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Estimating population trends using population viability analyses for the conservation of *Capra pyrenaica*

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Large herbivore populations can suffer important oscillations with considerable effects on ecosystem functions and services, yet our capacity to predict population fate is limited and conditional upon the availability of data. This study investigated the interannual variation in the growth rate of populations of *Capra pyrenaica* Schinz, 1838, and its extinction risk by comparing the dynamics of populations that were stable for more than two decades (Gredos and Tortosa-Beceite), populations that had increased recently (Tejeda-Almijara), and populations that were in decline (Cazorla-Segura) or extinct (the Pyrenees population; hereafter, bucardo). To estimate quasi-extinction threshold assessments (50% of population extinct in this study), which have implications for the conservation of the species, we used empirical data and the predictions derived from several theoretical models. The results indicate that when variance of log population growth rate reaches a specific threshold, the probability of quasi-extinction increased drastically. For *C. pyrenaica*, we recommend keeping population variance < 0.05, which will reduce the likelihood that the irruptive oscillations caused by environmental and demographic stochasticity will put the population at risk. Models to predict the dynamics of *C. pyrenaica* populations should incorporate temporal stochasticity because, in this study, it strongly increased the likelihood that a population declined.

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Introduction

The dynamics of ungulate populations are controlled naturally by negative density-dependence (Putman 1996, Brooks and Bradshaw 2006), ie, population growth rate declines as population size increases, generally because of intraspecific competition for limited resources. Density-independent factors, particularly climate, can limit population growth rate (Milner-Gulland 1994, Jacobson *et al.* 2004, Grøtan *et al.* 2008). In predator-free environments, the dynamics of ungulate populations are strongly influenced by a combination of stochastic variation in the environment and population density (Sæther 1997). Negative density dependence and environmental stochasticity influence body condition, which leads to a lag in the response of the population to changes in the environment. In the absence of predators, a stable equilibrium is unlikely to occur and the result is population fluctuations (Sæther 1997).

Classical models of population dynamics have shown that populations of large herbivores frequently increase to large sizes, which can have a severe impact on vegetation and lead to a degraded environment that, in turn, leads to a significant reduction in population size (Caughley 1976). Overcompensation occurs when population density exceeds the environment's carrying capacity (Clutton-Brock *et al.* 1991). Often, the result is irruptive oscillations in the sizes of ungulate populations (Clutton-Brock *et al.* 1991, McCullough 1997, Peterson 1999), which can be more significant when herbivorous wildlife share habitat with livestock, as occurs with ibex *Capra sibirica* (Bagchi *et al.* 2004). Similarly, deer densities rarely exceeded 5 individuals/km^2 but, in predator-free areas, densities reached 25–40 ind./km^2 in a semi-natural forest in Eastern Europe (Latham 1999). At such relatively high densities, competition can influence the susceptibility of ungulate to pathogens and the conservation of vegetation.

In most of the areas in Spain occupied by Iberian wild goat (formerly, Spanish ibex *Capra pyrenaica* Schinz, 1838), large predators are absent and, therefore, do not influence ungulate populations. In those areas, hunting, culling and poaching control wild ungulate populations, and disease outbreaks play an important role in some populations (Pérez *et al.* 2002). In Spain, the number of *C. pyrenaica* increased from 5000 in the 1960s to 50 000 individuals distributed among more than 50 populations at the end of the 20th Century (Alados 1985, 1997, Pérez *et al.* 2002). Nevertheless, the recent extinction of a subspecies (*C. p. pyrenaica*) (García-González and Herreo 1999), and drastic reductions in the sizes of some of the populations (eg, Cazorla-Segura population declined by more than 90% over four years) (Pérez *et al.* 2002) reinforces the need to understand extinction risk in populations of *C. pyrenaica*. Time-series analyses of population size can detect population trends and the factors that affect them. Ultimately, advances in the use of population viability analyses (PVA) to assess extinction risk and the probability of reaching a specific population threshold associated with specific management practices can be invaluable in devising conservation and management strategies (Dennis *et al.* 1991). PVA can be based on count data (number of individuals in the population), which is the type of data most likely to be available from managers (Morris and Doak 2002).

The objective of this study was to quantify the effect of variations in the values of parameters on population forecast. Following the recommendations of several authors (Morris and Doak 2002, Sabo *et al.* 2004), we applied several models to *C. pyrenaica* populations for which there was enough data (in Tejeda-Almijara, Tortosa-Beceite, and Gredos), and we assessed the success of the models statistically. We ignored the possible effects of measurement errors (eg, how errors in the assessment of population size might have inflated estimates of population variability), because we were interested in the importance of the variation in the model's parameters on the fate of population, not in the precision of the forecasts. To quantify the effect of temporal variability in population size on the long and short data-series of seven populations of *C. pyrenaica*, we evaluated a simple, density-independent, discrete-time model of exponential population growth with environmental stochasticity (Lande and Orzack 1988). That method underestimates the maximum growth rate used in generating time-series data when the population is density dependent, but is well-suited to slowly declining populations or space-limited populations near their carrying capacity (Sabo *et al.* 2004). To quantify the effect of the variance on relative extinction risk, we used the Ceiling model. To help in assigning priorities for management and conservation efforts, we generated time-series using different combinations of population parameters as a means of identifying the populations most at risk of extinction.

