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Demography, population dynamics and sustainability of the Patagonian sheep flocks

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Abstract

Sheep production is the main agricultural activity in Patagonia. Since the middle of the 20th century, sheep numbers have declined steadly. We used historical records of stock numbers in four ranches to analyze the importance of regional factors so as to explain the decline of the Patagonian sheep flocks. We found that the stocks of all the four ranches declined with a similar trend but fluctuated independently, thus reflecting a complex interaction between regional and local factors. Aboveground net primary production (ANPP) and vegetation physiognomy explained most of the differences in the flocks declining rates. We estimated demographic parameters for two ranches differing in their average annual growth rates. From these demographic parameters, we constructed deterministic and stochastic matrix models to establish the relative contribution of demographic processes to the observed decline. Matrix models projected a faster decline than that observed in the ranch used to calibrate the model. This suggests that the recorded demographic parameters could drive most stocks to extinction in less than 100 years. We concluded that the observed dynamics would be generated by demographic processes, but extinction is delayed or avoided by a continuous intake of animals. Ewe survival was the most important parameter in controlling the growth rate of the flocks. The environmental stochastic model showed that the growth of the stocks was highly sensitive

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to increases in the frequency of good years (those that produce a positive growth) and in the transition from normal years to bad years. All these evidences point out the existence of biological constraints to sheep production in Patagonia: ANPP and vegetation structure would control flock population dynamics throughout its effects on key demographic parameters, ewe survival and marking rate (a recruitment measure). Our model results suggest that the decline in sheep numbers, and hence the sustainability of the activity, is driven, to a large extent, by the demographic characteristics of the flocks.

Keywords: Sheep; Demography; Synchrony; Matrix models; Sustainability

1. Introduction

Sheep husbandry in Patagonia started at the beginning of the 20th century from European settlers (Soriano and Paruelo, 1990). The introduction of sheep led to dramatic economic, social and ecological changes in the region. Native vegetation has been almost the only source of forage for sheep. The flocks stay in the field all year round in paddocks often of thousands of hectares and they are exposed to extreme weather conditions (Golluscio et al., 1998; Paruelo et al., 1998a). Moreover, sanitary management is minimal. Flocks behave as ‘‘semi-natural’’ populations, i.e., populations with limited human intervention.

A generalized sheep stock reduction has been reported in Patagonia during the last five decades (Golluscio et al., 1998, 1999). The number of animals fell from 20 million in 1952 to 11 millions in 1993 (Golluscio et al., 1998). This decline has been observed at different spatial scales: individual ranches, counties, provinces and the whole region. Multiple causes may explain this reduction but most of them could be associated with two groups of factors:

1. Management decisions: they involve voluntary changes in the proportion of different species (cattle, goats and sheep), or changes in the number of sheep.
2. Demography: includes changes in age structure, sex ratio, survivorship and fecundity. Changes in these demographic variables are associated with changes in the forage availability, with extreme climatic events or with the effect of predators. These factors are not independent.

Although the reduction in the Patagonian sheep stocks is a well-known fact, its causes remain largely unknown. Studies on demography and population dynamics of Patagonian flocks are scarce. Olaechea et al. (1981, 1983) conducted a series of autopsy studies in order to establish the main causes of lamb mortality in four ranches of Río Negro province. Hall (2000) conducted an extensive regional analysis of the environmental controls of lamb recruitment in eleven ranches distributed along the provinces of Neuquén, Río Negro and Chubut in Argentina. To the best of our knowledge, those are the only studies on the demography of sheep flocks in

Patagonia. A critical step to describe flocks dynamics and its exogenous and endogenous controls is to know their demographic parameters.

In this article we used time series of stock numbers and estimated demographic rates:

1. To determine the average annual growth rates of sheep flocks in four ranches, and test the significance of some ecological covariates of these rates (Golluscio et al., 1998, 1999).
2. To estimate the importance of regional factors (i.e., climate, desertification) when explaining stock trends and fluctuations. To tackle this issue, we estimated synchrony (defined as the average cross-correlation among time series, se below) in animal numbers and annual growth rates. A significant synchrony in flock dynamics would reflect the action of regional factors (Koenig, 1999).
3. To study the relative contribution of demographic processes to stock decline. To do this, we compared demographic parameters of two flocks with different rates of decline from ranches with different ecological characteristics. Moreover, we built matrix models of population dynamics to determine if demographic parameters alone could mimic the observed dynamics in the two ranches studied. First, we applied a deterministic model that uses average demographic parameters, and then stochastic models that incorporate the effect of environmental variability on demographic parameters. The last models allowed us to determine if environmental stochasticity affects the conclusions derived from the deterministic scenario.

2. Study area

The study area is located in the northwest of Patagonia, in the so-called Occidental district (Soriano, 1956). The climate is temperate or cool-temperate, with mean annual temperatures ranging from 12 °C in the northeastern region to 3 °C in the southwestern region (Paruelo et al., 1998a). The mean temperature in the coldest month (July) is greater than 0 °C in all the extra Andean Patagonia (Fig. 1); however, toward the southwest, minimum absolute temperatures are lower than −20 °C. A characteristic of Patagonian climate is the predominance of strong "westerly winds" (Paruelo et al., 1998a). Maximum wind speeds (15 – 22 km h^{-1}) occur between September and January. Strong winds reduce the wind chill over the whole region by 4.2 °C (Coronato, 1993).

Precipitation shows a strong seasonal pattern, with most of the precipitation falling during winter (Fig. 1). From the Andes mountains and eastward, total annual precipitation decreases exponentially from 800 to 150 mm y^{-1} (Jobbágy et al., 1995). This precipitation gradient influences ecosystem vegetation (Jobbagy et al., 1996; Paruelo et al., 2004), and results in an eastward decline in aboveground net primary production (ANPP) from 900 to 390 kg ha^{-1} y^{-1} (Paruelo et al., 1998b).

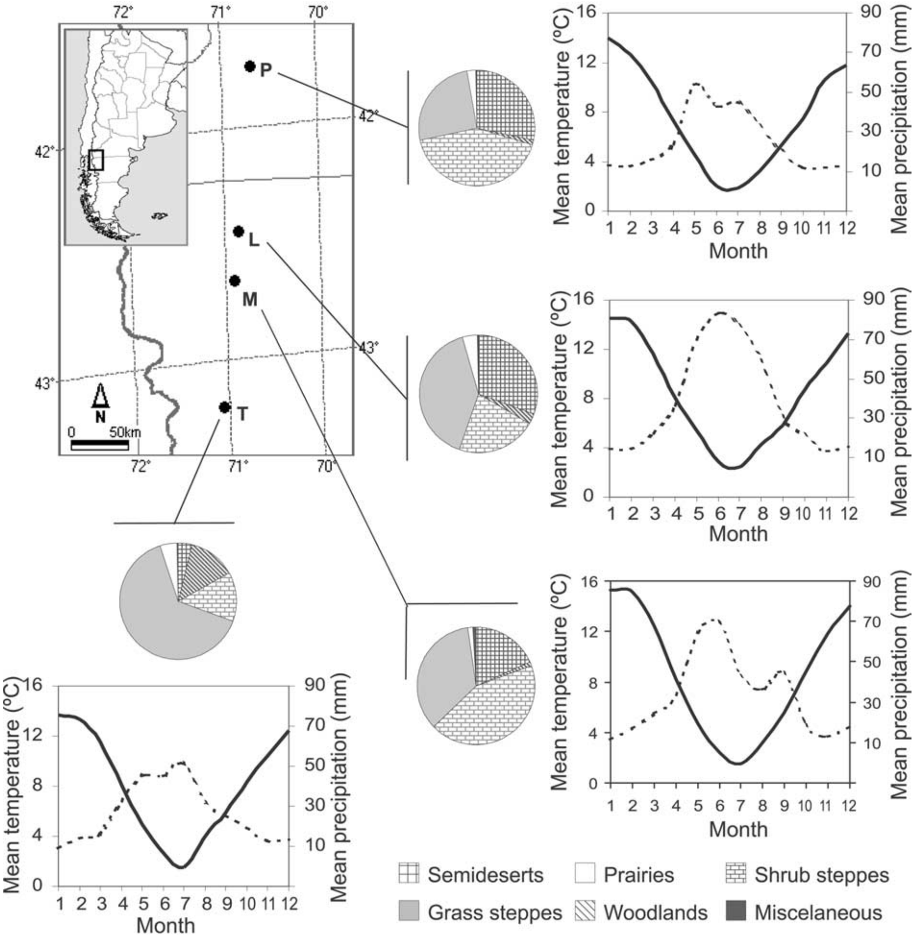
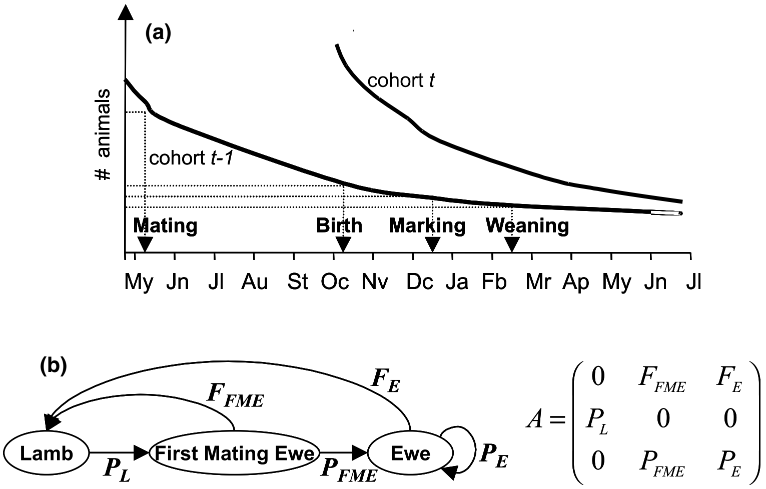


