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Environmental controls on lambing rate in Patagonia (Argentina): A regional approach

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Abstract

Sheep herd sustainability in Patagonia is limited by reproductive efficiency. As the herds graze on natural vegetation year round, efficiency is constrained by biophysical factors. Our aim was to characterize the environmental controls over effective lambing rate in northwest Patagonia. We related remotely sensed data [surface temperatures and Normal Difference Vegetation Index (NDVI), a surrogate for forage availability] and climatic information to lambing rates. A spatial model explained 63% of the variability in mean lambing rate, based on mean annual NDVI and mean spring surface temperature. The relative inter-annual variability in lambing rates was of similar magnitude to that of annual NDVI. Both lambing rate and NDVI were less variable than climatic factors. Two regional temporal models explained approximately 25% of the variability, based on NDVI values representative of ewes' nutrition during late gestation and lambing. These models predicted, with 65% and 76% accuracy respectively, the occurrence of better-than-average and worse-than-average yearly lambing rates. These results provided insights into the factors limiting reproduction, and they form the basis for important decision tools for ranch managers. Prediction of lambing rates based on remotely sensed data will reduce the uncertainty and risk in sheep production, increasing the economic sustainability of sheep production.

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Keywords: Climatic controls; Effective lambing rate; Forage availability; Northwest Patagonia; Reproductive efficiency; Spatial and temporal patterns

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1. Introduction

As in many semi-arid regions of the world, animal production based on extensive grazing of native rangeland has historically been the main economic activity in Patagonia (Soriano, 1983; Ares et al., 1990). Sheep herds graze large areas of natural grasslands and shrublands all year round, and the populations are sustained by internal replacement of ewes and wethers. Average historical stocking densities range from as low as 0.2 sheep/ha to over 2.4 sheep/ha, depending on precipitation and proportion of meadows in the ranch (Golluscio et al., 1998a). The population dynamics of the herds are subject to variations in forage availability and to extreme winter weather conditions, which determine high mortality and/or low lambing rates. Initial overestimates of rangeland carrying capacity by European settlers and continuous grazing of heterogeneous areas have led to overgrazing of palatable species (Golluscio et al., 1998a), and a significant decline in sheep numbers in the region (INDEC, 1993). This degradation, combined with decreasing wool prices in the late 20th century, has compromised the Patagonian sheep industry's ecological and economic sustainability (Golluscio et al., 1998a).

Given the practice of internal replacement, the lambing rate (percent of ewes giving birth to a live lamb) determines the population's sustainability and the herd's capacity to generate surplus animals. Selection of individuals and the sale of lambs are dependent on this surplus. The actual lambing rate is generally not measured on ranches. The only index of reproductive efficiency commonly available is the effective lambing rate, defined as the number of lambs alive at marking (approximately 3 weeks after lambing) relative to the number of ewes at marking. This index summarizes the genetic (breed, selection) and environmental (health, management, forage availability, weather) constraints on reproductive efficiency that act throughout the reproductive cycle.

Given the characteristics of the Patagonian sheep herds, animal productivity is strongly dependent on environmental factors. Little is known of the relative importance of different factors as controls of the reproductive indices of the herds. It is necessary to identify the environmental variables that are effectively limiting reproductive efficiency to be able to generate management practices or technologies to alleviate their negative effect on sheep herds' productivity (represented, for example, by lamb production).

There is abundant evidence relating reproductive efficiency in sheep to both genetics and environmental factors at specific periods in the reproductive cycle. Breed and breeders' selection objectives can determine differences in reproductive efficiency. Ewes are susceptible to reproduction illnesses, such as brucellosis, which cause abortions (Irazoqui, 1981; Eales et al., 1983). They are also affected by parasites, which decrease the general productive efficiency (Irazoqui, 1981). The effect of health on reproductive efficiency is affected by management decisions. Management can also control reproductive efficiency directly, by defining time period and type of mating, assistance during lambing and care of orphan lambs (Alexander and Peterson, 1961; Irazoqui, 1981), or indirectly, through shearing practices and nutrition (Irazoqui, 1981).