Methods

Capra pyrenaica is a medium-sized, mountain-dwelling ungulate that occurs over most of Spain's mountain ranges (Pérez *et al.* 2002). Each year, regional refuge authorities perform complete counts of *C. pyrenaica,* and their official census reports form the basis for this study. The Pointage-flash method (Berducou *et al.* 1982) entails counting simultaneously all of the individuals in area. The area is divided into sectors, which are visited simultaneously by a number of trained rangers. Censuses are conducted during the rut season, when the animals are engaged in mating activities in open areas and are easily detected. In this study, the census error was considered constant, assuming similar sampling error in the different areas and years. With the exception of the extinct bucardo subspecies *C. pyrenaica pyrenaica*, all the populations were hunted. All the populations included in the study were inside national game reserves, excluding the bucardo population that inhabited a National Park (Ordesa and Monte Perdido). With the exception of bucardo and the population in Gredos (*C. p. victoriae*), the populations were *C. p. hispanica* (based on the classification by Cabrera 1911).

Estimating the best-fit model based on long data time-series

With sufficient data, it is possible to fit population models to data and to compare density-dependent and density-independent models. In our study, three populations (Tejeda-Almijara, Tortosa-Beceite, and Gredos) had enough data to perform the analysis. The following three models were fit to the data using nonlinear least squares regression of log (N_{t+1}/N_t) against N_t, based on complete censuses recorded at fixed time intervals:

Density-independent model (Lewontin and Cohen 1969):

$$\log(N_{t+1} / N_t) = r \tag{1}$$

Ricker model (Ricker 1954):

$$\log(N_{t+1} / N_t) = r(1 - N_t / K) \tag{2}$$

Theta logistic model (Gilpin and Ayala 1973), which is a generalization of the logistic model:

$$\log(N_{t+1} / N_t) = r[1 - (N_t / K)^{\theta}] \tag{3}$$

where N_{t+1} and N_t are population size at time t+1 and t, r is the log population growth rate, K is the carrying capacity, and theta, θ, is a positive parameter that reflects the importance of density dependence in the population forecast. In the analyses, log was used to represent the natural logarithm.

It was necessary to use a contiguous time-series data for the analysis; therefore, we extrapolated linear estimates using the nearest censuses and then identified the best-fit model. To determine whether the interpolation of data influenced the results, the same analyses were performed on censuses that had contiguous data.

We calculated the residual variance, *Vr*, which is the mean squared deviation between the observed values of log (N_{t+1}/N_t) and the values predicted by the model. For each model, maximum log likelihood values were calculated following Morris and Doak (2002). The simplest best-fit model was identified using the corrected Akaike Information Criterion, $\mathrm{AIC_c}$ (Burnham and Anderson 1998).

Estimating extinction probabilities using stochastic density-dependent models

The probability of quasi-extinction was calculated using each of the density-dependent models with computer simulation in Matlab 7 (after Morris and Doak 2002). The quasi-extinction threshold is defined specifically for the critical population size of concern. In our study, 50% of the actual population size was used as the quasi-extinction threshold. To estimate the probability of reaching a specific population size threshold given an actual population size, the models were run through 5000 iterations. For each year, the computer generated a random number, z_t, that had mean = 0 and variance = 1, which reflects environmental stochasticity, ε_t, when multiplied by σ (square root of the population variance), was substituted into the following equation:

$$N_{t+1} = N_t \exp\left\{ r\left[1 - \left(\frac{N_t}{K}\right)\right] + \varepsilon_t \right\} \tag{4}$$

To estimate the confidence intervals for the quasi-extinction probabilities, we used a nonparametric bootstrap with 5000 repetitions (Hilborn and Mangel 1997).

Estimating population parameter based on short time-series data

When data series are short, population parameters cannot be calculated using the former approaches and an alternative method is required. One option is to calculate population parameters using a simple, stochastic, density-independent, discrete-time model expressed as follows:

