

Predicting population survival under future climate change: density dependence, drought and extraction in an insular bighorn sheep

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Summary

1. Our understanding of the interplay between density dependence, climatic perturbations, and conservation practices on the dynamics of small populations is still limited. This can result in uninformed strategies that put endangered populations at risk. Moreover, the data available for a large number of populations in such circumstances are sparse and mined with missing data. Under the current climate change scenarios, it is essential to develop appropriate inferential methods that can make use of such data sets.

2. We studied a population of desert bighorn sheep introduced to Tiburon Island, Mexico in 1975 and subjected to irregular extractions for the last 10 years. The unique attributes of this population are absence of predation and disease, thereby permitting us to explore the combined effect of density dependence, environmental variability and extraction in a ‘controlled setting.’ Using a combination of nonlinear discrete models with long-term field data, we constructed three basic Bayesian state space models with increasing density dependence (DD), and the same three models with the addition of summer drought effects.

3. We subsequently used Monte Carlo simulations to evaluate the combined effect of drought, DD, and increasing extractions on the probability of population survival under two climate change scenarios (based on the Intergovernmental Panel on Climate Change predictions): (i) increase in drought variability; and (ii) increase in mean drought severity.

4. The population grew from 16 individuals introduced in 1975 to close to 700 by 1993. Our results show that the population’s growth was dominated by DD, with drought having a secondary but still relevant effect on its dynamics.

5. Our predictions suggest that under climate change scenario (i), extraction dominates the fate of the population, while for scenario (ii), an increase in mean drought affects the population’s probability of survival in an equivalent magnitude as extractions. Thus, for the long-term survival of the population, our results stress that a more variable environment is less threatening than one in which the mean conditions become harsher. Current climate change scenarios and their underlying uncertainty make studies such as this one crucial for understanding the dynamics of ungulate populations and their conservation.

Key-words: Bayesian state space model, bighorn sheep, climate change, density dependence, population dynamics

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Introduction

Earth's climate is changing faster than the Intergovernmental Panel on Climate Change (IPCC 2001) models predicted (Rahmstorf *et al.* 2007). As a consequence, the fate of a wide range of species is increasingly uncertain (Stenseth *et al.* 2002; Thomas *et al.* 2004). A poor understanding of the relationship between population dynamics and environmental variability hinders conservation efforts to prevent population extinctions (Hulme 2005).

Ecological theory has struggled to determine the mechanisms that influence wild populations. Debate has focused mainly on comparing the importance of environmental effects and density-dependent feedback mechanisms (Coulson, Milner-Gulland & Clutton-Brock 2000; Jacobson *et al.* 2004). The study of simplified systems, for which sources of variability other than those mentioned above are either controlled or absent, represent a valuable opportunity to inform the debate. For example, some ungulate populations not exposed to predation and diseases are bounded by a combination of environmental variability and density-dependent interactions (Choquenot 1991; Saether 1997; Coulson *et al.* 2001; Jacobson *et al.* 2004). Particularly for those living in xeric environments, food shortages in response to environmental variability can strongly limit their dynamics (Sinclair, Dublin & Borner 1985; Choquenot 1991; Mduma, Sinclair & Hiborn 1999). As a result, they can show over-compensatory density dependence that translates into wide population fluctuations (Grenfell *et al.* 1992; Clutton-Brock *et al.* 1997; Larter *et al.* 2000). However, the variable nature of some of the environmental conditions they are exposed to can promote oscillations of the same magnitude as density-dependent effects (Coulson *et al.* 2000), and therefore the key driver of their population dynamics is not always clear-cut.

Historically, ungulate populations have been intensively managed (Wright 1999). Interactions between the extraction regimes employed, environmental variability and over-compensatory density dependence adds another level of complexity that has practical consequences to successful management (Wright 1999, Milner *et al.* 2006). For example, desert bighorn sheep (*Ovis Canadensis* Shaw), has undergone strong management pressures as a consequence of its conservation status and the limited number of wild populations (Bleich, Wehausen & Holl 1990; Torres, Bleich & Wehausen 1994). Re-introductions into historical ranges have been widely implemented with little or no knowledge about the species' tolerance to environmental variability and the strength of its density-dependent interactions.

Such has been the case of the bighorn sheep population on Tiburon Island, Mexico, which was initially introduced in 1975 with the expectation that it could become a source to repopulate the species' historical range in Sonora and other states (Montoya & Gates 1975). The Island had important advantages over the mainland in that it provided the ideal habitat for the species and all major predators were absent, particularly mountain lions. The population grew from 16 to around 700 individuals in less than 20 years (Lee & Lopez-Saavedra 1993) and, after 1996, was subjected to considerably uneven yearly extractions, which seemed to have an important influence in its dynamics (see

Table 1. Number of hours flown (hour), sheep sighted per year, and number of sheep extracted during survey years

Year	Hours flown	Sheep counted	Sheep extracted
1975	0·0	*16	0
1984	3·0	**45	0
1993	4·7	293	0
1996	4·5	287	16
1997	4·1	227	60
1998	3·3	215	0
1999	3·0	130	129
2001	3·9	218	7
2003	5·1	306	8
2006	3·7	366	8

*Actual size of the introduced group. **DeForge & Valdes (1984).

Table 1; Lee 2001; Medellin *et al.* 2005). Since two of the three major causes of mortality for the species are absent for this population, namely predation (Hayes *et al.* 2000; Festa-Bianchet *et al.* 2006) and diseases (Gross, Singer & Moses 2000), it is most likely affected by food quality and availability determined by droughts (Young 1994; Epps *et al.* 2004).

