \exp\left(-\dfrac{a + c_l v_i}{e_l v_i}\right) & \text{if } v_i < v_{\text{thresh}} \\ \exp\left(-\dfrac{a + c_h v_i}{e_h v_i}\right) & \text{if } v_i \geq v_{\text{thresh}}. \end{cases} \quad (14)$$

The ED is analogous to a dynamic carrying capacity that changes as a function of snow depth, v_i. It is interesting to consider this quantity for management purposes, as it estimates the instantaneous number of animals the habitat could support.
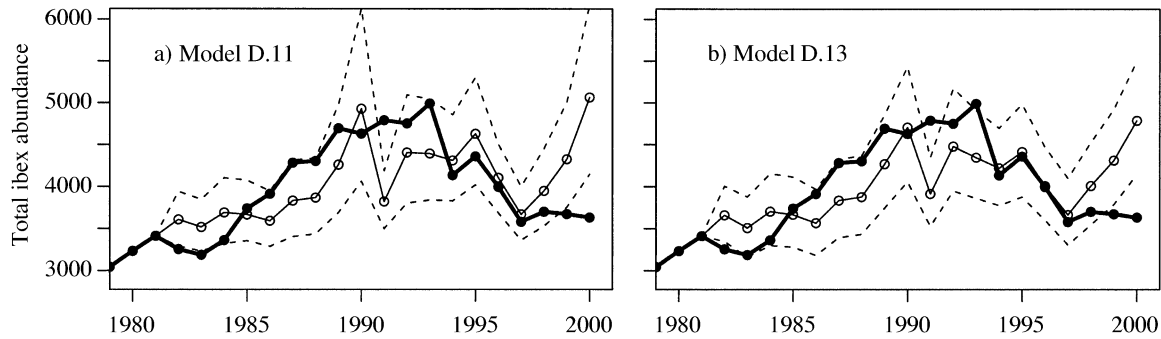
Fig. 3. Out-of-sample prediction: predictions of two of the candidate models trained using only the first half of the ibex census and Serrù climate data (19 years, 1962–1980). Panel (a) is for model D.11, and panel (b) is for model D.13 (models are defined in Table 3, and their expressions are given in Appendix D). The model predictions of the relative population change, y, have been translated into n, the resultant total population size, so that model performance in reproducing the eruption is more evident. In both plots, observations are shown with a thick line, the thin solid line is the mean of 1000 stochastic predictions, and the dashed lines are the 5th and 95th percentiles of those predictions.

Historical n_i^* values compare favorably with observed total ibex counts (Fig. 4). Changes in the ED largely mirror the population variations before the eruption, and increase dramatically in the 1980s. Mismatches between the ED and the actual ibex population, both in the few years around 1975 and in the years of the eruption, serve as a reminder that although these simple models perform remarkably well at qualitatively reproducing the gross features of the population variability, they are unaware of the more complex dynamics of this population (see *Discussion*).

Because of the long life expectancy of ibex (Toïgo et al. 1997), a population's reaction to a sudden change in the environment would not be instantaneous, but would take some time to manifest itself in full (e.g., Murray 1993). The inherent delay in the reaction of a population to changes in its environment is functionally equivalent to a low-pass filter, which attenuates higher frequencies while leaving longer-term variability untouched (Oppenheim and Schafer 1989). In Fig. 4 the ED has been smoothed by low-pass filtering the snow-depth data used in Eq. 13 and Eq. 14. Estimates of the ED obtained in this fashion should be considered at

most suggestive of the real carrying capacity of the system.

DISCUSSION

Changes in the total Alpine ibex population in the Gran Paradiso National Park (GPNP) are negatively affected by population density, by winter snow depth, and by the interaction between these two variables. Our results suggest that the population growth in the 1980s was mainly due to increased adult survival, although the series of mild winters may have also increased recruitment (Appendix E). We will first discuss the implications of these results, then consider the limitations of our study.