$$N_{t+1} = N_t \exp(r + \varepsilon) \tag{5}$$

where ε is the error term, which is normally distributed with mean = 0 and variance = σ^2. Population growth follows a lognormal distribution and, therefore, the natural logarithm of population size is normally distributed. In Spain, population censuses were not performed annually, and variance increases more rapidly as the time between measurements increases. To avoid violating the assumption of homogeneity of variances, the rate of population change was transformed by dividing log population growth rate by, x_i [ie, $y_i = \log(N_{i+1} / N_i) / x_i$]; where x_i is the square root of the time elapsed between two , *i*, censuses ($\sqrt{t_{i+1} - t_i}$) (Morris and Doak 2002); y_i was regressed as a dependent variable against x_i and the intercept of the regression was forced through 0. The slope of the regression, *r*, is the log population growth rate, which is > 0 when population growth rate is > 1 and is < 0 when population growth rate is < 1. The confidence intervals of *r* were derived from $\hat{r} - t_{\alpha,q-1}\,\mathrm{SE}(\hat{r}), \hat{r} + t_{\alpha,q-1}\,\mathrm{SE}(\hat{r})$, where *t* is Student's *t*-statistic; *q* is the number of censuses on which a regression was performed, and SE is the standard error. The variance of the log population, σ^2 is the mean squared error of the regression multiplied by *q*/*q*-1 (Dennis *et al.* 1991). The confidence intervals for σ^2 were obtained from the χ^2 distribution as $(q-1)\sigma^2 / \chi^2_{0.025,q-1}\,(q-1)\sigma^2 / \chi^2_{0.975,q-1}$.

We examined the first order autocorrelation residuals and, to determine whether any censuses had a disproportionate influence on the parameter estimations, we did diagnostic tests on outliers. The tests involved computing the Pearson correlation coefficient between the residuals of years 1 to *q*-1 *vs.* the residuals of years 2 to *q*. We used *dw* option in *proc reg* from SAS V9.1.

Estimating extinction probabilities using the Ceiling model and short time-series data

When the mean log population growth rate is > 0 and temporal stochasticity can be assumed to be low, the density-independent model predicts that a population will grow to an infinite size; however, density-dependent effects will occur as the population increases. The Ceiling model (Lande 1993, Morris and Doak 2002) estimates the mean time ($\overline{T}$) to reach the quasi-extinction threshold in a simulated population that has a known mean log growth rate, *r*, and variance σ^2. For that model, we used population parameters derived from the density-independent model. The Ceiling model assumes density-independent behaviour below the upper threshold of abundance (*K* – carrying capacity), but the population does not exceed that ceiling.

$$\overline{T} = \frac{1}{2rc}\left[e^{2ck}(1 - e^{-2ck}) - 2cd\right] \tag{6}$$

for $c = r / \sigma^2$, $d = \ln(N_c / N_x)$, $k = \ln(K / N_x)$.

If the population starts at the ceiling (*K* – carrying capacity), that is, $N_c = K$, and the population is extinct at N_x = 1, then

$$\overline{T} = \frac{1}{2rc}\left[K^{2c} - 1 - 2c\log K\right]. \tag{7}$$

Results

Identification of the best-fit model based on large time-series data

In our study, the Tejeda-Almijara, Tortosa-Beceite and Gredos population had almost complete data series. Consequently, the parameter values obtained from the extended (with time-series completed by extrapolation) and reduced (without extrapolation) data sequence were similar. For example, in the Ricker model, the estimates of *r* in the Tejeda-Almijara population from the extended and reduced data sequence were 0.171 and 0.175, respectively. To find the simplest best-fit model, we used Akaike Information Criterion ($\mathrm{AIC_c}$). In the three former populations, the Ricker model had the highest weights and lowest $\Delta\mathrm{AIC_s}$ (Table 1). When the parameters of the Ricker logistic equation were used, in Tejeda-Almijara, Tortosa-Beceite, and Gredos, as the size of the *C. pyrenaica* populations increased, population growth rate declined (Fig. 1).

To this point, we have assumed that the impact of environmental factors on population growth is independent between years; however, temporal environmental autocorrelation, ρ, might lead to deviations in the population growth rate that are correlated among years. For example, bad weather in one year might depress population growth rate for several years. If population growth rate is correlated in time and environmental deviations can be assumed to be independent, predictions of the risk of extinction can be inaccurate. In the Tejeda-Almijara (ρ = 0.16, *p* = 0.38), Tortosa-Beceite (ρ = –0.01, *p* = 0.96), and Gredos (ρ = 0.02, *p* = 0.88) populations, the first-order environmental autocorrelations were not significant.

Relationship between population parameters and probability of extinction

To estimate the probability of reaching the quasi-extinction threshold (50% of the population) in Tejeda-Almijara, we used Ricker logistic models and ran 5000 iterations starting from the initial population size in each of the 5000

Table 1. Least-squares parameter estimates from each model (r, K, θ), residual variance (Vr), number of parameters (p) and Akaike Information Criterion (AIC_c) of *Capra pyrenaica* populations with long time-series data.