Fig. 1. Map of the study area showing the four ranches considered. Graphs show mean monthly temperature (solid line) and mean monthly precipitation (broken line). Pie charts show the proportion of physiognomic units in each ranch.

In the boundary with the sub-Antarctic forests, *Festuca pallescens* dominates the grass steppes. Toward the east, the total cover decreases and shrub proportion increases (*Mulinum spinosum*, *Adesmia campestris* and *Senecio filaginoides*), although grass stratum is still abundant (*Stipa speciosa*, *Stipa humilis*). These grass–shrub steppes dominate the Occidental district (Paruelo et al., 1991; León et al., 1998).

The four ranches studied occupy an area of more than 400,000 has. They are distributed on a strip parallel to the Andes, from Río Negro province to the center of Chubut province (between 41° S and 43° S and around 71° W, Fig. 1), and span over the major climatic gradients on the study area. The ranches were originally part of British companies settled in Patagonia by the end of the 19th century and they basically show the same production structure and a relatively similar management



$$A = \begin{pmatrix} 0 & F_{FME} & F_E \\ P_L & 0 & 0 \\ 0 & P_{FME} & P_E \end{pmatrix}$$

Fig. 2. (a) Events in the sheep life cycle and management practices. Mating, lamb births, marking, and weaning. (b) Diagram of the life cycle and the population projection matrix associated. F_{E} is ewe fecundity, F_{FME} is first mating ewes fecundity, and P_{L}, P_{FME} and P_{E} are the annual survival probabilities for lambs, first mating ewes and ewes, respectively.

(Golluscio et al., 1998). As far as we know, no other sources of long term records of production are available in the area.

The northernmost ranch ("*P*", Rio Negro province, 41° 40′ S, 70° 38′ W) occupies 41800 ha and is dominated by shrub–grass steppes (Fig. 1). The southernmost ranch ("*T*", Chubut province, 43° 20′ S, 70° 7′ W) is located 300 km from *P*, and has an approximate area of 175,000 ha. It is dominated by grass, grass–shrub steppes and by the steppe–forest ecotone, showing the highest mean annual productivity (Paruelo et al., 2004). The other two ranches are located in Chubut ("*L*", 42° 24′ S, 70° 53′ W, has an area of 108,500 ha and "*M*", 42° 43′ S y 71° 1′ W, has an area of 81,000 ha) between *"P"* and *"T"*. One of them (*"L"*) spans over the broadest precipitation and vegetation gradient, from forest to semidesert, whereas the other (*"M"*) is dominated by shrub, shrub–grass and grass–shrub steppes.

Sheep give birth in September–October, and lambs are marked in December. The number of lambs marked divided by the number of ewes at mating (marking rate) is a recruitment rate descriptor often used (Battro, 1992b). Lambs are weaned in February. During May–June, ewes are mated (Fig. 2(a)).

3. Methods

3.1. Data

Data were obtained from annual animal records from each ranch. We used time series of ewe numbers at marking (December) to estimate synchrony. Only those years available for all ranches were used. We obtained time series of marking rate (number of lambs marked in December divided by the number of females at mating) for ranches *P* (1928–2000) and *T* (1911–1999) only.

For ranch *P*, the number of ewes, first mating ewes and lambs was recorded for two months without animal movements (intakes and offtakes) each year (May and December for ewes, December and February for lambs, and July and December for first mating ewes). This allowed us to estimate the annual survival probabilities in order to build the matrix models (see below). The information available from ranch *T* was for ewes only. No data was available for ranches *L* and *M*. Data on intake and offtake of animals was not available. ANPP and vegetation physiognomic characteristics (proportion of different plant functional types) were estimated from satellite data, as described in Paruelo et al. (2004).

3.2. Analysis of time series of sheep numbers

In order to estimate the average annual growth rate for each flock, we log-transformed the time series of female numbers and regressed them against time. The slope of these regressions represents the average intrinsic rate of increase (r) during the period, whereas $R = e^r$ represents the average annual growth rate. The four average growth rates obtained were regressed against ANPP, the percentages of prairies, grass steppes and semideserts. These variables were selected because they represent the forage resources available for sheep.

Synchrony was estimated from the average cross-correlation coefficient (RS) among the raw time series of the flocks (Koenig, 1999; Bjornstad et al., 1999; Cattadori et al., 2000). This coefficient reflects the correlation among trends, and it is not a synchrony coefficient *sensu stricto*. To overcome this problem we calculated the average cross-correlation coefficient among the series of annual growth rates. These were obtained from the log-transformed, first-differenced series (r_t). These transformations remove the trends and normalize the series (Chatfield, 1989):

$$r_t = \log\left(\frac{N_{t+1}}{N_t}\right), \tag{1}$$

where N_t is the number of females at time t and N_{t+1} is the number of females at time $t + 1$. Confidence intervals for cross-correlation coefficients were generated by bootstrapping (Koenig, 1999; Bjornstad et al., 1999), since stocks and annual growth rates are not independent among years. We generated 10,000 bootstrap replicates for the average cross-correlation calculated from flock series and annual growth rate series. We regressed pairwise cross-correlation (in flock time series and annual growth rate series) against the distance between pairs of ranches to determine if flocks from ranches located close to each other showed higher similarity in dynamics.

3.3. Matrix population models

Matrix population models are widely used as tools to derive management practices of endangered wild populations and exploited populations (Doak et al., 1994;

Legendre and Colbert, 1995; Lesnoff, 1999; Caswell, 2001; Fieberg and Ellner, 2001). The general form of matrix population models is

$$\mathbf{n}_{t+1} = \boldsymbol{A}_t \times \mathbf{n}_t, \tag{2}$$

where $\mathbf{n}_t$ is a column vector, containing the number of individuals in each stage at time t, and $\boldsymbol{A}_t$ is a square matrix containing the stage-specific demographic rates. Post-multiplying the matrix by the vector yields the population and the stage size trajectories along time. According to the assumptions on the variability of the demographic rates, the projection matrix may take different forms. We describe only those forms considered in this study: deterministic and stochastic matrix models.