Nutrition during the weeks before mating has an important effect on ovulation and lambing rates (Gunn, 1983; González et al., 1997; McDonald et al., 1997). Subnutrition during the first weeks after conception is an important cause of loss of embryos (Robinson, 1983). The ewe's nutrition and body condition during the last third of the gestation period are critical in determining the lamb's birth weight (Irazoqui, 1981; Mukasa-Mugerwa et al., 1994). Low birth weights significantly increase the risk of perinatal deaths from starvation (Alexander and Peterson, 1961; Scales et al., 1986; Mukasa-Mugerwa et al., 1994), thereby affecting reproductive efficiency. Nutrition during this period also affects the ewe's milk production, as it does early in the lactating period (Ratray, 1992; Burfening and Kott, 1994), and through this, the lamb's probability of survival (McCance and Alexander, 1959).

There is substantial inter- and intraannual variability in vegetation growth and forage availability in Patagonia (Jobbágy et al., 2002), which add greater complexity to the management of the herd's nutrition. Lambing occurs very close to the beginning of the growing season. Small changes in this date could potentially have a very important effect on the lambing rate, due to its impact on the ewes' nutrition during this critical period. Shifts in the beginning of the growing season are closely related to winter temperatures (Jobbágy et al., 2002).

Weather can also affect lamb survival. Lambing occurs when temperatures are commonly still low, rain and snow are still probable, and the herds are unprotected during this period. These climatic factors, added to the winds common in the region (Paruelo et al., 1998a) characterize a harsh environment for lamb survival (Irazoqui, 1981; Coronato, 1999), especially if they have a low birth weight (Irazoqui, 1981; Eales et al., 1983).

As in many arid and semi-arid rangelands, the main constraints on the reproductive efficiency of sheep herds in northwestern Patagonia are forage availability, the synchronization between forage supply and demand, and temperature and precipitation at different time periods in the reproductive cycle. Climatic variables could have two effects: a direct effect on lamb survival, between lambing and marking (Coronato, 1999), and an indirect one due to its effect on vegetation growth and forage availability (Jobbágy et al., 2002). The overall objective of this study is to identify the environmental controls that determine the effective lambing rate's spatial and temporal patterns. We sought to answer the following questions: (1) Which environmental variables best explain the regional variations in effective lambing rate in northwestern Patagonia? (2) What is the magnitude of the inter-annual variations in effective lambing rate, and how does it compare to environmental variability? (3) Which environmental variables explain the inter-annual variance in effective lambing rate? The answers to these three questions will allow us to propose specific, quantitative hypotheses on the environmental constraints on sheep production in NW Patagonia, allowing efforts destined to making production more efficient, economically viable and ecologically sustainable to concentrate on these factors.

2. Methods

2.1. Study area

This study was based on data obtained from 11 ranches in northwestern Patagonia, east of the Andes range. All 11 ranches are within a 22,000 km² rectangle, extending between 39°35'S and 45°40'S, and from 70°20'W to 71°25'W. Sheep ranches in this area are extensive, covering thousands to hundreds of thousands of hectares. The dominant breed is Merino, and sheep usually graze a single paddock year round. Both ewes and wethers are shorn once a year. Mating takes place in the late fall. Lambing occurs in the early spring, with ewes two to more than 6 years old giving birth, usually to one lamb. Not all ewes produce a lamb every year, so lambing rates are usually well below 100%. How low this rate is will determine whether these populations can maintain their size, for the given range of reproductive ages in the herd. Marking occurs approximately 3 weeks after lambing, and is the first time lambs are counted.

The climate in NW Patagonia is temperate to cold, with mean annual temperatures ranging between 5 and 9 °C (Paruelo et al., 1998a). Westerly winds coming over the Andes Mountains generate a precipitation gradient from west to east, with mean annual values ranging from 800 to 150 mm yr⁻¹ (Jobbágy et al., 1995). This gradient is correlated to changes in vegetation structure and function. Grasslands are found in a narrow strip running north to south, to the east of the deciduous temperate forests (Soriano, 1956; Golluscio et al., 1982; Paruelo et al., 2004). Further east, total plant cover decreases, and the proportion of shrubs increases, constituting a grass-shrub steppe (Soriano, 1956; Golluscio et al., 1982). Above-ground primary productivity decreases from 900 kg ha⁻¹ yr⁻¹ in the grassland to 390 kg ha⁻¹ yr⁻¹ in the semideserts (Paruelo et al., 1998b). The seasonality of vegetation growth and the inter-annual variability of primary productivity also vary (Paruelo et al., 1998b).