Model	Least –squares parameter estimates				Akaike Information Criterion (AIC_c)			
	r	K	θ	Vr	p	AIC_c	Akaike weights	Δ AIC_c
				Tejeda-Almijara				
Density independent	0.044			0.019	2	–32.73	0.031	6.27
Ricker	0.171	1318		0.015	3	–39.00	0.704	0
Theta logistic	0.094	1504	6.237	0.0143	4	–37.04	0.265	1.96
				Tortosa-Beceite				
Density independent	0.054			0.017	2	–43.23	0.0002	16.49
Ricker	0.232	4682		0.011	3	–59.72	0.759	0
Theta logistic	0.209	4687	1.297	0.011	4	–57.43	0.241	2.29
				Gredos				
Density independent	0.020			0.0041	2	–109.60	0.003	6.37
Ricker	0.163	5609		0.0034	3	–115.97	0.722	0
Theta logistic	0.093	5603	2.267	0.0036	4	–113.83	0.248	2.14

bootstrap iterations. In the three populations, the probability of quasi-extinction was almost zero but, with the variance set to 0.1 the probability that the population would be reduced to half increased dramatically. When environmental stochasticity was set to 0.1, the 50-year simulation estimated that the quasi-extinction probability was 56% in Tejeda-Almijara, 66%, in Tortosa-Beceite, and 92% in Gredos (Fig. 2).

In one of the populations that has experienced significant reductions in the last century, Cazorla-Segura, the model predicted a quasi--extinction probability after 50-years simulation of 44% when starting from the actual initial population size (1324 individuals in 2007) (Fig. 3). In the Cazorla-Segura population, the probability of extinction increased over the course of the 50-year simulation. In the extinct bucardo population, when starting from the largest population size (30 individuals in 1982), the model predicted a quasi-extinction probability after 50-year simulation of 84% (Fig. 3). In the bucardo population, the quasi-extinction probability increased dramatically in the first 10 years of the simulation. At bucardo, the predicted probability of total extinction was 55% (Fig. 4).

Temporal stochasticity and the extinction probabilities derived from the Ceiling model

The higher the σ^2, the more rapidly a population is likely to go extinct. Thus, it is important to know whether temporal inter-annual variation in population size affects the predicted extinction probabilities. Although no *C. pyrenaica* population in our study had a growth rate that differed significantly from zero, the sizes of the populations in Sierra Nevada increased by more than a magnitude of 10 since the 1960s (which was observed previously in the populations at Tejeda-Almijara and Tortosa-Beceite), but the bucardo population went extinct, and the Cazorla-Segura population decreased. Nevertheless, the variance in those populations ranged from 0.005 in the Gredos population to 0.6 in the extinct population (bucardo) (Table 2). The autocorrelation of the regression residuals, which indicates temporal autocorrelation, was statistically significant in the Tortosa-Beceite and bucardo populations, only. No outliers were detected.

The Ceiling model can calculate the mean time ($\overline{T}$) to reach the quasi-extinction threshold in a simulated population that has a mean log