Deterministic models: In these models $\boldsymbol{A}_t$ can be constant or can vary in deterministic ways (density or frequency dependent models or models in which parameters are deterministic functions of environmental variables). We considered deterministic models with constant elements only. Variability in demographic rates is considered negligible in this kind of models and matrix parameters are obtained by averaging over sites or time intervals. All the relevant information on the long-term population dynamics can be calculated analytically from the matrix: the asymptotic growth rate (λ_1, the matrix dominant eigenvalue), the stable stage distribution (the right eigenvector associated to λ_1) and the reproductive values associated with each stage (the left eigenvector associated to λ_1). Sensitivity and elasticity (relative sensitivity) analyses of λ_1 with respect to matrix parameters (Legendre and Colbert, 1995; Caswell, 2001) are often performed.

P was the only ranch with data suitable to extract complete demographic information. For this reason, we constructed matrix models only for this ranch. Parameters were based only on females (we assumed a sex ratio 1:1). The age classes were those usually used by ranch managers: lambs (aged 7 months), first mating ewes (between 7 and 19 months) and ewes (more than 19 months). Sheep which are 6-year old are removed from the flocks. This was represented in the model because in survival estimation the sheep removed were considered as dead animals. We built Leslie–Lefkovitch models (Fig. 2, Lefkovitch, 1965; Caswell, 2001).

Annual survival probabilities were estimated from the difference in animal numbers at two times (see Section 3.1) assuming a constant force of mortality over the year (Caswell, 2001). This method assumes a constant stage-specific mortality μ over an interval Δt (a month in our situation), and estimates the monthly survival probability as:

$$P_{\text{monthly}} = \mathrm{e}^{-\mu\cdot\Delta t}. \tag{3}$$

We estimated the monthly mortality (μ) probability for each stage by fitting an exponential curve to female numbers in each stage recorded during two months each year. Then, we obtained the stage-specific annual survival as $\mathrm{e}^{-\mu\cdot 12}$. Standard life table methods were not used because they would confound survivorship with the movement of animals among ranches. We considered a "sheep year" (from June$_t$ to June$_{t+1}$) as the matrix projection interval. According to the sequence of events in the life cycle of sheep, fecundity was calculated as the product of marking index and lamb recruitment probability (lamb survival from marking to the next year

June). Thus, we calibrated the matrix according to a post-breeding census (Caswell, 2001). Marking rate for the first mating ewes was assumed to be 85% of ewe marking rate. In such way, we derived the series of annual demographic parameters and constructed a series of annual matrices. Average demographic parameters were used in the deterministic projection. We constructed the response surface of λ_1 respect to ewe survival and fecundity. To do this, we kept the average demographic parameters and varied ewe survival and fecundity rates only, in order to build the new matrices.

We had access to data on the number of ewes and ewes dead in May–June each year for ranch *T*. Then, we estimated ewe annual survival in year *t* by dividing the number of dead ewes in year $t + 1$ by the ewe number in the year *t*. We applied this method because offtake of animals was not included in records from ranch *T*. Marking rate was estimated in the same way as for *P*. To obtain an estimate of λ_1 for ranch *T*, we superimposed the observed ewe annual survival and fecundity rates for this ranch on the response surface of λ_1 with respect to those parameters in ranch *P*. Although this approximation is conservative (assumes that remaining parameters are the same for ranches *P* and *T*), it allowed us to obtain a possible range of values of λ_1 for ranch *T*.

The annual demographic parameters calculated were adjusted to different statistical distributions using Kolmogorov–Smirnov Goodness-of-fit tests (Zar, 1996). We applied the arcsin transformation to data on survival, and then performed a *t*-test with pooled variance (Zar, 1996) to compare the average ewe survival probabilities between ranches *T* and *P*. For marking index comparisons, the *t*-test was performed without transforming data because the distribution of this parameter for both ranches fitted to a normal distribution (see below). Both tests were one tailed.

Stochastic models. These models allow us to include environmental variability in demographic rates. To do this, an entire matrix or parameters values are selected in each iteration according to a probabilistic rule. Selecting matrices (random transition matrix approach, "RTM" Fieberg and Ellner, 2001) or matrix elements from their distributions (parametric matrix model approach, "PMM" Fieberg and Ellner, 2001) depends on the covariation among vital rates (trade offs among components of the life cycle). If covariation exists and is to be maintained, the easiest way to preserve it is to select entire matrices. In order to establish if there was covariation among demographic parameters, we calculated the Pearson correlation matrix among the annual demographic rates estimated independently (ewe survival, first mating ewe survival, marking rate and recruitment probability). Probability values for the correlations were estimated by bootstrapping (Manly, 1991).

Given the covariation patterns found (see Section 4), we followed the random transition matrix approach. The environment was modeled as a completely random process, without memory of its previous state. To estimate memory in the series for ranch *P*, we analyzed the detrended time series of animal numbers and the series of asymptotic annual growth rates produced by each annual matrix, using autocorrelograms and partial autocorrelograms (Chatfield, 1991). In order to add memory to the model we constructed a Markov chain model for the environment (Silva et al., 1991; Beissinger, 1995; Caswell, 2001). We examined the observed distribution of asymptotic annual growth rates (those produced by each annual matrix) and classified each year as "bad", "normal" or "good", according to its matrix asymptotic annual growth rate (below the 25% percentile, between the 25% and 75% percentiles or above the 75% percentile). We re-classified the growth rate series (as series of bad, normal or good years) and constructed the "environmental" transition matrix. This matrix determined the sequence of environmental states: for a bad year, we selected a population matrix from the lower 25% percentile of the λ_1 distribution at random; for a normal year, we selected a population matrix from the intermediate 50% percentile; and for good a year, we selected a population matrix from the upper 25% percentile. The subdominant eigenvalue of the environmental matrix (ρ) represents the lag 1 autocorrelation between the "environmental" states. If ρ is positive, we may expect runs of years of the same type. If ρ is negative, we may expect alternation of "environmental" states. Finally if $\rho \cong 0$, the sequence of years is completely random (and this model reduces itself to the model without memory).

A single run of each stochastic model, represents just one of the possible flock trajectories. We generated 10,000 replicated flock trajectories, iterated 1000 years each, in order to obtain Montecarlo confidence intervals (Manly, 1991; Caswell, 2001) for flock sizes, growth rates and quasi-extinction times (see below). In these models, two growth rates describe flocks growth: the growth rate of the mean population size ($\log(\mu)$) and the time averaged growth rate or stochastic growth rate ($\log(\lambda_s)$) (the mean growth rate of the replicated flocks). Quasi-extinction time was defined as the first time when the number of animals fell below some threshold (1% of the initial flock in our case).

When we assume independent and identically distributed environments (the model without memory), $\log(\mu)$ is equivalent to the mean matrix dominant eigenvalue (Tuljapurkar, 1997; Caswell, 2001). In the case of the Markov chain environmental model, $\log(\mu)$ is defined as the dominant eigenvalue of the matrix $B_1 = A \times (P \otimes I)$, where A is a diagonal block matrix, with the mean population matrices associated to each environmental state in the corresponding diagonal, P is the environmental Markov transition matrix, I is the identity matrix and "$\otimes$" denotes the Kronecker product ($P \otimes I$, is defined as the product of each element of matrix P by matrix I, Caswell, 2001). The growth rate of the mean population size and the stochastic growth rate are related by the expression:

$$\log(\mu) = \log(\lambda_s) + \frac{\sigma^2}{2}, \tag{4}$$

where σ^2 is the population size variance. This expression shows that $\log(\lambda_s) \leqslant \log(\mu)$. The size of this difference reflects the impact of environmental variability on the population dynamics. For each time in each replicate, the annual growth rate for year t is given by Eq. (1). For each replicated flock trajectory, the stochastic growth rate is given by the Heyde–Cohen estimator (Caswell, 2001):

$$\log(\lambda_s) = \frac{1}{T} \sum_{t=0}^{t=T-1} r_t. \tag{5}$$

The average stochastic growth rate across the simulation replicates will be the final estimator of log (λ_s):

$$\overline{\log(\lambda_s)} = \frac{1}{TR}\sum_{i=0}^{i=TR-1}\log(\lambda_s)_i, \tag{6}$$

where TR is the number of replicated stock trajectories (10,000), T is the number of iterations in each replicate (1000), and N_t is the flock size at time t.