A key challenge to drawing inference from any small, controlled population is that its dynamics incorporate sources of uncertainty that cannot easily be tackled under a traditional statistical framework. Most modelling approaches are forced to adopt a clear separation between the deterministic process and the variability due to stochastic processes, particularly when the goal is to discern the effect of different sources of variability. Bayesian hierarchical state space models allow us to treat each source of uncertainty as being conditionally related to the process to be modelled (Clark & Bjornstad 2004). This framework entails a more realistic treatment of uncertainty with the added advantage that it is not limited by model dimension (i.e. number of parameters). Also, a common problem in ecological data sets is the presence of missing data. This method uses a probabilistic framework during inference to predict missing data while exploring parameter space.

This study explores the strength of density dependence and environmental regulation on the Tiburon Island bighorn sheep population, using Bayesian state space models that incorporate extractions and explicitly consider different sources of uncertainty for a small data set. We then use stochastic simulations with the resulting models to explore extinction probabilities under the combined effect of density dependence, environmental variability and different levels of extraction for future climates change scenarios.

Materials and methods

STUDY AREA

The study area is Tiburon Island (~29·0°N, 112·0°W), the largest island in the Gulf of California (1028 km²), 3 km off the coast of Sonora, Mexico. The island is crossed by two mountain ranges ('sierras') from north to south; Sierra Kun Kaak, the highest (600 m

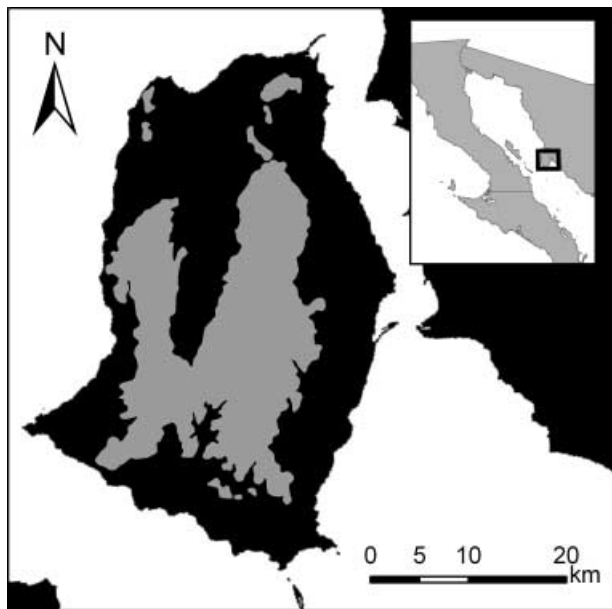


Fig. 1. Tiburon Island on the Gulf of California, Mexico. The two main mountain ranges are outlined in grey: the Sierra Kun Kaak to the east and the Sierra Menor to the west.

above sea level) to the east; and the Sierra Menor to the west (Fig. 1). These constitute the bulk of the 400 km² of suitable habitat for the species. The vegetation communities on the island are characteristic of the Sonoran desert, dominated by deciduous shrubs and succulent cacti and a few deciduous trees (Ezcurra, Equihua & Lopez-Portillo 1987). Annual rainfall varies from 75 to 375 mm, with two wet seasons: the first from December through March and the second from July to September (Ezcurra & Rodriguez 1986).

DATA COLLECTION

In 1975, 16 desert bighorn sheep (*Ovis canadensis mexicana* Merriam) were introduced to Tiburon Island. Fourteen ewes and two rams survived (Montoya & Gates 1975). These animals were relocated from the Sonoran mountain ranges facing the island, some 5 km away. In 1984, DeForge and Valdez (1984) reported the first aerial survey, followed by eight more in 1993, 1996 to 1999, 2001, 2003, and 2006 (Lee 2001; R. Lee, unpublished data). All surveys were performed in mid-October to early November. Due to the prohibitive costs of performing this type of surveys, data are available for a limited number of years, most of which were not consecutive.

Based on studies for which areas with known numbers of desert bighorn sheep were repeatedly flown (Miller *et al.* 1989; Remington & Welsh 1989; R. Lee, unpublished data), it has been established that the proportion of the population detected per hour flown is close to 0.09 sheep h⁻¹. Thus, to standardize our data, we divided the number of sheep counted at each occasion by the number of hours flown. Observation errors were further accounted for within the modelling framework (see Bayesian state space models section below).

POPULATION GROWTH MODELS

The basic deterministic structure of our model assumes that the population at time t (n_t) is a function of its size at time $t - 1$ and an individual growth parameter (r_t), being of the form

$$n_t = n_{t-1} \exp(r_t) - E_t,$$

where E_t corresponds to the number of animals that have been extracted between $t - 1$ and t . Although n_t is a continuous variable, we can calculate it as the expected number of sheep in the 400 km² of available habitat on the Island (Turchin 2003). This facilitates incorporating the actual number of sheep extracted E_t into the model as well as finding a closer approximation of the actual population size from this density. For simplicity, we will refer to this area wide density, n_t , as the expected number of sheep.