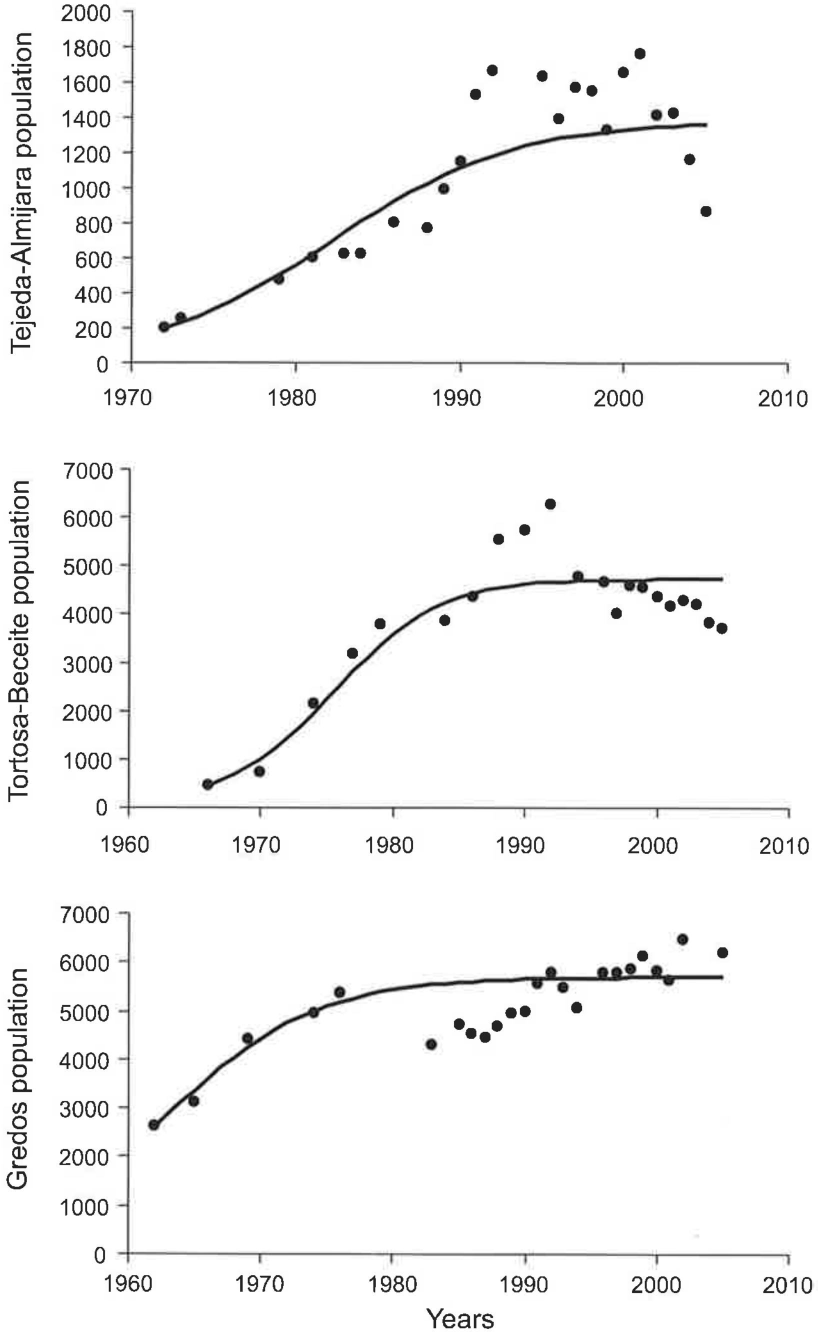

Fig. 1. Best-fit model for *Capra pyrenaica* populations in (a) Tejeda-Almijara, (b) Tortosa-Beceite and (c) Gredos exhibiting the density-dependent population dynamics using the parameters of the Ricker logistic equation obtained after 5000 bootstrap iterations. The mean ± SE population parameters were $r = 0.171 \pm 0.028$, $K = 1379.7 \pm 451.9$ in Tejeda-Almijara; $r = 0.232 \pm 0.056$, $K = 4732.8 \pm 588.9$ in Tortosa-Beciete; and $r = 0.166 \pm 0.035$, $K = 5697.9 \pm 526.9$ in Gredos.

population growth rate r of 0.01 and variance σ^2 that ranges from 0.1 to 0.6. At a mean log population growth rate of 0.01 (close to carrying capacity), an increase in the variance from 0.1 to 0.2 or higher leads to a significant reduction in the mean time to quasi-extinction (Fig. 5). If the

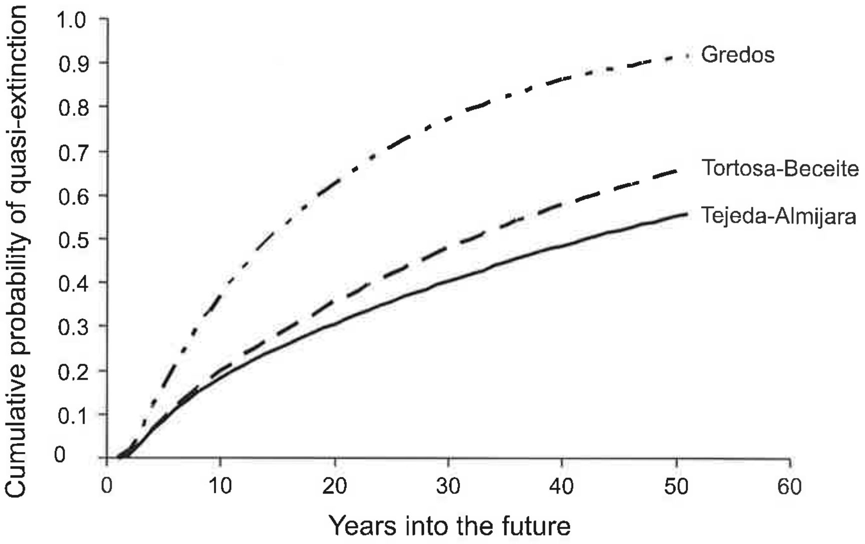

Fig. 2. Probability of reaching 50% of the initial population size in the *Capra pyrenaica* population in Tejeda-Almijara, Tortosa-Beceite and Gredos, Spain, based on simulations that used 5000 replicate trajectories and an environmental stochasticity $\sigma^2 = 0.1$.