We performed the stochastic sensitivity analysis of log (λ_s) for the random transition matrix model in order to see if environmental variability affected the conclusions extracted from the deterministic perturbation analysis. For the Markov chain environmental model, we estimated numerically the sensitivity of the different population dynamics statistics (log (λ_s), log (μ), mean quasi-extinction time and its standard deviation) to changes in each environmental matrix parameter. Once a parameter was changed, the other column parameters were also modified to keep the column sums equal to 1 (Caswell, 2001). In such a way, we studied the effect of hypothetical environmental changes.

3.4. Estimation of net sheep movement rate

Preliminary results indicated that the annual growth rate estimated from the deterministic model in ranch P was lower than the observed annual growth rate. We estimated the annual movement rate needed to generate the observed annual growth rate by using a harvested matrix model:

$$\boldsymbol{n}_{t+1} = \boldsymbol{H}\times\boldsymbol{A}\times\boldsymbol{n}_t \tag{7}$$

In this model, $\boldsymbol{A}$ is the constant (deterministic) matrix for ranch P, $\boldsymbol{H}$ is a diagonal matrix whose elements are $h_i = 1 + m_i$ and m_i is the proportion of animals (relative to previous year stock number) imported or exported from stage i (stage-specific annual movement rate, AMR). We estimated m_i for each stage separately (at a given time only one element in the matrix $\boldsymbol{H}$ is different from 1). We modified each h_i from 0.5 (offtaking half the animals from the stage) to 1.5 (intaking a number of animals equal to half the animals in the stage), and we obtained the annual growth rate for each AMR value (λ_h the dominant eigenvalue of the matrix $\boldsymbol{H}\times\boldsymbol{A}$). Then, we projected the population from 1928 to 1991, according to λ_h. We considered an initial size equal to the flock size in 1928. We compared the observed series of females at mating associated with the trajectories projected by each harvested matrix model using likelihood methods, assuming independent log-normal errors (Pascual and Adkinson, 1994; Hilborn and Mangel, 1997). For each value of h_i and each pair of points (observed and projected by the harvested model in year t), we calculated the negative log-likelihood as

$$L_t(h_i) = \log(\sigma) + \frac{1}{2}\cdot\log(2\cdot\pi) + \frac{d_t^2}{2\sigma^2}, \tag{8}$$

where σ^2 is the residual variance resulting from the fit, and d_t^2 is the squared difference between the logarithms of observed and projected flock sizes at time t. Summing across all years for each h_i we obtained the total log-likelihood for that value of h_i Then we obtained m_i as $(h_i - 1)$. The value of h_i (and m_i) that minimizes the log-likelihood ($\boldsymbol{L}_{\min}$) is the maximum likelihood estimator of the AMR. Likelihood confidence intervals (95%) were obtained as the values of h_i that corresponds to $\boldsymbol{L}_{\min} + 1.92$ (where 1.92 is the critical value of a χ^2 distribution with 1 degree of freedom, Hilborn and Mangel, 1997).

4. Results

4.1. Analysis of the time series

The maximum annual rate of decline of sheep numbers was 0.47% (*M*) and the minimum was 0.08% (*T*). The other ranches showed similar values than ranch *M* (*P* 0.40% and *L* 0.33%, Fig. 3). All regressions were significant. The declines in ranches *M*, *L* and *P* were not significantly different. Despite ranch *T* showing the greatest growth rate, the 95% confidence interval for the growth rate of ranch *T* did not include values greater than 1. The variable that mainly explained growth rate variance (in terms of r^2 and significance) was ANPP (Fig. 4). The other variables (percentage of prairies, grass steppes and semideserts) showed patterns that suggest a relationship, but they are not significant.

Stocks numbers showed a weak but significant correlation in long term trends ($\mathrm{RS}_{\text{flock}}$ ($95\%_{\text{bootstrap Confidence Interval}}$) = 0.221 (0.074, 0.359)). However, annual growth rates did not show this pattern (RS_{rt} ($95\%_{\text{bootstrap Confidence Interval}}$) = 0.061(−0.050, 0.163)). These results indicate that stock dynamics are not in phase, i.e, all of them are falling with similar slopes (mainly ranches *M*, *P* and *L*) but fluctuating independently (Fig. 3). Cross-correlation between pair of ranches did not depend on the distance among them. The regression of pairwise cross-correlation in stock series against distance was not significantly ($\mathrm{RS}_{\text{stock}} = 0.35 - 0.001 \times \text{distance}$, $r^2 = 0.029$, $p = 0.745$). Regression of pairwise cross-correlation in annual growth rates on distance was not significant either ($\mathrm{RS}_{\text{rt}} = -0.17 + 0.002 \times \text{distance}$, $r^2 = 0.204$, $p = 0.368$).

4.2. Demographic parameters

Survivorship of all stages in ranch *P* and of ewes in ranch *T* fitted to beta distributions (Table 1). Ewe marking rate, fitted slightly better to normal distribution than to log-normal distribution in both ranches (Table 1).

Ewe survival and marking rate were significantly higher in ranch *T* than in ranch *P* ($t_{\text{survival}} = 2.696$, $df = 91.6$, $p < 0.01$ and $t_{\text{marking rate}} = 4.037$, $df = 114.4$, $p < 0.001$).

The following pairs of independently estimated parameters showed a significant but weak positive correlation in ranch *P*: ewe survival and lamb recruitment probability ($r = 0.511$, $p < 0.05$), first mating ewe survival and lamb recruitment

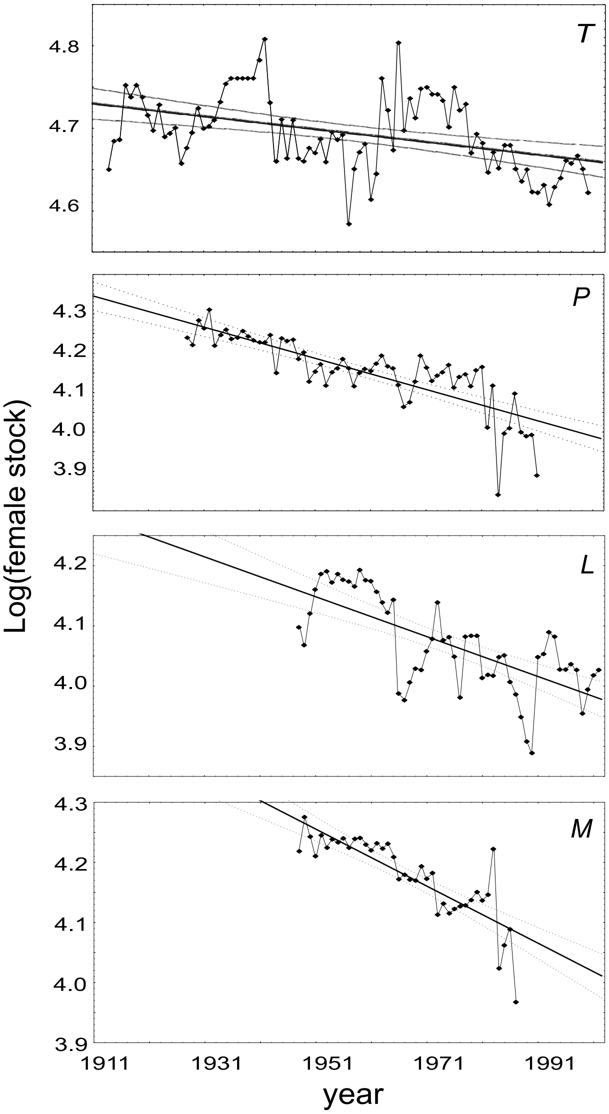


Fig. 3. Time series of log-transformed stocks in the four ranches studied. Regression lines with 95% confidence intervals are shown. The letters in the upper right corner of each graph indicates the ranches. Regression results for each ranch were: (*T*) log (stock) = 6.2 – 0.0008 × year, $r^2 = 0.181$, $p < 0.001$, $R = 0.9992$, (*P*) log (stock) = 11.91 – 0.0040 × year, $r^2 = 0.665$, $p < 0.001$, $R = 0.9960$, (*L*) log- (stock) = 10.62 – 0.0033 × year, $r^2 = 0.483$, $p < 0.001$, $R = 0.9976$, (*M*) log (stock) = 13.51 – 0.0047 × year, $r^2 = 0.697$, $p < 0.001$, $R = 0.9963$.