By letting $\log(n_t) = x_t$, the process follows a linear structure. Thus, it is necessary to integrate E_t into a logarithmic expression, which can be accomplished by solving for the term $e_t = \log |1 - ((E_t)/(n_{t-1}e^t))|$. Thus, in the absence of extractions, e_t is null, and negative otherwise. The final version of the basic deterministic equation is.

$$x_t = x_{t-1} + r_t + e_t = f(x_{t-1}) \quad \text{eqn 1}$$

We tested six competing models: three with varying degrees of density dependence and three versions of the first models but with environmental effects (i.e. drought) included. The first (or null) assumes that r_t is only a function of individual birth and death rates, summarized by the parameter β_0 , with no dependence on population density.

$$x_t = x_{t-1} + \beta_0 + e_t \quad \text{eqn 2a}$$

The second model is the stochastic Gompertz model, which has a limited effect of density dependence since r_t is proportional to the natural logarithm of n_{t-1} (i.e. x_{t-1})

$$x_t = x_{t-1} + \beta_0 + \beta_1 x_{t-1} + e_t \quad \text{eqn 2b}$$

where β_1 accounts for the effect of density dependence. The third model is the stochastic Ricker model, with a larger effect of density dependence than the previous model, with r_t linearly related to n_{t-1}

$$x_t = x_{t-1} + \beta_0 + \beta_1 n_{t-1} + e_t \quad \text{eqn 2c}$$

To incorporate drought into the models, we obtained summer (July, August and September) standardized precipitation index (SPI) data for 1975 to 2006, from the North American Drought Monitor (Heim 2002; Svoboda *et al.* 2002). We selected summer precipitation since it conditions primary productivity during the following seasons, which are in turn key for ewes' reproductive success (Turner & Hansen 1990). The data were collected at the National Oceanic and Atmospheric Administration (NOAA) weather station located at Santa Rosalia, Baja California Sur, 170 km south-west of Tiburon Island, the closest in the sea of Cortez (available online)¹. This index represents the probability of recording a given amount of precipitation, standardized so that the median is equal to 0. Negative index values correspond to drought while wet conditions are positive. As the dry or wet conditions become more severe, the index becomes progressively more negative or positive; an index smaller than -2 indicates extreme drought conditions.

We incorporated the effect of drought on the three competing population growth models as

$$x_t = f(x_{t-1}) + \beta_2 d_t + \varepsilon_t \quad \text{eqn 3}$$

1. (<http://www.ncdc.noaa.gov/oa/climate/monitoring/drought/nadm/spi-data-files.html#doc>)

where d_t is the averaged summer SPI value at year t , and β_2 is the parameter relating it to x_t . A preliminary analysis that included an interaction between drought and density dependence did not yield conclusive results, therefore we decided that equation (3) had the correct resolution for the amount of data and our modelling approach.

BAYESIAN STATE SPACE MODELLING FOR POPULATION GROWTH

For most wildlife surveys, the number of individuals seen (o_t) represents an observed fraction of the population, which can vary based on a range of factors independent from the process itself, such as observer experience, visibility, vegetation density, etc. (Miller *et al.* 1989; Remington & Welsh 1989). This implies that modelling such systems can be improved by explicitly separating the error associated to the observed data and that associated to the underlying state, represented by the process. To achieve this, we followed Clark and Bjornstad's (2004) modelling approach, which considers the pair of equations.

$$x_t = f(x_{t-1}) + \varepsilon_t \tag{eqn 4a}$$

$$y_t = g(x_t) + w_t \tag{eqn 4b}$$

where equation (4a) represents the process model with x_t , as in equation (1), the log of the underlying state (i.e. population size or density) at time t , and ε_t a Gaussian error term [$\varepsilon_t \sim N(0, \sigma^2)$] that accounts for the variability not explained by $f(x_{t-1})$. The observation or data model is represented by equation (4b), where y_t is the log of the observed number of individuals [$\log(o_t)$] at time t , standardized by effort, in this case per hour flown, $g(x_t)$ is the function that relates the observations to the underlying state; $g(x_t) = x_t - \alpha = y_t$, where α is the log of the proportion of individuals seen per hour flown (i.e. 0.09 in this case), and w_t is a normally distributed error term [$w_t \sim N(0, \tau^2)$] that accounts for observation error. By modelling the number counted with respect to the real number as a log-normal regression, we make certain that no negative estimates of the population size arise during inference, while accounting for the increase in error with population size. The conditional posterior of x_t is

$$\frac{p(x_t | x_{t-1}, x_{t+1}, y_t, \mathbf{B}, \sigma^2, \tau^2)}{p(x_{t+1} | f(x_t; \mathbf{B}), \sigma^2) p(y_t | g(x_t; \alpha), \tau^2)} \propto p(x_t | f(x_{t-1}; \mathbf{B}), \sigma^2) \times \tag{eqn 5}$$

where \mathbf{B} is the vector of β parameters that describe the population growth process. Change in population size is a first order Markov process, in which the probability of a given population size at time t (x_t) is conditionally dependent on the processes immediately connected to it; its size at time $t - 1$ and $t + 1$, and to the observed number of individuals (y_t) at time t (5). In this case, the model does not need to be conditioned on the initial population size since this is known for the Tiburon Island bighorn sheep population ($n_0 = 16$ sheep). For missing observations, the third factor on the right-hand side of equation 5 is not included. It can be expected that in these cases the predictive intervals around x_t will be comparatively larger than for those for which y_t is known.

The full Bayesian model incorporates prior information in the form of (i) variation on the error terms using conjugate inverse gamma distributions, $\sigma^2 \sim IG(s_1, s_2)$ and $\tau^2 \sim IG(s_3, s_4)$; (ii) a prior distribution for the parameters in the process models: $\mathbf{B} \sim N(\mathbf{B}_0, \Lambda)$, where \mathbf{B}_0 is a vector of mean values for the parameters and Λ is a covariance matrix; and (iii) for the data model $\alpha \sim N(\alpha_0, v^2)$. The prior for $\beta_0 = 0.3$ is informative based on previous reported values of the intrinsic growth rate for the species under similar conditions (Deming 1961, Woodgerd 1964, Singer, Zeigenfuss & Spicer 2001).