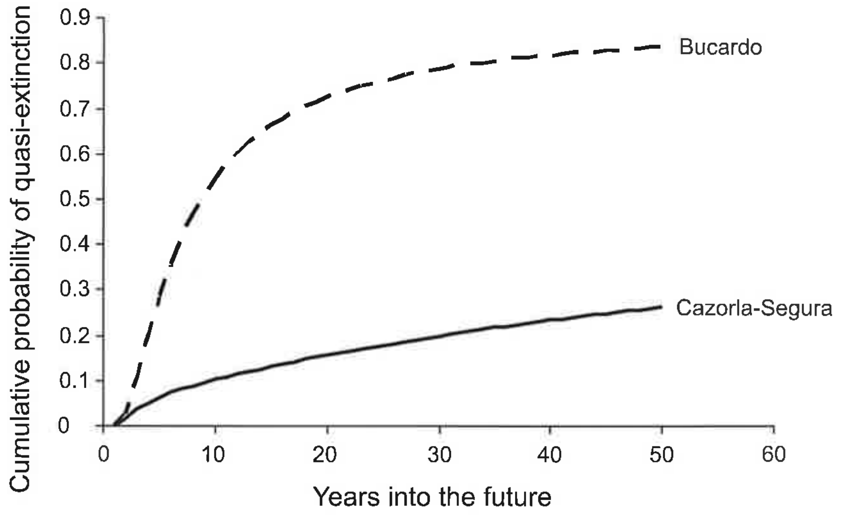

Fig. 3. Probability of quasi extinction for the Cazorla-Segura and bucardo populations of *Capra pyrenaica* in Spain as predicted by the Ricker logistic model. After 5000 bootstrap iterations, the mean ± SE population parameters were $r = 0.032 \pm 0.068$ and $K = 4045.8 \pm 96406$ in Cazorla-Segura, and $r = -0.09 \pm 0.1$ and $K = 85.1 \pm 253.8$ in the bucardo population.

variance increases to 0.6, the mean time to reach the extinction threshold is about 100 years, even though the mean growth rate is > 0. When the variance is low (~ 0.1), an increase in the size of the natural reserve increases the carrying capacity and, consequently, the mean time to extinction increases rapidly. Thus, the relative extinction risk is influenced by the height of the ceiling (carrying capacity) and the mean and variance of the log population growth rate.

Based on the data from the extinct bucardo population ($r = -0.04$, $\sigma^2 = 0.6$), the estimated

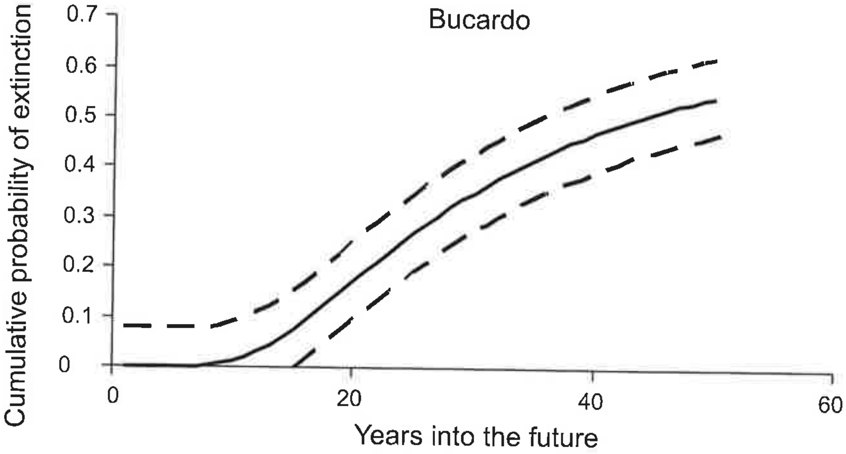

Fig. 4. Mean probability of extinction and confidence limits for the bucardo population of *Capra pyrenaica* in Spain from an initial population size of 30 individuals and simulations using 5000 replicate trajectories.

Table 2. Mean log population growth rate, r, number of observations, q, and population variance, σ^2, and first order autocorrelation residuals, p, calculated for *Capra pyrenaica* populations with density-independence. CI is 95% confidence limit. * significance $p < 0.05$.

Population	q	r			σ^2			p
		CI <	mean	< CI	CI <	mean	< CI	
Bucardo	16	–0.207	–0.040	0.128	0.313	0.573	1.374	–0.627*
Cazorla-Segura	19	–0.094	0.032	0.158	0.101	0.177	0.386	–0.131
Sierra Nevada	6	–0.031	0.071	0.173	0.023	0.058	0.351	–0.308
Ronda	9	–0.038	0.027	0.092	0.015	0.033	0.121	0.424
Tejeda-Almijara	22	–0.017	0.044	0.105	0.017	0.028	0.058	0.218
Tortosa-Beceite	20	0.003	0.054	0.105	0.013	0.023	0.050	0.426*
Gredos	23	–0.002	0.020	0.042	0.003	0.005	0.009	–0.121