probability ($r = 0.289$, $p < 0.05$). Ewes showed the highest mean annual survival, with the lowest dispersion, whereas lamb survival exhibited the opposite pattern (lowest mean and highest dispersion, Fig. 5).

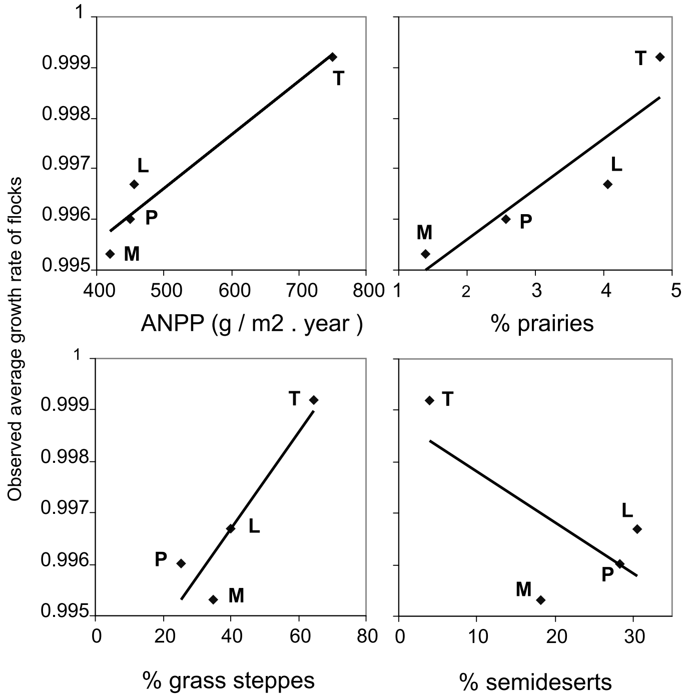


Fig. 4. Regressions of observed average annual growth rate (R) against (a) aboveground net primary production (ANPP), $R = 0.991 + 1 \times 10^{-5} \times (\text{ANPP})$, $r^2 = 0.939$, $p < 0.05$, (b) percentage of prairies, $R = 0.994 + 0.001 \times (\%\text{prairies})$, $r^2 = 0.813$, $p = 0.098$, (c) percentage of grass steppes, $R = 0.993 + 9 \times 10^{-5} \times (\%\text{grass steppes})$, $r^2 = 0.844$, $p = 0.081$, (d) percentage of semideserts $R = 0.999 + 1 \times 10^{-4} \times (\%\text{prairies})$, $r^2 = 0.496$, $p = 0.296$.

Table 1
Results of the Kolmogorov–Smirnov Goodness-of-fit tests

	Ranch *P*			Ranch *T*		
	K_s	*P*	D_s	K_s	*P*	D_s
Lamb survival	0.091	0.672	Beta	–	–	–
FME survival	0.132	0.227	Beta	–	–	–
Ewe survival	0.123	0.287	Beta	0.079	0.748	Beta
Ewe MR	0.111	0.406	Normal	0.068	0.869	Normal

K_s is the Kolmogorov–Smirnov statistic, p is the probability value associated and D_s is the best fit distribution. FME means first mating ewe, and MR means marking rate.

4.3. Matrix population models

The growth rate associated to the deterministic transition matrix was $\lambda_1 = 0.961$, and the stock fell below the 1% of the initial stock (15,800 animals) in simulation year 113 (Fig. 6(a)). The sensitivity and elasticity analyses highlighted that the most important parameters determining the flock growth rate were ewe survival and fecundity (Table 2).

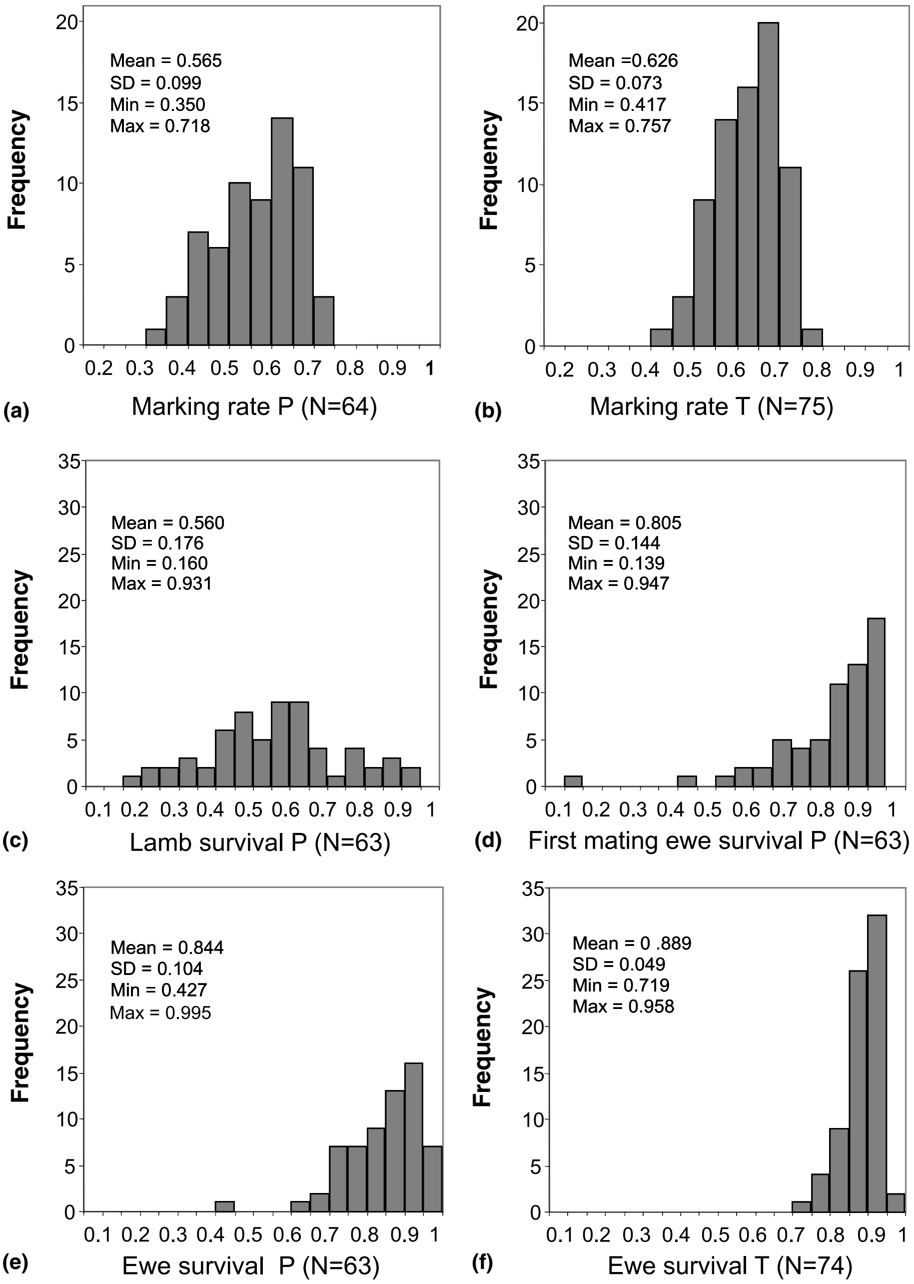


Fig. 5. Observed distribution of demographic parameters for ranches *P* (a,c,d,e) and *T* (b,f).