Models in ecology usually describe historical changes in population size rather than predict them, but this study tests the predictive power of population models including density-dependent and climate effects over a period of $\sim$20 years (about three ibex generations). Information on total counts and snow depth collected over the first part of the study successfully predicts the population increase of the 1980s and the subsequent decline in the 1990s, but fails to reproduce the apparent

Fig. 4. Equilibrium density (ED) population level, n_i^*, for the two final candidate models (D.11 and D.13). Also shown is the actual total ibex count (thick solid line) during the study period. The ED values were computed using Eqs. 13 and 14 with a low-pass filtered series of average snow depths at Serrù in order to suppress high-frequency variability (see *Results: Testing model predictive ability*). A six-point Hann window was used for the low-pass filtering of snow depths.
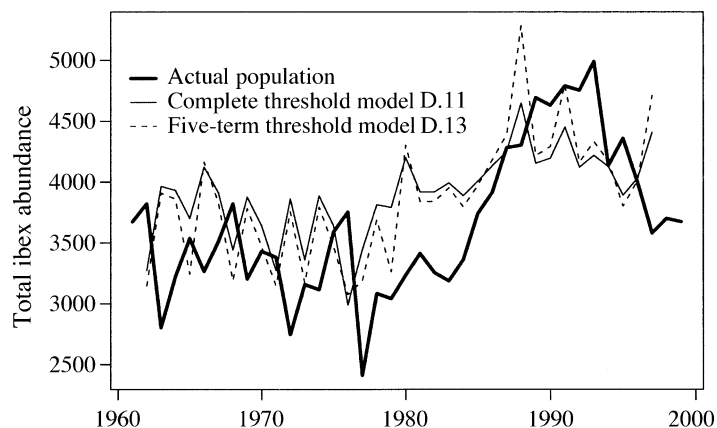
stability of the population after 1997. It is striking that the models can predict this dramatic population change, since their parameters were determined only by total population size and snow depth in the first half of the study period, when the population remained well below the levels attained in the second half.

Variability of vital rates affecting recruitment could explain some of the observed population changes. Reviews of ungulate population dynamics (Sæther 1997, Gaillard et al. 1998, 2000) suggest that juvenile survival, and to a lesser extent fecundity, especially of young females, can vary considerably from year to year. Recently, Gaillard et al. (2000) detailed a framework of incremental responses in vital rates as population density increases. This pattern begins with an increase in the age of primiparity, followed by increased juvenile mortality, then increased yearling mortality and, in extreme cases, decreases in adult fecundity and survival. Because climate extremes tend to have a stronger impact on population growth at high rather than at low population density (Sæther 1997, Forchhammer et al. 1998b, Portier et al. 1998, Post and Stenseth 1999, Post et al. 1999, Coulson et al. 2000), we expected sharply reduced juvenile survival during high-density periods associated with harsh winters. However, this does not appear to be the case. Indeed, changes in juvenile survival cannot explain the substantial increase in the ibex population after 1985. Although the number of kids counted increased with the number of adult females, the number of yearlings was only slightly higher during the population increase than before (Fig. 1). During the eruption, from ca. 1983 to ca. 1990, adult survival increased while weaning success and kid survival remained stable or decreased (Appendix E). Consequently, the increase in population following years of low snow depth could be attributed mostly to increased adult survival. This conclusion is at odds with evidence from other ungulate studies suggesting that adult mortality is relatively insensitive to changes in climatic conditions because adults tend to be in better body condition than juveniles and have a lower surface-to-mass ratio (Jorgenson et al. 1997, Gaillard et al. 2000; but see Fryxell 1987, Gunn et al. 1989, and Owen-Smith 1990). As Gaillard et al. (1998) pointed out, adult survival has a very high elasticity. Therefore, a small increase in this vital rate over a short run of years could lead to a substantial increase in population growth.