To assign a prior to β_1 , we used previous estimates of average densities (2 sheep km⁻²) for populations of the same subspecies assumed to have reached carrying capacity (DeYoung *et al.* 2000). The available sheep habitat on the island is about 400 km², which means that the carrying capacity K should be somewhere around 800 sheep, thus, the prior β_1 for the Ricker model is $\beta_1 = -\beta_0/K = -0.0004$, and for the Gompertz model it is $\beta_1 = -\beta_0/\log(K) = -0.05$ (both were rounded to the first significant digit). We set the diagonal elements of the covariance matrix Λ at 10. We fixed the mean prior α_0 for the detection proportion α based on estimates from studies that established the proportion of sheep observed per hour flown in areas with known population sizes around 0.09 sheep h⁻¹ (Miller *et al.* 1989; Remington and Welsh 1989; R. Lee personal communication). Thus, the final joint posterior is

$$p(\mathbf{B}, \alpha, \sigma^2, \tau^2, \mathbf{x} | \mathbf{y}) \propto \overbrace{\prod_{t=2}^T N(x_t | f(x_{t-1}), \mathbf{B}, \sigma^2)}^{\text{Process model}} \times \overbrace{\prod_{t \in O} N(y_t | \alpha + x_t, \tau^2) N(\mathbf{B} | \mathbf{B}_0, \Lambda) N(\alpha | \alpha_0, v^2)}^{\text{Data model Priors for params.}} \times \overbrace{IG(\sigma^2 | s_1, s_2) IG(\tau^2 | s_3, s_4)}^{\text{Priors for errors}} \tag{eqn 6}$$

where T is the number of years covered by the time series and O is the set of years with observed data. Posterior distributions for the parameters are obtained by sampling using a Markov chain Monte Carlo scheme (MCMC, Gelfand & Smith 1990). For conditional posteriors with conjugate distributions, the parameters are sampled directly. For nonconjugate conditional posteriors (i.e. the likelihood function in this case), a Metropolis algorithm is used. This process uses jump distributions centred on the estimates from the previous iteration, to propose new parameters at each step. If the proposed parameters have larger support from the data and priors, they are updated. The process is maintained for several thousand steps after convergence is reached, leaving aside what is called the 'burn-in' initial sequence. The remaining sequence in turn permits to build posterior densities and to estimate credible intervals for the parameters. (For more details on the modelling approach, see Clark & Bjornstad 2004.) We ran each model for 100 000 steps with a burn-in of 50 000. To avoid calculating any of the following statistics from autocorrelated estimates (i.e. estimates from contiguous MCMC steps), we thinned the results by keeping only 300 values separated by 150 steps.

For model selection, we constructed predictive distributions of y obtained from the sampling process and calculated from the thinned sequences of parameters (i.e. which had already reached convergence), and applied a predictive criterion (D_m) for each model m , calculated from the sum of a goodness-of-fit (G_m) and a penalty (P_m) terms (Gelfand & Ghosh 1998).

We performed all our analysis on the open source software R (R Development Core Team 2008). The R code for several examples of state-space models for time series of this sort will be available at <http://www.nicholas.duke.edu/people/faculty/clark>.

EFFECT OF DROUGHT AND EXTRACTION ON THE POPULATION SURVIVAL PROBABILITY

Based on the IPCC projections, we explored two possible scenarios of drought change: (i) an increase in drought variability (i.e. increase in SPI standard deviation values; σ_{SPI}); and (ii) an increase in mean drought (i.e. decrease in SPI mean values; μ_{SPI}).

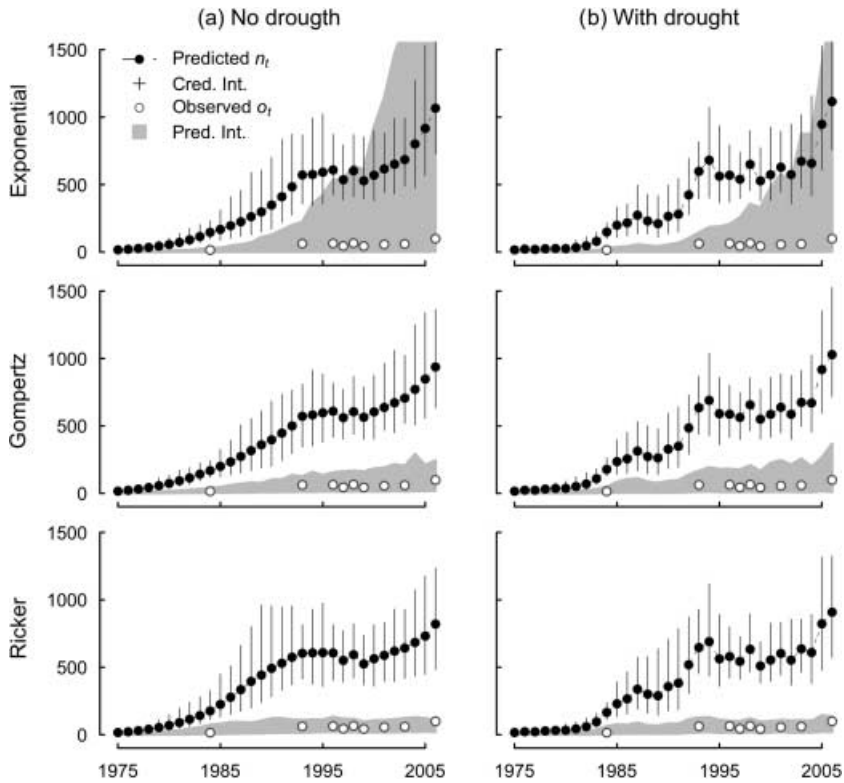


Fig. 2. Result from MCMC sampling for all models. The solid dots represent the mean n_t values for the predicted (expected) population size, the vertical lines are the 95% credible intervals for the estimated population sizes (n_t), the open gray circles are the observed number of sheep per hour surveyed (o_t), and the gray surface is the 95% predictive interval [i.e. the range of predictions for the observations (o_t), not for the actual population sizes (n_t)]. The plots are organized in two columns, (a) no drought included and (b) drought included, and the rows correspond to the model type.