2.2. Data collection

We selected ranches in this region using two criteria. The first was the availability of historical records of effective lambing rate (*porcentaje de señalada*) for over 10 years and, if possible, monthly precipitation and temperature. We only used data from ranches with regular sanitary plans and that bred Merino sheep extensively. We applied this second criterion in an attempt to reduce the variations in management practices between ranches. In Patagonia, the only program that objectively evaluates the productive characteristics of rams (PROVINO) does not include reproductive characters in its evaluations (Mueller, 1997). Therefore, we assumed that the genetic differences in reproductive efficiency between ranches were negligible. Even given these constraints, the data obtained from each of the 11 ranches varied (Table 1). We were unable to incorporate stocking rate, an important management variable for this analysis, due to the heterogeneity in the spatial and temporal resolution of this information between ranches.

Table 1
 Synthesis of the data obtained for each ranch, identifying the periods for which there are records for each environmental variable

Ranch ^a	Effective lambing rate	Annual precipitation	Monthly precipitation	Snowfall	Temperature: absolute maxima and minima	Temperature: mean maxima and minima	NDVI	Surface temperature
N1	1976–1999	1977–1995	1977–1995	1977–1995	—	—	1981–1999	1981–1999
N2	1976–1995	1977–1997	1977–1997	1979–1996	1978–1997	1978–1997	1981–1999	1981–1999
RN1	1971–1997	1969–1993	1969–1993	—	—	(INTA) 1970–1990	1981–1999	1981–1999
RN2	1928–1998	1966–1985	1966–1985	1966–1985	1966–1999	1966–1999	1981–1999	1981–1999
RN3	1978–1993	1992–1998	1992–1998	1992–1998	—	—	1981–1999	1981–1999
C1	1970–1999	1981–1992	—	—	—	—	1981–1999	1981–1999
C2	1948–1999	Mean	Mean	—	Mean	Mean	1981–1999	1981–1999
C3	1984–1998	1948–1999	1948–1999	1971–1990	1962–1999	1962–1999	1981–1999	1981–1999
C4	1955–1999	1975–1995	1975–1995	—	1981–1995	1981–1995	1981–1999	1981–1999
C5	1974–1999	1955–1999	1955–1999	1971–1990	—	—	1981–1999	1981–1999
C6	1978–1999	1995–1999	1995–1999	1995–1999	—	—	1981–1999	1981–1999
		1979–1999	1979–1999	1979–1999	1979–1999	1979–1999	1981–1999	1981–1999

^aRanch names contain the initials of the province they are in (N: Neuquén, RN: Río Negro, C: Chubut) and a number. INTA in RN1 refers to data obtained from the National Agricultural Technology Institute in the city of Bariloche, Province of Río Negro, which is close to RN1. For C1 we were only able to obtain mean values for the region (“Mean”), with no yearly records from the ranch.

We used the Normalized Difference Vegetation Index (NDVI) as a surrogate for forage availability. This satellite-measured, reflectance-based index is linearly related to the fraction of photosynthetically active radiation (PAR) absorbed by a canopy (Gallo et al., 1985; Goward et al., 1994; Law and Waring, 1994). Above-ground net primary productivity (ANPP) is directly proportional to the annual integral of absorbed PAR, and estimates of radiation use efficiency (Monteith, 1981) allows the relation between NDVI and ANPP to be modelled (Potter et al., 1993; Ruimy et al., 1994). Such relationships have been described for grasslands and shrublands around the world (Goward et al., 1985; Tucker et al., 1985; Diallo et al., 1991; Prince, 1991; Paruelo et al., 1997, 2000) and preliminary data showed the same pattern for the study area (Jouve, 2003). ANPP is the main determinant of forage availability (Paruelo et al., 1999), which justifies our use of NDVI as a simple and easily obtained indicator of forage availability.

Remote sensing data has also been used to estimate surface temperatures. At-sensor radiance in the thermal infrared portion of the electromagnetic spectrum is predominantly due to surface and atmospheric emittance. This emittance is proportional to the fourth power of the temperature of the emitting body. Split-window techniques were used to model surface temperature based on data from channel 4 (10.3–11.3 μm) and channel 5 (11.5–12.5 μm) of the AVHRR/NOAA sensor (Sobrino et al., 1991, 1993). These techniques provide a theoretical justification for correcting temperature measurements for atmospheric absorption by regressing the surface temperature of interest against remotely sensed brightness temperatures obtained at two different wavelengths within the same atmospheric window (in this case, the 10.5–12.5 μm window, dominated by water vapour absorption) (Sobrino et al., 1991; Kidder and Vonder Haar, 1995).