Deep snow may cause direct mortality of all age classes in the guise of avalanches. Alternatively, snow depth may have had a relatively stronger effect on the survival of senescent ibex, those older than about 10–12 years (Toïgo et al. 1997). The absence of predation on adults and the high survival of prime-aged ibex likely meant that a substantial proportion of the adult ibex reach senescence. It is possible that a series of years with low snow depth increased the average longevity of adults and thus the average age of the pop-

ulation. Very little is known about the effects of density and climate on survival of senescent adult ungulates, partly because sample sizes of known-age old individuals accumulate very slowly (Gaillard et al. 2000). Some studies, however, do suggest that older ungulates are sensitive to unfavorable weather: in greater kudu (*Tragelaphus strepsiceros*) the survival of older females is affected by drought more than the survival of prime-aged females (Owen-Smith 1990), and in Dall sheep (*Ovis dalli*) severe winter weather affects the survival of old but not prime-aged ewes (Burles and Hoefs 1984). More recently, Garrott et al. (2003) showed that in an unhunted population of elk, the survival of females older than nine years declined with increasing snow depth, while the survival of younger females was only affected by an exceptionally severe winter. In ibex, the adult-male aggregate survival rate was substantially more variable than that of adult females (Appendix E), indicating that survival of adult males may be more sensitive to environmental conditions.

The rapid population decline after 1993 despite the lack of an accompanying resurgence in snow depth is a potential signature of density-dependent dynamics. Both kid survival and weaning success may have begun to decline in the late 1980s, and therefore the decline may have been partly due to lower recruitment. As indicated by Festa-Bianchet et al. (2003), an increase in average ibex age would likely cause an increase in average adult mortality, which could lead to the appearance of density-dependent mortality when none may exist. Without data on known-age animals, we cannot properly assess the level of density dependence in adult survival.

The inability of the threshold models' out-of-sample predictions (see *Testing model predictive ability*, above, and Fig. 3) to fully reproduce observed population variability in the 1997–2000 period is consistent with the attribution of the eruption to enhanced adult survival. Since the simple models described in this paper do not take the age structure of the population into account, they cannot reproduce the effects of increased mortality due to the aging of the population. The apparent density-dependent mortality suggested by Festa-Bianchet et al. (2003) could explain much of the decrease in population size during 1993–1997. The predicted sharp decline in population growth in 1991 (Fig. 3b) is caused by a moderately high winter snow depth, which has a disproportionately strong effect because of its nonlinear interaction with the high population level in 1991 (Fig. 1). This failure could be attributed to several causes, but a likely candidate is the model's inability to consider the cumulative effects of successive years of low snow depth (Garrott et al. 2003), which could render the population more able to withstand a single year of high snowfall. The nonlinear model also predicts a strong rebound of the population in the period 1997–2000, due to continued low snow
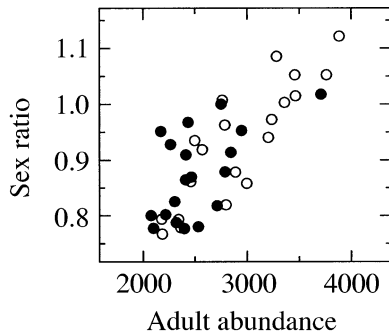
FIG. 5. Adult sex ratio (ratio of males to females) plotted against total number of adult ibex ($r = 0.79$). Open circles represent years with average snow depth at Serrù below the mean of 126 cm; solid circles represent years with average snow depth above the mean. The correlation between sex ratio and adult ibex abundance in years of low snow depth (open circles) is stronger ($r = 0.86$) than that in years of high snow depth (solid circles, $r = 0.58$).

levels during a period of low density. Recent censuses indicate, however, that while the adult portions of the population may be recovering, kid survival remains depressed (Appendix E). This may be due to a lagged effect of high density in the 1990s on kid survival or on age of primiparity. If lag effects only occur following years of very high density, models like the ones discussed here should be expected to fail.

Other studies of sexually dimorphic ungulates typically report that adult sex ratio becomes increasingly female biased as density increases (Clutton-Brock et al. 1997, Jorgenson et al. 1998), although adult male mortality is generally not density dependent (Clutton-Brock et al. 1997, Jorgenson et al. 1997). In the ibex population observed by Toïgo et al. (1997), no significant sexual differences in survival of prime-aged adults was found, a result that suggests an even sex ratio. Population counts of ibex in the GPNP suggest a weak positive relationship between population size and adult sex ratio (Fig. 5).