We ran Monte Carlo simulations for both scenarios varying extraction numbers (E_t) from 0 to 100 sheep. For the first scenario, we gradually increased the variability in SPI from $\sigma_{\text{SPI}} = 0$ to $\sigma_{\text{SPI}} = 4$. Similarly, we changed the mean SPI values from $\mu_{\text{SPI}} = 0$ (i.e. the current value) to $\mu_{\text{SPI}} = -1.5$. We used 1000 simulations for each combination of E_t and σ_{SPI} or μ_{SPI} , each of which accounted for a 100-year population trajectory. We obtained the SPI values by randomly sampling from a normal distribution [scenario (i) $\text{SPI} \sim N(0, \sigma_{\text{SPI}})$; (ii) $\text{SPI} \sim N(\mu_{\text{SPI}}, 2)$]. We randomly selected 1000 sets of parameters from the list of estimates obtained from the MCMC estimation, which we applied to each of the simulations. We calculated the proportion of populations that survived at the end of each simulation, which we interpreted as the probability of population survival (p) under the extraction and drought conditions.

Results

DATA COLLECTION

After 1993, the estimated population size (N) fluctuated around a mean estimated n of 686 sheep ($\text{SD} = 191$; Table 1). This represents an average density of 1.72 sheep km^{-2} for the suitable habitat on the Island.

MODEL SELECTION

The model with the lowest D_m value was the Ricker model with no environmental effect followed by the same model with drought (Fig. 2, Table 2). Although within the range of values reported for several species, the initial individual growth rate parameter obtained ($\beta_0 = 0.31$; Table 2) for the first model was,

as expected, higher than previous estimates for translocated populations of desert bighorn sheep in the western USA (highest reported is $\beta_0 = 0.23$ for Pool Creek, Colorado; Singer *et al.* 2001), the highest sustained initial growth rate reported for the species being $\beta_0 = 0.27$ by Woodgerd (1964) for Wildrose Island, Montana. The higher β_0 is consistent with the fact that there are no natural predators or major external diseases for the species on the island. We also estimated the mean carrying capacity as $K = \beta_0/\beta_1 = 652$ sheep.

The predictive accuracy of the exponential model is dramatically reduced by the end of the study (Fig. 3). This is likely because this model does not assume density dependence, and thus the stochastic nature of the predictive method yields a wide range of estimates for the observed number of sheep (o_t), which translates into wide predictive intervals that increase with longer t . This stresses the importance of density dependence as a regulatory mechanism for this population.

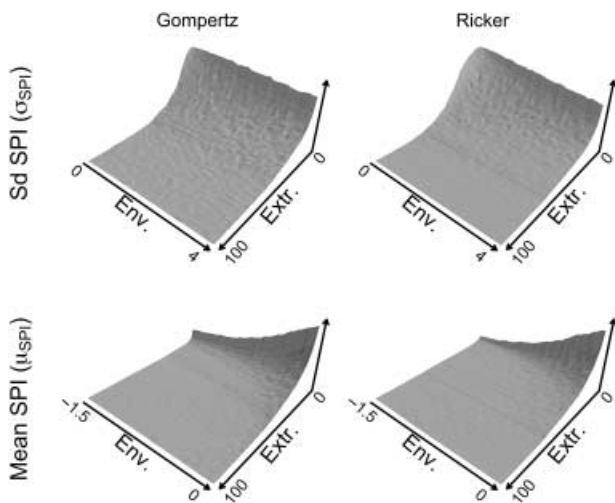
For the following section of the analysis, we used both the Ricker and Gompertz models with drought effects since both had considerably smaller D_m values than the exponential version (see Fig. 2, predictive intervals). In both cases, the 95% credible interval for drought parameter (β_2) did not include 0.

EFFECT OF DROUGHT AND EXTRACTION ON THE POPULATION SURVIVAL PROBABILITY

Our results show that an increase in drought variability (σ_{SPI}) has a limited effect on population survival with respect to an increase in extraction (E_t). Nonetheless, it still predicts that a

Table 2. Summary of results from predictive loss test for the effect of density dependence and environmental variability on the Tiburon Island bighorn sheep population, and estimated 2.5, 50%, and 97.5% quantiles for each parameter