Almost 50% of the combination of values of ewe fecundity and survival in ranch *T* resulted in $\lambda_1 > 1$ (the area to the right of the thick line, inside the broken square in

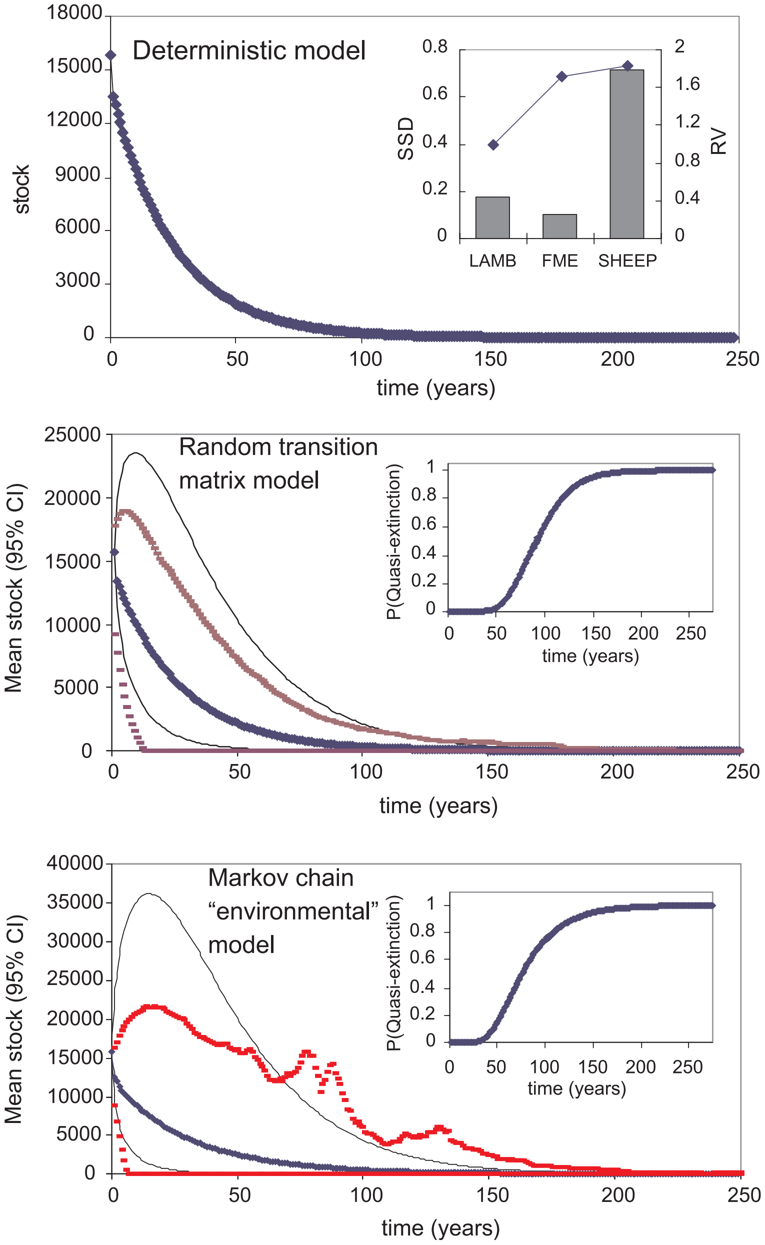


Fig. 6. Stock dynamics simulated from matrix models for ranch *P*(a) deterministic model. The graph in the upper right corner represent the stable stage distribution (SSD, bars) and reproductive values (VR, lines). (b) The ensemble dynamics of the random transition matrix model (10000 replicates). The diamonds represent the mean population size, with bootstrap 95% confidence intervals (squares) and log-normal 95% confidence intervals (solid lines). The graph in the upper right corner is the cumulative distribution of quasi-extinction times. (c) The ensemble dynamics of the markovian environment matrix model. The references are the same than those of the random transition matrix model.

Table 2
Sensitivity and elasticity matrices of λ_1 respect to the deterministic matrix model parameters

	Sensitivity of λ_1			Elasticity of λ_1		
	L	FME	E	L	FME	E
L	0.086	0.046	0.380	0	0.008	0.078
FME	0.159	0.086	0.706	0.086	0	0
E	0.189	0.101	0.823	0	0.078	0.751

"L" is lambs, "FME" is first mating ewes and "E" is ewes.

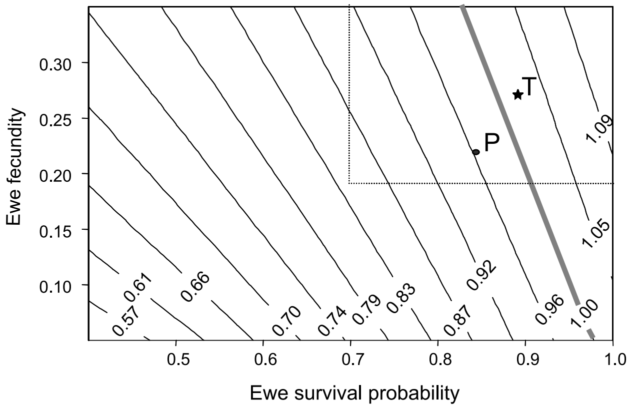


Fig. 7. Response surface of λ_1 in the space of ewe survival probability and fecundity for ranch *P*. The thick line represents the value of $\lambda_1 = 1$. The upper right broken line square represents the observed range of ewe survival and fecundity for *T*. The dot corresponds to the growth rate obtained for the mean parameter values of ranch *P*, and the star the same for *T*.

Fig. 7), when superimposed on the response surface of λ_1 generated for ranch *P*. On the contrary, most of the combinations of observed parameters for ranch *P* generated $\lambda_1 < 1$ (the area to the left of the thick line, Fig. 7).

The stage-specific net annual movement rates (AMR) that generated the observed growth rate for *P* ($\lambda_{obs} = 0.996$) were 1.047 for ewes, 1.354 for first mating ewes and 1.349 for lambs. These rates represent annual intake rates of 4.66%, 35.38% and 34.85% of the previous year numbers of female ewes, first mating ewes and lambs, respectively. Lamb imports produced the minimum negative log-likelihood, indicating that the most likely process was a mean annual lamb intake of 34.85% of the previous year female lamb number. 95% profile likelihood confidence intervals in AMR (1.341, 1.356) produced growth rates of (0.995, 0.996), respectively (Fig. 8). An intake of 39.5% of the previous lamb stock was needed to obtain a $\lambda_1 = 1$.

The stochastic growth rate generated from multiple runs of the random transition matrix model was $\lambda_s = 0.953$ (Fig. 6(b)), whereas the growth rate of the mean was $\mu = 0.961$. The mean quasi-extinction time was 95.76 years (SD = 29.45 years, upper right corner, Fig. 6(b)). These values were similar to those produced by the deterministic model. Stochastic sensitivity and elasticity patterns showed a strong positive correlation with their deterministic counterparts ($r^2 = 0.999$, $p < 0.01$).