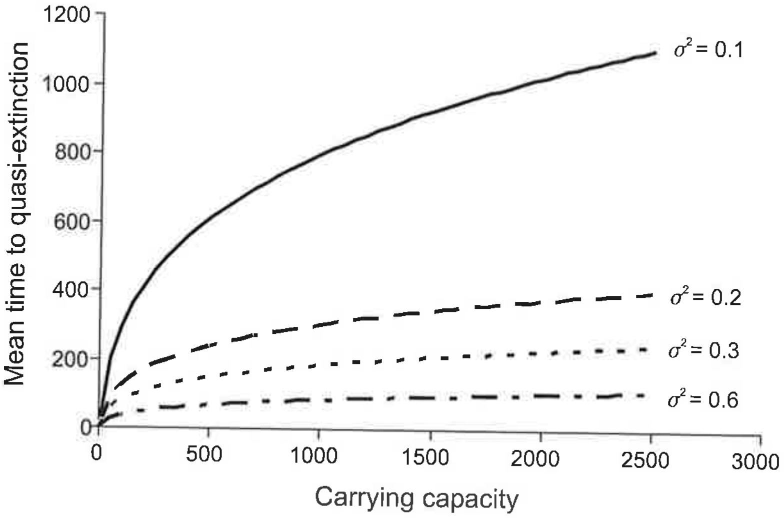

Fig. 5. Estimates of the mean time to extinction for simulated *Capra pyrenaica* populations in Spain starting at carrying capacity with a log growth rate $r = 0.01$, and a variance σ^2 ranging from 0.1 to 0.6 using the Ceiling model.

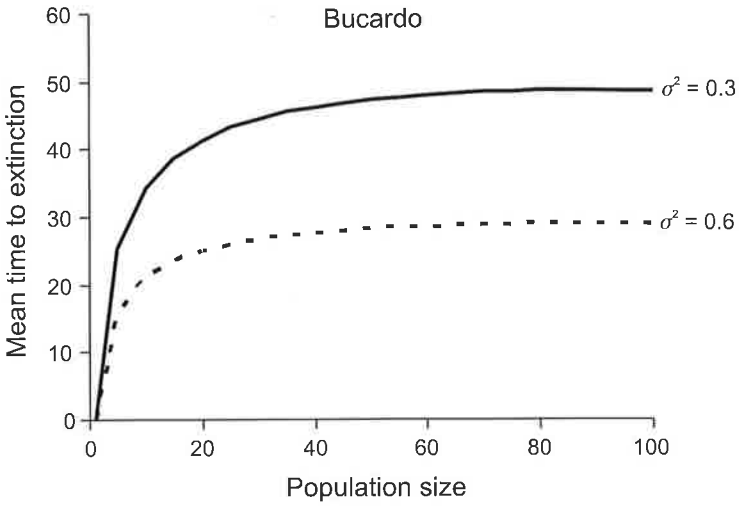

Fig. 6. Probabilities of quasi extinction predicted by the Ceiling model for the bucardo population of *Capra pyrenaica* in Spain with rate $r = -0.04$ and variance σ^2 ranging from 0.3 and 0.6.

mean time to extinction for the *C. pyrenaica* population was only 40 years when the initial population size was 30 individuals (Fig. 6). In fact, despite conservation efforts, in 2000 the population became extinct, approximately 20 years after the 1982-census (n = 30 individuals).

Discussion

In this study we demonstrated that, although *C. pyrenaica* is regulated by density-dependent mechanisms, the importance of environmental stochasticity is significant because the populations that exhibited the greatest stochastic variation were those that had the highest extinction risks.

In the *C. pyrenaica* populations, the density-independent models generated mean log population growth rates that did not differ significantly from equilibrium, but generated high variance. The bucardo population had a variance of 0.6, which might have contributed to its extinction. In the Cazorla-Segura population, a variance of 0.2 was associated with a ten-fold decrease in the size of the population in four years. Although most of the populations had variances of about 0.05, the Gredos population had a variance of 0.005, which reflected the population's stability. The likelihood that a population declined was strongly influenced by temporal stochasticity. Thus, efforts to draw conclusions about the dynamics of natural *C. pyrenaica* populations should include temporal stochasticity, particularly because predictions for temperature increases in mid-latitudinal mountain areas of Europe ranges between 5.3 and 2.9°C by 2085 (Nogués-Bravo *et al.* 2007), which will have a significant impact on the diversity of mountain ecosystems (Walter *et al.* 2005). In particular, climate variation influences environmental stochasticity in ungulates populations (Sæther 1997, Grøtan *et al.* 2008). Despite the self-regulating nature of density-dependent processes, the stochasticity of environmental influences on birth and survival rates favour random fluctuations in natural populations, which might lead those populations to a high risk of extinction.