Model	G_m	P_m	D_m	Quantile	σ^2	τ^2	α	β_0	β_1	β_2
Ricker	0.47	1.76	2.22	50%	0.0231	0.0403	-2.366	0.3096	-0.00046	
				2.5%	0.0075	0.0054	-2.510	0.1995	-0.00091	
				97.5%	0.1130	0.2549	-2.198	0.5044	-0.00024	
Ricker with SPI	0.4	2.34	2.73	50%	0.0224	0.0294	-2.369	0.1958	-0.00037	0.4144
				2.5%	0.0066	0.0047	-2.526	0.0462	-0.00074	-0.0418
				97.5%	0.1105	0.1929	-2.228	0.3869	-0.00014	0.8769
Gompertz	0.39	3.24	3.63	50%	0.0197	0.0378	-2.386	0.6060	-0.08487	
				2.5%	0.0053	0.0074	-2.516	0.2827	-0.14085	
				97.5%	0.1160	0.1846	-2.231	0.9130	-0.03224	
Gompertz with SPI	0.54	3.92	4.46	50%	0.0203	0.0286	-2.406	0.4204	-0.06750	0.4437
				2.5%	0.0051	0.0060	-2.555	0.1001	-0.12252	-0.0580
				97.5%	0.0962	0.1409	-2.251	0.7616	-0.01538	0.8915
Exponential with SPI	5.57	14.24	19.8	50%	0.0308	0.0316	-2.381	0.0409		0.5602
				2.5%	0.0093	0.0054	-2.531	-0.0529		0.0510
				97.5%	0.1281	0.1836	-2.220	0.1616		1.0975
Exponential	4.68	22.68	27.36	50%	0.0446	0.0357	-2.367	0.1397		
				2.5%	0.0144	0.0046	-2.525	0.0548		
				97.5%	0.1745	0.1987	-2.227	0.2427		

**Fig. 3.** Predicted probability of population survival under increasing extraction (Extr.) and environmental forcing (drought; Env.) with Gompertz and Ricker models. We tested two drought change scenarios: (a) increase in SPI variability (i.e. standard deviation, σ_{SPI}); and (b) reduction in mean SPI values (i.e. increase in drought conditions, μ_{SPI}).

less variable environment reduces the probability of extinction (Fig. 3). On the other hand, an increase in average drought conditions (μ_{SPI}) affects in a similar proportion the probability of survival as E_t (Fig. 3).

Discussion

FACTORS AFFECTING THE TIBURON ISLAND'S BIGHORN SHEEP POPULATION

Our results show that the Tiburon Island's bighorn sheep population is bounded by a combination of density dependence, environmental variability and extractions. In the absence of

predation and diseases, this population grew from a small founding population of 16 individuals to an average size of around 700 sheep; comparatively faster than other populations of the species (Woodgerd 1964; Singer *et al.* 2001). Anomalous cases of initial growth rates of 0.329 to 0.365 were reported by Deming (1961) for a herd introduced into Hart Mountain, Oregon in 1954, but were only sustained for the first three years after introduction. However, in the absence of predation and major diseases, it is not surprising that this population was capable of maintaining such sustained growth.

None of the models tested explained entirely the population's fluctuations (see values for σ^2 Table 2), even those that had stronger support from the data. An important issue is that, due to the coarse nature of the data, we were unable to distinguish between factors affecting fecundity and juvenile and adult mortality. It is likely that with a data set with which we could distinguish different ages or stages, we would be able to further improve the predictive accuracy of the model (Coulson *et al.* 2001). However, despite these limitations, namely the small number of sample points and the lack of stage or age resolution common to many data sets, our modelling approach has considerably good predictive accuracy as shown in Fig. 2.

Although the inclusion of drought did not improve the accuracy of the models, the effect of this variable was significant to close to 95% confidence in both weak and strong density-dependent models. Thus, this supports the assumption that environmental variability, particularly summer droughts, can represent a discernable limiting factor for the species (Gaillard, Festa-Bianchet & Yoccoz 1998). It is during this time that ewes enter oestrous and are lactating (Turner & Hansen 1990), which means that a reduction in food supply due to drier conditions can promote a decline in recruitment as a result of higher lamb mortality.

The climate on Tiburon Island is characteristic of the Sonoran Desert, with hot summers and relatively mild winters (Ezcurra & Rodriguez 1986). The outcomes of this

scarce precipitation and subsequent drought are reductions in food quality and quantity, which are a strong population control mechanism for other ungulate populations (Sinclair *et al.* 1985; Choquenot *et al.* 1990; Mduma *et al.* 1999). In this case, the lack of predation and diseases and the subsequent rapid population growth, together with considerable variable drought conditions, could be responsible for the current fluctuations around the carrying capacity (close to 650 sheep). Moreover, these wide fluctuations are responding to the latter and trigger over-compensatory density dependence regulations (Clutton-Brock *et al.* 1997; Larter *et al.* 2000). Such fluctuations could be a response to delayed effects on vital rates that, with a more complete data set, could be better explained by the inclusion of lags into the models (Turchin 1990; Turchin, Taylor & Reeve 1999).

CLIMATE CHANGE AND POPULATION SURVIVAL

One of the IPCC long-term climate change predictions, which follows the IS92a scenario (doubling of atmospheric carbon dioxide concentration, moderate economic growth, and 'business as usual' in curbing anthropogenic emissions), predicts that there will be no significant changes in mean drought in the region, with possible increases in drought variability (Collins, Tett & Cooper 2001; Mitchell *et al.* 2004). Under this scenario, our results suggest that the major external force on the population will be management-related extractions. However, assuming that no extractions are implemented, our model still predicts a reduction in survival probability with higher environmental variability. Under scenario (ii), that predicts an increase in mean drought as foreseen by models A2 and B2 of the IPCC, the synergistic effect of drought and extractions of medium to large numbers of individuals dramatically affects population survival. In this case, even with the moderate changes projected by models A2 and B2, our results suggest that, with a constant extraction rate of 20 sheep per year, the risk of extinction could increase from 50% to 70%, the extreme case being almost 90% (Fig. 3). Similar simulations with extractions every two years still yielded the same results.