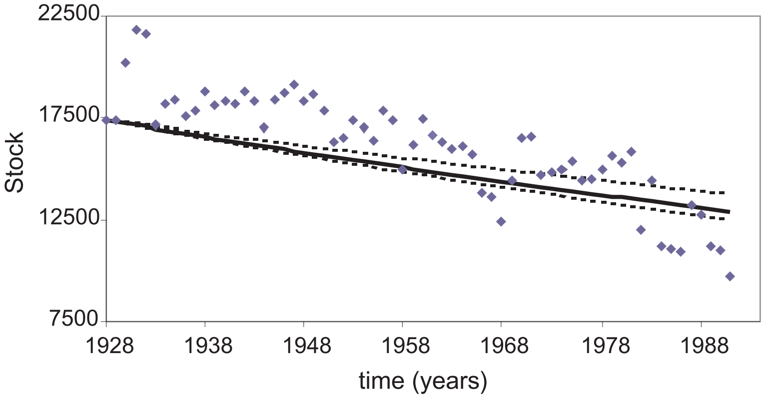


Fig. 8. Observed temporal dynamics of stocks numbers for ranch *P* and projections based on model that incorporate net annual "migration" rate. Diamonds are the observed series of females at mating ("stock"), the solid line is the dynamics estimated by the maximum likelihood estimator of the stage specific animal movement rate, and the broken lines are the 95% profile likelihood confidence intervals.

Detrended flock time series showed significant autocorrelations (AC) at lags of one and two years (AC(1) = 0.276, AC(2) = 0.310). We have found that partial correlation (PAC) was significant at a lag of only one year for detrended flock series PAC(1) = 0.276, and detrended asymptotic growth rate series PAC(1) = 0.335. These patterns in autocorrelation and partial autocorrelation functions are characteristic of Markov processes (lag one autoregressive processes, Chatfield, 1991). For this reason, we included memory in the stochastic matrix model. Nevertheless, including memory in the model did not alter previous conclusions substantially (Fig. 6(c)). The condition of the year (bad, normal or good) showed a positive autocorrelation ($\rho = 0.524$) that was greater than that observed in the detrended flock series and asymptotic growth rate series. This resulted from the fact that the highest transition rates are located in the diagonal of the "environmental" matrix (Table 3). The stochastic growth rate produced by the Markov environmental model was lower than the RTM stochastic growth rate ($\lambda_s = 0.943$), but the mean growth rate was higher, $\mu = 0.969$. The mean quasi-extinction time was 83 years (SD = 34.99 years). These could be explained by the stationary probability distribution of environmental states: in the long run, 29% are bad years, 50% are normal years, and 21% are good years. If we had not considered memory (RTM model) the stable distribution of year conditions would have been uniform (i.e., in the long run all conditions would have a fre-

Table 3
Environmental transition matrix for the markovian environment matrix model

	Bad	Normal	Good
Bad	0.438	0.323	0
Normal	0.500	0.548	0.400
Good	0.062	0.129	0.600

The matrix is read from columns to rows.

quency of 33.3%). The incidence of good years in the Markov model will be less than in the RTM model.

The stochastic growth rate derived from the Markov model was particularly sensitive to changes in the transition from normal years to bad years, and to changes in the probability of persistence of good years (Fig. 9). These patterns are reflected in the steepness of the response of the log (λ_s) respect to environmental transitions. log (λ_s) was insensitive to transitions from bad years to good years, and from good years to bad years.

An increase in the transition from normal years to bad years (an increment in the incidence of bad years) could have catastrophic consequences on sheep stocks, whereas an increase in the persistence on good years could have the opposite effects

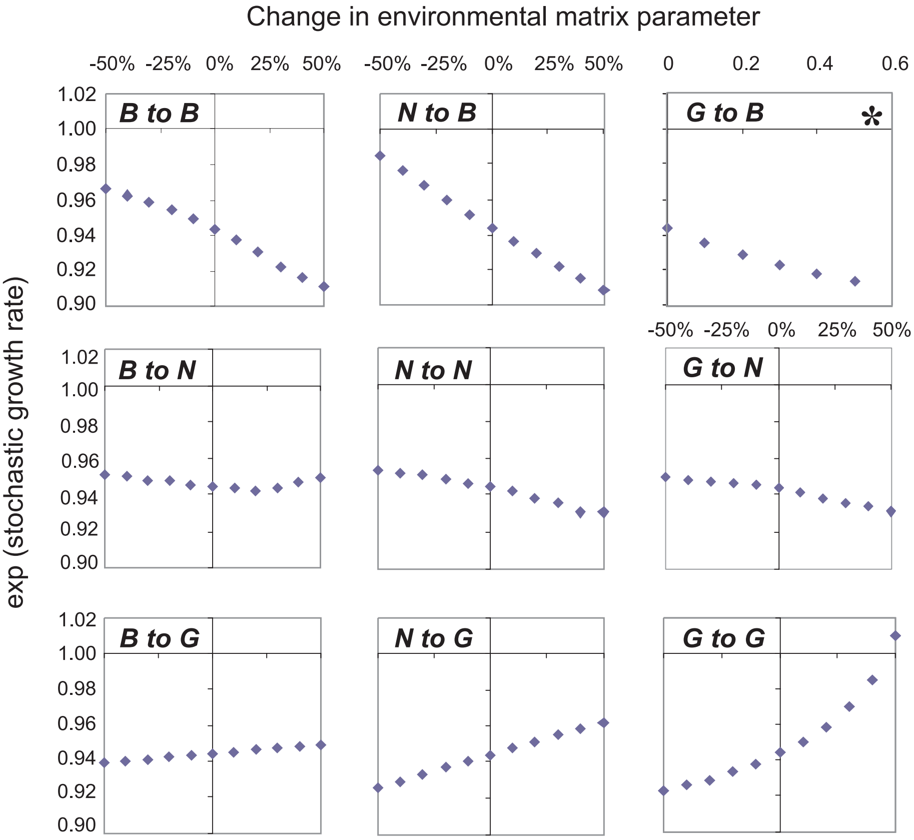


Fig. 9. Sensitivity of stochastic growth rate to percentage changes in the environmental matrix parameters. The environmental transitions are shown, i.e., N to G means "from normal years to good years", and B to N means "from bad years to normal years". (*) Because this parameter is zero in the environmental matrix, we did not express the changes as percent of original value. The stochastic growth rate is exponentiated, to interpret it as an average annual growth rate (i.e., R).

(Fig. 9). The mean growth rate, and mean quasi-extinction time showed the same patterns.

5. Discussion

We found that the population dynamics resulting from the observed demographic parameters may explain an important part of sheep flocks decline in Patagonia. Our analyses suggest that the observed stock decline could be attributed to a decrease in recruitment due to reduced marking rates during the last part of the period analyzed. The population dynamics of sheep flocks seem to have a strong biological constraint. The analysis of time series revealed that the mean annual growth rates showed a significant positive correlation with the ANPP, and positive correlations (but marginally non-significant) with some structural characteristics of the vegetation, the percentage of prairies and grass steppes in the ranch. The relationship between demographic parameters and ecosystem attributes (ANPP and vegetation structure) provides empirical evidence for the relationship between sheep stocks decline and the desertification process. Many authors showed that this degradation (mainly due to sheep overgrazing and mismanagement) led to a reduction in ANPP (Aguiar et al., 1996) and to changes in plant physiognomy (shrub encroachment and a reduction in plant cover) (León and Aguiar, 1985; Perelman et al., 1997; Paruelo and Aguiar, 2003). In this article, we have showed that changes in vegetation feedback to sheep flocks by affecting demographic parameters.

Although the four flocks studied showed a similar trend during most of the 20th century, the observed decreases were not in phase. The lack of real synchrony (i.e., in annual growth rates) highlights the importance of local factors or changes in the controls of the population dynamics. Jobbágy et al. (2002) showed that the length of the growing season and the dates of maximum productivity and the start of the growing season varied spatially in Patagonia across temperature and precipitation gradients. If annual growth rates are controlled by some of these variables (through survival and/or fecundity), flocks inhabiting areas with similar ANPP, but showing differences in growing season lengths and date of start, will present different growth rates. A strong effect of the date of start of the growing season has been found on the marking rate (Paruelo, unpublished). Another cause for the lack of real synchrony could be management decisions: intake and offtake of animals would mask the synchrony in dynamics produced by ecological or environmental controls.