Values of NDVI and surface temperature ($^{\circ}\text{C}$) for each ranch were extracted from 10-day composite images from AVHRR/NOAA (Holben, 1986), whose spatial resolution is 8 km. These images were obtained from the Distributed Active Archive Center (Goddard Space Flight Center; ftp://daac.gsfc.nasa.gov/data/avhrr/continent/south_america), and were processed using ERDAS Imagine software, Version 8.2 (Leica Geosystems, Atlanta, Georgia, USA). For each month, the value used for each variable for a given ranch corresponded to the average of three consecutive images (composites of three 10 day intervals), and of a rectangle of pixels that included the total area of the ranch. These rectangles varied in size from 8 (2×4) to 56 (7×8) pixels. Most ranches have irregular shapes, so these rectangles were substantially larger than the ranches themselves, which served to reduce the effect of geolocation errors on the selection of pixels within the ranch boundaries. Before averaging the data, we corrected abnormal values. We eliminated negative values of NDVI, assuming they indicated zero PAR absorbed. For winter months, we replaced these values with zeros. During the rest of the year, we eliminated them completely, since they most likely resulted from pixel contamination or processing errors. We also eliminated surface temperatures greater than 59°C or less than -20°C . This range was selected considering that the highest value for soil surface temperature registered in the region is 62°C (S.R. Verón, unpublished data), and the lowest value of air temperature found in the records used was -28°C . If abnormal

values occurred in more than 75% of the pixels of any given ranch, we eliminated the value for that date, since due to the heterogeneity of the surface conditions, the calculated values would not be expected to represent the whole ranch.

We calculated a series of potentially important attributes of precipitation, air and surface temperatures and NDVI (monthly, seasonal and annual means, maxima, minima, ranges). We also selected a subset of these attributes based on the known critical time periods in the ewe's reproductive cycle: mating (May and June), lambing (October and November) and between lambing and marking (December).

2.3. Statistical analysis

2.3.1. Spatial patterns of mean effective lambing rate

We used stepwise multiple regression (Snedecor and Cochran, 1980) to identify the variables most associated with the spatial variability in mean annual effective lambing rate (mELR). We calculated the means for the 1981–1999 period, for which we had remotely sensed data. We used the different combinations of environmental variables (NDVI, precipitation, air and surface temperatures) described above as independent variables. We developed separate stepwise regression models using all the environmental variables integrated over different time periods (annual, seasonal, during mating, lambing and between lambing and marking). We selected the variables from each time period that were most associated with the spatial variations in mELR, and combined them in further stepwise regression procedures with the most related variables from other time periods, until we reached a maximum proportion of the variance explained. We analysed the sensitivity of the coefficients of the best regression model to the actual sites used to fit it, by repeating the regressions with only 10 ranches, eliminating one site at a time.

Based on the best regression model, we generated a map showing the spatial patterns of expected mean effective lambing rate using ERDAS Imagine's Model Maker module.

2.3.2. Inter-annual variability in effective lambing rate

We analysed the inter-annual variability in effective lambing rate and its relation with the variability of environmental factors by comparing the relative variance (coefficient of variation = standard deviation/mean) of the ELR with that of the main environmental variables. We modelled the probability that a given year's lambing rate was lower than the equilibrium effective lambing rate (eELR; *señalada de equilibrio*), defined as the lambing rate below which a herd of ewes cannot maintain its size without immigration. The eELR is calculated by representing the herd of ewes with a simplified age structure, considering a constant annual mortality for all categories, and defining the age at first and last mating (Battro, 1992). These three population parameters determine the ratio of individuals in different age classes and the proportion of individuals that are reproductive. The eELR is calculated as the ratio between the yearly number of lambs (male and female) that need to survive to marking to provide enough females to replace the ewes that die annually, and the number of reproductive ewes. This calculation includes male lambs

simply to be consistent with managers, who record total effective lambing rate, rather than female effective lambing rate.