The effect of temporal stochasticity on population dynamics are such that populations will decrease in size faster than they would without variation. Demographic and environmental stochasticity can reduce population viability, but the data needed to calculate demographic variance is not always available; therefore, quasi-extinction rates are recommended over extinctions thresholds (Morris and Doak 2002). In addition, sampling error artificially increases the temporal variability (Freckleton *et al.* 2006), which underscores the need to perform accurate censuses, to calculate sampling uncertainty, and remove its effects on temporal stochasticity. With the range of variances in the populations at Tejeda-Almijara, Tortosa-Beceite, and Gredos, the probabilities of quasi-extinction (50% of the actual population size) were close to 0. Nevertheless, the probability of reaching 50% of extinction increased dramatically when the variance was 0.1, which is a particular concern for harvested populations, where a second intrinsic demographic process operates. An indirect consequences of a strongly biased sex ratio is that very few animals reach senescence and, consequently, some females do not have an opportunity to mate (Langvatn and Loison 1999). Harvested populations have disproportionately larger juveniles classes, which are more vulnerable to the effects of environmental stochasticity (Eberhardt 1977, Escós and Alados 1991, Gaillard *et al.* 2000). Thus, it is reasonable to predict larger variation in population growth rate of harvested populations (Gordon *et al.* 2004). Indeed, other studies have shown that an increase in the adult survival rate from 0.87 to 0.91 stabilized the population trajectory (Escós *et al.* 1994). Harvesting all of the age and sex classes proportionally might compensate for the negative effect of an increased environmental stochasticity on the trajectories of harvested populations.

The Tejeda-Almijara *C. pyrenaica* population data best fit a Ricker logistic model. Nevertheless, the theta parameter was high (θ = 6.24), which reflects the importance of density on the population trajectory in the Theta logistic model. The harvesting practices in the area contributed to the high theta value. Since 1996, when the Tejeda-Almijara population was close to its carrying capacity, it has been harvested at 0.1% of its size, which has enhanced artificially the density-dependent effect.

Simple diffusion models that assume density-independent population growth are not realistic for populations that live within the confines of refuges. At high densities in confined areas, populations of large mammals exhibit reductions in fecundity and juvenile survival (Eberhardt 1977, Clutton-Brock *et al.* 1987, Portier *et al.* 1988, Gaillard *et al.* 2000), which result from self-regulating processes that are density-dependent (Dennis and Taper 1994, Foley 1994). In our study and others (Sabo *et al.* 2004), comparisons of simple diffusion methods for estimating population viability using density-dependent models revealed that density-independent methods underestimate maximum growth rate and overestimate the variance compared to the results of the Ricker model. In addition, Sabo *et al.* (2004) demonstrated that those density-independent models fit the data very well when the need to detect the risk was most important, ie, when populations were declining to near extinction levels and when they fluctuated near their carrying capacity.

The Ceiling model is relatively straightforward and can calculate of the mean time to reach a specific population size given the growth rate, environmental variance, and carrying-capacity of the population (Lande 1993, Morris and Doak 2002). Although the Ceiling model does not estimate the form of the density-dependence, it can play an important role in assessing the dynamics of real populations when the quantity or quality of the data do not permit the parameterization of more complex nonlinear population models (Sabo *et al.* 2004). The Ceiling model can confirm whether the size of the refuge, which influences the carrying-capacity of an area, and the environmental variance play a significant role in predicting mean time to reach extinction for populations near equilibrium. In the *C. pyrenaica* populations that were close to equilibrium, when environmental variability was increased from 0.1 to 0.2 and higher, the mean time to reach extinction declined significantly. In the Ceiling model, when the variance was 0.1, the mean time to extinction declined linearly as the size of the protected area was reduced, but dropped dramatically when population carrying-capacity was about 500 individuals. Herbivore-vegetation models predict that an increase in the heterogeneity of resources increases the stability of populations because low-quality resources act as a buffer against starvation during stressful periods (Owen-Smith 2004). Kie *et al.* (2002) emphasized the important influence that habitat heterogeneity has on the distribution of large herbivores in comparison to variation in home range size. Indeed, the optimal size of the reserve will depend on habitat quality and habitat heterogeneity. We conclude that a minimum refuge size is needed to satisfy the requirements of the animals and to ensure that the population will have a high probability of persisting.

In our study, the accuracy of the Ceiling model was evident when we compared the predicted mean time to extinction with known extinctions. For example, the bucardo population, which was extinct by 2000 (García-González and Herreo 1999), exhibited a predicted mean time to extinction of 40 years for its more optimistic forecast based on the population sizes observed in the first half of the 20th Century.

In conclusion, variation in the growth rate of wild Iberian goat populations in Spain, rather than simple mean rates is the most informative and cost-effective parameter to evaluate when estimating the relative risk of population extinction and assigning priorities in conservation efforts and management practices. Furthermore, variance in population growth is a manifestation of a population's ability to withstand environmental stochasticity. A population that is capable of maintaining a stable population trajectory in a changing environment is probably better adapted to such environment. In our study, we concentrated on simple counts of entire populations within specific protected areas, which has been the standard census method for *C. pyrenaica* populations in Spain since the start of their recovery in the 1960s. These censuses had some sampling error that might have influenced our results and inflated our estimated environmental variance, but we assumed that these effects were common to all the censuses included in the analyses and that all of the populations were affected similarly. It is possible that populations at risk be surveyed more intensively, which would minimize the amount of variance due to sampling error in those populations that are most strongly affected by temporal stochasticity in population size.

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