Our analyses showed that the stocks are not sustainable given by the observed demographic parameters. The inclusion of historic environmental variability did not modify the results obtained using a deterministic model. The behavior of stochastic models could be explained by the fact that 60% of the annual transition matrices produced negative growth rates. Most of these matrices occurred in recent years, and had eigenvalues progressively more negative. Deterministic sensitivity and elasticity patterns revealed that λ_1 is highly responsive to variations in sheep survival. Ewe survival sensitivity (0.823) implies that an incremental change "Δ" in P_E will produce a change of $0.823 \times \Delta$ in λ_1 (Caswell, 2001). The same change in ewe fecundity would produce a much lower effect on λ_1 (i.e., $0.380 \times \Delta$). This highlights the importance of taking into account ewe survival when analyzing stock sustainability. Although the stage corresponding to lambs is most sensitive to weather conditions (i.e., years with harsh winters), and showed the greatest variability in survival; according to the sensitivity analyses results lamb survival has a much lower impact on the growth rate than ewe survival or fecundity. Gaillard et al. (1998, 2000) found that this pattern is common in large herbivores. These authors showed that, despite the low relative impact on growth rate of immature stages (lambs is our case) compared to adult stage (ewes), immature stages may be critical components of population dynamics, due to the high temporal variation exhibited. In our case, including temporal variability in demographic rates (through stochastic matrix models) did not affect sensibility. These results contribute to the discussion initiated by Gaillard et al. (2000): for sheep flocks in Patagonia, population dynamics depend more on ewe survival (as showed by stochastic sensitivity), than on a highly variable lamb survival (Fig. 5).

Until now, stock sustainability has been defined as the difference between the real (observed) marking rate and the equilibrium marking rate (the marking rate needed to maintain the stock, i.e., $\lambda_1 = 1$, Battro, 1992a,b). A constant mortality for all age stages is assumed to calculate the equilibrium marking rate. Without any information about age-specific mortality rates, this assumption is a good starting point. However, a more realistic evaluation of sustainability can be done using the deterministic or stochastic growth rates and the quasi-extinction times. Of course the use of such statistics depends on the availability of long term data on age-specific rates of fecundity and survival, or on the possibility to simulate them based on their hypothesized distributions or environmental controls. The stochastic model formulations are very useful for evaluating the effects of environmental variability on stocks dynamics, as well as the effect of exceptionally bad years (“catastrophic years”). The sensitivity analysis of the Markov environmental model showed that the only environmental scenario that ensures a positive growth rate was associated to a persistence of good years 50% higher than the observed in the period 1928–1991 (around 0.9). This is almost impossible since it would generate very long sequences of good years. On the contrary, a continued decline is expected, given the environmental autocorrelation patterns showed by the environmental transition matrix.

Assuming that ranch *T* has the same lamb and first mating ewe survival probabilities as ranch *P* (a very conservative assumption), and considering observed ewe survival and marking index in ranch *T*, we obtained a lower variability in the growth rate and a higher mean growth rate than those obtained for ranch *P*. This indicates a lower impact of the environmental variability in the demographic parameters of ranch *T*. Moreover the asymptotic growth rate predicted by the model for ranch *T* was greater than one. Demography (birth–death process) by itself could rapidly drive ranch *P* stock to extinction and could produce stock increases in ranch *T*. Decline was more pronounced in ranch *P* when we included environmental stochasticity (as a completely random process or as a Markov proccess). The differences between observed and projected dynamics imply that some other processes are involved in generating the observed dynamics. When we included the estimated stage-specific net movement rates, an average intake rate of 34.85% of the number of female lambs in the previous year was needed over the period to generate the observed dynamics. Moreover an annual intake of 39.5% of the previous year female lamb stock would produced $\lambda_1 = 1$. These rates are net rates i.e., they represent the balance between intake and offtake. Records of animal intake and offtake were not available for any ranch. However, some very fragmentary information for some ranches indicates that our estimates of the AMR are reasonable (Golluscio, personal communication). Summarizing, the models suggest that some sustainable ($\lambda_1 > 1$) ranches (i.e, ranch *T*) would act as a source of animals for non-sustainable ($\lambda_1 < 1$) ranches (i.e., ranch *P*). The obvious outcome would be a generalized reduction in stocks. The persistence of some sheep ranches depends on the existence of a supply of animals from other ranches. Given the trends in the number of animals, these source ranches are being progressively less likely. Moreover, movement of animals into a non-sustainable ranch (intake) would avoid the operation of potentially important feedback processes resulting from the relationships between demographic parameters and vegetation attributes (Fig. 4). Adding animals from external sources would increase the chances of overgrazing, leading to an increase on degradation processes which, in turn, reduce ANPP and prairies and grass steppes areas. A reduction on such vegetation variables would, in turn, impact demographic and population dynamics patterns.

One critical assumption of our model is that annual survival is estimated from data from the two months of each year without imports and exports. Although we avoid the confusion between survival and imports, we could have overestimated or underestimated the annual survival probabilities. Ewe annual survival was estimated extrapolating survival between May and December to the rest of the year; first mating ewe annual survival was obtained extrapolating survival from July to December; whereas lamb survival was estimated extrapolating from December to February. Thus, ewe and first mating ewe survival could be underestimated, because we considered the period of the year with harshest weather conditions. Nevertheless, mark-recapture studies (we have marked 400 animals in ranches *P* and *M*, in order to obtain more reliable estimates of survival and fecundity) in process are yielding results that support our results and assumptions.

A more mechanistic approach is required to identify the controls of the demographic rates that generated the observed dynamics. This would involve the explicit consideration of additional variables: environmental variables (temperature and precipitation on critical periods, El Niño Southern Oscillation index), vegetation and landscape attributes, incidence of predation, etc., as determinants of demographic parameters. Moreover, modeling management variables would improve the understanding of the system. Available evidences suggest where to start searching for the controls of the demographic rates. Hall (2000) found that almost 50% of the spatial variability in the marking index in eleven ranches in Patagonia (ranches *T* and *P* included) was explained by the annual mean of the Normalized Difference Vegetation Index (an spectral index highly correlated to ANPP) and surface temperature in spring (critical period in the sheep life cycle, when the birth of lambs occurs). According to this model, stocks would have a greater marking rate in more productive and warmer sites. Golluscio et al. (1998) showed that the stock density in the study area was positively correlated with the area of meadows. Although this is an indicator of management decisions upon the use of forage resources, it points out the capacity of certain communities to sustain a greater number of animals (enhancing survival). Olaechea et al. (1981, 1983) showed that almost 70% of lamb mortality was due to the combined effect of weather severity and starvation. The same authors showed that between 5% and 10% of mortality was caused by predators, mostly red foxes (*Pseudalopex culpaeus*) and pumas (*Felis concolor*). Evidences from different natural and partially managed systems have demonstrated an effect of climatic oscillations (El Niño Southern Oscillation and the North Atlantic Oscillation) on the demography and population dynamics of several species: muskox (*Ovibos moschatus*) and caribou (*Rangifer tarandus*) in Greenland (Forchhammer et al., 2002), Soay sheep (*Ovis aries*) in Scottish islands (Catchpole et al., 2000; Coulson et al., 2001), several species of rodents and their avian and mammal predators in northern Chile (Lima et al., 1999, 2002), and a weak effect mediated through the precipitation regime on eleven ungulate species in South Africa (Ogutu and Owen-Smith, 2003). El Niño phenomenon has a significant impact on regional precipitation (Paruelo et al., 1998a). Spring precipitation (September to November) is higher during El Niño events. This can have positive effects on survival through an increase in productivity and simultaneous negative effects due to a decrease in perceived temperature.

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