MODELLING AND INFERENCE FROM SMALL DATA SETS

Ecological data of the type we analysed here are extremely common; species that are too costly to follow, or those that are rare or endangered are typical cases for which the data available are scarce and incomplete. Measurement uncertainty and missing observations result in data sets with few data points that tend to be considered inappropriate for inference and decision-making. However, under the current trends in climate change and diversity loss, it is essential to face the statistical challenges that these data sets entail. Thus, in conjunction to understanding the factors influencing the Tiburon Island population dynamics, the aim of this project was to develop a modelling framework that facilitated using such types of data sets and still being able to draw useful conclusions. In that sense, our analyses stress the sensitivity that wild

ungulate populations have toward changes in mean environmental conditions and emphasize the need for more conservative management and conservation plans under climate change, based on robust predictive models and ecological information.

Acknowledgements

We thank Carlos Manterola and Manuel Valdes for coordinating and providing major support for the project, the Seri Government for their permission to work on Tiburon Island, and the Seri Bighorn team, Francisco Navarro and Felipe Rodriguez for their help in data collection and logistics, Dalia Amor Conde, Sean McMahon, Jessica Metcalf, Joe Sexton, Benjamin Poulter, Sandra Cavalieri and Paul Stoy for their reviews and comments, as well as two anonymous reviewers for their valuable suggestions. This project was supported by CEMEX, BIOCONCIENCIA and Wildlife Trust, as part of the National Recovery Plan for Bighorn Sheep led by the Dirección General de Vida Silvestre of the Mexican Federal Government (SEMARNAT), Unidos Para la Conservación, A.C., and the Institute of Ecology, National Autonomous University of Mexico.

References

- Bleich, V.C., Wehausen, J.D. & Holl, S.A. (1990) Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conservation Biology*, **4**, 383–390.
- Choquenot, D. (1991) Density-dependent growth, body condition, and demography in feral donkeys: testing the food hypothesis. *Ecology*, **72**, 805–813.
- Clark, J.S. & Bjornstad, O.N. (2004) Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology*, **85**, 3140–3150.
- Clutton-Brock, T.H., Illius, A.W., Wilson, K., Grenfell, B.T., MacColl, A.D.C. & Albon, S.D. (1997) Stability and instability in ungulate populations: an empirical analysis. *The American Naturalist*, **149**, 195–219.
- Collins, M., Tett, S.F.B. & Cooper, C. (2001) The internal climate variability of HadCMw, a version of the Hadley Center coupled model without flux adjustments. *Climate Dynamics*, **17**, 61–81.
- Coulson, T., Milner-Gulland, E.J. & Clutton-Brock, T. (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society B: Biological Sciences*, **267**, 1771–1779.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M., Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Nature*, **292**, 1528–1531.
- DeForge, J.R. & Valdez, R. (1984) Status of investigations of desert bighorn sheep in Sonora, Mexico. *Desert Bighorn Council Transactions*, **28**, 41–43.
- Deming, O.V. (1961) Bighorn sheep transplants at the Hart Mountain National Antelope Refuge. *Desert Bighorn Sheep Council Transaction*, **5**, 56–57.
- DeYoung, R.W., Hellgren, E.C., Fulbright, T.E., Robbins, Jr., W.F. & Humphreys, I.D. (2000) Modeling nutritional carrying capacity for translocated desert bighorn sheep in Western Texas. *Restoration Ecology*, **8**, 57–65.
- Epps, C.W., McCullough, D.R., Wehausen, J.D., Bleich, V.C. & Rechel, J.L. (2004) Effect of climate change on population persistence of desert-dwelling mountain sheep in California. *Conservation Biology*, **18**, 102–113.
- Ezcurra, E. & Rodrigues, V. (1986) Rainfall patterns in the Gran Desierto, Sonora, Mexico. *Journal of Arid Environments*, **10**, 13–28.
- Ezcurra, E., Equihua, M. & Lopez-Portillo, J. (1987) The desert vegetation of El Pinacate, Sonora, Mexico. *Vegetatio*, **71**, 49–60.
- Festa-Bianchet, M., Coulson, T., Gaillard, J.M., Hogg, J.T. & Pelletier, F. (2006) Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1537–1543.
- Gaillard, J.M., Festa-Bianchet, M. & Yoccoz, N.G. (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends in Ecology & Evolution*, **13**, 58–63.
- Gelfand, A.E. & Ghosh, S.K. (1998) Model choice: a minimum posterior predictive loss approach. *Biometrika*, **85**, 1–11.
- Gelfand, A.E. & Smith, A.F.M. (1990) Sampling-based approach to calculating marginal densities. *Journal of the American Statistical Association*, **85**, 398–409.
- Grenfell, B.T., Price, O.F., Albon, S.D. & Clutton-Brock, T.H. (1992) Overcompensation and population cycles in an ungulate. *Nature*, **355**, 823–826.