A bias in the sex ratio toward males during the eruption would be consistent with a scenario in which adult male ibex react more strongly than adult females to changes in climatic conditions. Ibex males likely enter the winter in worse body condition than females because of strenuous activity during the rut. A similar situation was reported for red deer in Norway, where the survival of adult stags was affected by spring weather, while the survival of adult hinds was not (Loison and Langvatn 1998). A series of mild winters could therefore have a greater positive effect on male survival than on female survival. A detailed long-term study of marked individuals initiated in 1999 will address the hypothesis that adult males, and possibly older males in particular, are more sensitive to climatic conditions than adult females.

A serious limitation of our data set is the low level of resolution of age classes in the census data. Age

structure plays an important role in ungulate population dynamics, because of strong age-dependent schedules of reproduction and survival (Bérubé et al. 1999, Loison et al. 1999, Gaillard et al. 2000). As discussed above, the shortcomings of the models presented in this paper may be in part due to the fact that they have no means of considering the age dependence of important processes (Coulson et al. 2001a).

In conclusion, our analysis of the time series of ibex counts in the GPNP reveals that an interaction of density and climatic conditions was responsible for most of the interannual change in total population. A simple model did a satisfactory job of reproducing observations, and predicted a major change in the total population size over a period longer than two ibex generations. Changes in ibex density during the population eruption were apparently due to changes in adult-ibex survival and may indicate an overall aging of the population. The rapid decline in ibex counts during 1993–1997 may be due to density-dependent mortality of senescent adults. Unlike other species of sexually dimorphic ungulates, this ibex population does not show an increasingly female-biased adult sex ratio as density increases.

It appears that for about 25 years the GPNP ibex population was mostly limited by the episodic occurrence of harsh winters characterized by large amounts of snowfall. When snow accumulations decreased after 1982, the population increased substantially. Other long-term studies of ungulate population dynamics recognize a strong role of climate (Messier 1991, 1994, Portier et al. 1998, Solberg et al. 1999, Coulson et al. 2000). Density dependence may not be detected if extrinsic factors prevent populations from reaching densities where food limitation affects vital rates (Crête and Courtois 1997). The Alpine ibex population at GPNP may have entered a dynamic regime in which density dependence, possibly including new lag effects, will play a different role over the coming decade than it has in the past.

The results of our study imply that changes in the amount of snow falling on the Alps could have drastic effects on ibex populations. At this time, predictions about regional effects of global climate change are limited, and it is generally agreed that more accurate predictions for high-altitude ecosystems will depend on future generations of climate models and data analysis systems (see e.g., the web site for CLIVAR, an international research program on climate variability and predictability).[6] Ibex and other Alpine ungulates may provide sensitive indicators to the advance effects of any such changes (Forchhammer et al. 1998b, Post et al. 1999), and thus populations such as this one deserve careful monitoring over the coming decade. In addition, dramatic population changes of such a large herbivore

[6] URL: ⟨http://www.clivar.org⟩

would have profound long-term consequences for several other components of the alpine ecosystem.

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APPENDIX A

Census data for the Alpine ibex population (Gran Paradiso National Park, Italy) and corresponding climate data (snow depth, temperature, and precipitation) are available in ESA's Electronic Data Archive: *Ecological Archives* E085-043-A1.

APPENDIX B

Results of diagnostic tests on model residuals are available in ESA's Electronic Data Archive: *Ecological Archives* E085-043-A2.

APPENDIX C

Correlations of changes in total fall ibex count with climate variables are available in ESA's Electronic Data Archive: *Ecological Archives* E085-043-A3.

APPENDIX D

Model equations are available in ESA's Electronic Data Archive: *Ecological Archives* E085-043-A4.

APPENDIX E

Aggregate vital rate data are available in ESA's Electronic Data Archive: *Ecological Archives* E085-043-A5.