- Gross, J.E., Singer, F.J. & Moses, M.E. (2000) Effects of disease, dispersal, and area on bighorn sheep restoration. *Restoration Ecology*, **8**, 25–37.
- Hayes, C.L., Robin, E.S., Jorgensen, M.C., Botta, R.A. & Boyce, W.M. (2000) Mountain lion predation of bighorn sheep in the peninsular ranges, California. *Journal of Wildlife Management*, **64**, 954–959.
- Heim, Jr. R.R. (2002) A review of twentieth-century drought indices used in the United States. *Bulletin of the American Meteorological Society*, **83**, 1149–1165.
- Hulme, P.E. (2005) Adapting to climate change: is there scope for ecological management in the face of a global threat? *Journal of Applied Ecology*, **42**, 784–794.
- IPCC (2001) *Climate Change 2001: Synthesis Report. A Contribution of Working Groups I, II and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Jacobson, A.R., Provenzale, A., von Hardenberg, A., Bassano, B. & Festa-Bianchet, M. (2004) Climate forcing and density dependence in a mountain ungulate population. *Ecology*, **85**, 1598–1610.
- Larter, N.C., Sinclair, A.R.E., Ellsworth, T., Nishi, J. & Gates, C.C. (2000) Dynamics of reintroduction in an indigenous large ungulate: the wood bison of northern Canada. *Animal Conservation*, **4**, 299–309.
- Lee, R. (2001) *The current status of desert bighorn sheep on Tiburon Island*. Report prepared for the Center of Ecology of the Autonomous University of Mexico.
- Lee, R. & Lopez-Saavedra, E.E. (1993) Helicopter survey of desert bighorn sheep in Sonora, Mexico. *Desert Bighorn Council Transaction* **37**, 29–32.
- Mduma, S.A.R., Sinclair, A.R.E. & Hiborn, R. (1999) Food regulates the Serengeti wildebeest: a 40-year record. *Journal of Animal Ecology*, **68**, 1101–1122.
- Medellin, R.A., Manterola, C., Valdez, M., Hewitt, D.G., Doan-Crider, D. & Fulbright, T.E. (2005) History, ecology, and conservation of the pronghorn antelope, bighorn sheep, and black bear in Mexico. *Biodiversity, Ecosystems, and Conservation in Northern Mexico*. (eds J.L. Cartron, G. Ceballos & R.S. Felger), pp. 387–404. Oxford University Press, Oxford, UK.
- Miller, R., Remington, R., Lee, R.M., Van den Berge, R. & Haderlie, M. (1989) *Efficiency of Bighorn Sheep Helicopter Surveys*. Arizona Game and Fish Department. Special report, Phoenix, Arizona.
- Milner, O.S.M., Bonenfant, C., Mysterud, A., Gaillard, J.M., Csanyi, S. & Stenseth, N.C. (2006) Temporal and spatial development of red deer harvesting in Europe: biological and cultural factors. *Journal of Applied Ecology*, **43**, 721–734.
- Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M. & New, M. (2004) *A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: observed record (1901–2000) and 16 scenarios (2001–2100)*. Working Paper 55, Tyndall Centre for Climate Change Research Norwich (Vol. in review).
- Montoya, B. & Gates, G. (1975) Bighorn capture and transplant in Mexico. *Desert Bighorn Council Transaction*, **40**, 28–32.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Rahmstorf, S., Cazenave, A., Church, J.A., Hansen, J.E., Keeling, R.F., Parker, D.E. & Somerville, R.C.J. (2007) Recent climate observations compared to projections. *Science*, **316**, 709.
- Remington, R. & Welsh, G. (1989) Surveying bighorn sheep. *The Desert Bighorn Sheep in Arizona* (ed. R. Lee), pp. 63–81. Arizona Game and Fish Department, Phoenix, Arizona.
- Saether, B.E. (1997) Population dynamics of large herbivores: a search for mechanisms. *Trends in Ecology & Evolution*, **12**, 143–149.
- Sinclair, A.R.E., Dublin, H. & Borner, M. (1985) Population regulation of Serengeti wildebeest: a test of the food hypothesis. *Oecologia*, **65**, 266–268.
- Singer, F.J., Zeigenfuss, L.C. & Spicer, L. (2001) Role of patch size, disease, and movement in rapid extinction of bighorn sheep. *Conservation Biology*, **15**, 1347–1354.
- Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K.S. & Lima, M. (2002) Ecological effects of climate fluctuations. *Science*, **297**, 1292–1296.
- Svoboda, M., LeComte, D., Hayes, M., Heim, R., Gleason, K., Angel, J., Rippey, B., Tinker, R., Palecki, M., Stooksbury, D., Miskus, D. & Stephens, S. (2002) The drought monitor. *Bulletin of the American Meteorological Society*, **83**, 1181–1190.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Torres, S.G., Bleich, V.C. & Wehausen, J.D. (1994) Status of bighorn sheep in California, 1993. *Desert Bighorn Council Transactions*, **38**, 17–28.
- Turchin, P. (1990) Rarity of density dependence or population regulation with lags? *Nature*, **344**, 660–663.
- Turchin, P. (2003) *Complex Population Dynamics. A Theoretical Empirical Synthesis*. Princeton University Press, Princeton, New Jersey.
- Turchin, P., Taylor, A.D. & Reeve, J.D. (1999) Dynamical role of predators in population cycles of a forest insect: an experimental test. *Science*, **285**, 1068–1071.
- Turner, J.C. & Hansen, C.G. (1990) Reproduction. *The Desert Bighorn. Its Life History, Ecology, and Management* (eds G. Monson & L. Sumner), pp. 145–151. The University of Arizona Press, Tucson, Arizona.
- Woodgerd, W.R. (1964) Population dynamics of bighorn sheep on Wildrose Island. *Journal of Wildlife Management*, **28**, 381–391.
- Wright, R.G. (1999) Wildlife management in the National Parks: questions in search of answers. *Ecological Applications*, **9**, 30–36.
- Young, T.P. (1994) Natural die-offs of large mammals: implications for conservation. *Conservation Biology*, **8**, 410–418.

Received 9 December 2008; accepted 14 January 2009

Handling Editor: Tim Coulson