2.3.3. *Temporal patterns of effective lambing rate*

We pooled the yearly data (1982–1999) on effective lambing rate and environmental variables from all 11 ranches to analyse the temporal dynamics. Given the variation between ranches, we used mixed linear regression procedures (Littell et al., 1996), with the ranch as a random effect. As the software package we used (proc MIXED in SAS 9.1, SAS Institute Inc., Cary, North Carolina, USA) does not offer stepwise procedures for mixed models, we first regressed effective lambing rate on each of the individual yearly biophysical variables (analogous to the ones used when analysing the spatial patterns). We selected those variables that were significantly correlated ($p < 0.05$), and combined them in all possible pairwise combinations. We used Akaike's Information Criterion (AIC_c) to rank these models. Because of the heterogeneity in the data available (Table 1), different models were fit to different specific samples. We were therefore unable to rigorously compare models using AIC_c , which requires all models be fit to the same data (Burnham and Anderson, 2002). We grouped the models based on sample size (sample sizes in each group did not vary by more than nine), and selected the best model with significant coefficients (95% confidence intervals did not overlap zero) from each group. To analyse the sensitivity of the parameters we generated four datasets of effective lambing rate, each differing from the original dataset in that 15 randomly selected points were eliminated. We used each of these four datasets independently to fit each of the mixed models we were evaluating. We compared the new parameter values from each repetition to the parameter values obtained when fitting the complete dataset. Given the variation in availability of the independent variables data, the number of validation points eliminated in these four datasets varied, but were never less than 45 in total. To evaluate the prediction accuracy of these temporal models we used each variant to predict the 15 points we had eliminated, and analysed the correlation between observed and predicted values of yearly lambing rate.

3. Results

3.1. *Spatial patterns of mean effective lambing rate*

The 11 selected ranches varied widely in area (7500–159,500 ha; Table 2), covering a significant portion of the size spectrum of ranches in this area. Their mean effective lambing rates ranged from 57.0% (C1) to 76.9% (RN3) and the environmental variables covered a broad range of conditions (Table 2). Based on their mean climatic variables, the ranches fall into three groups. The first group had mean annual precipitation higher than 600 mm and moderate mean annual surface temperatures (between 15 and 18 °C). The second and third groups both had less than 500 mm mean annual precipitation, but differed in mean annual surface temperatures. One of these groups included ranches located in southern Chubut

Table 2
Description of reproductive efficiency and biophysical variables of the ranches used in this study^a

Ranch	Mean lambing rate (%)	Mean annual precipitation (mm)	Mean NDVI (ratio) ^b	Mean surface temperature (°C) ^c	Area (ha) ^d	Humid meadows (% area) ^d
N1	64.2	279.3	0.23	21.8	32,500	2.4
N2	73.8	414.3	0.30	20.3	23,000	2.4
RN1	72.9	668.9	0.36	15.5	57,500	9.3
RN2	62.5	325.3	0.22	18.6	41,000	4.0
RN3	76.9	614.4	0.37	16.6	22,500	18.7
C1	57.0	512.4	0.29	14.7	7500	9.0
C2	67.1	458.6	0.27	19.2	115,000	14.9
C3	76.2	372.6	0.34	12.6	11,350	2.5
C4	65.7	315.2	0.27	17.3	81,000	6.6
C5	63.4	398.6	0.32	14.1	18,500	10.5
C6	65.8	315.3	0.37	13.1	159,500	6.3

^aRanch names are the same as in Table 1.

^bNormalized Difference Vegetation Index, calculated using channels 1 and 2 from AVHRR/NOAA satellite images.

^cThe surface temperature values are based on channels 4 and 5 of the AVHRR/NOAA images.

^dAreas and percent areas with humid meadows (*mallines*) are approximate.

(C1, C3, C5 and C6), with mean surface temperatures lower than 15 °C (Table 2). The other group with relatively low precipitation (N1, N2, RN2, C2 and C4) presented mean surface temperatures higher than 17 °C (Table 2).

Two environmental variables explained 63.5% of the spatial variability in mean effective lambing rate (mELR) ($p = 0.02$, $N = 11$) (Fig. 1). These were the mean annual NDVI (from January to December; mNDVI) and the mean surface temperature during spring (September, October and November; sST). Both variables explained a significant proportion of the variability, with mNDVI showing greater correlation (partial $r = 0.80$, $p = 0.005$) than sST (partial $r = 0.64$, $p = 0.05$). The regression model that quantifies their relationship with the mELR is

$$\text{mELR} = 127.9(\pm 34.4)\text{mNDVI} + 1.4(\pm 0.6)\text{sST} + 3.6(\pm 19.8). \quad (1)$$

Therefore, mELR increased as mNDVI and sST increased. Non-linear transformations or interactions between environmental variables did not increase the proportion of the spatial variability explained.

The sensitivity analysis of the regression coefficients showed that neither the coefficients of mNDVI nor the ones of sST varied more than one standard error (S.E.) from those shown in Eq. (1). In none of the 11 regressions using 10 ranches did the intercept of the equation differ significantly from zero ($p > 0.10$).

We used Eq. (1) to generate a map of expected mean effective lambing rate in non-forested NW Patagonia, given the environmental characteristics of each 8 km × 8 km

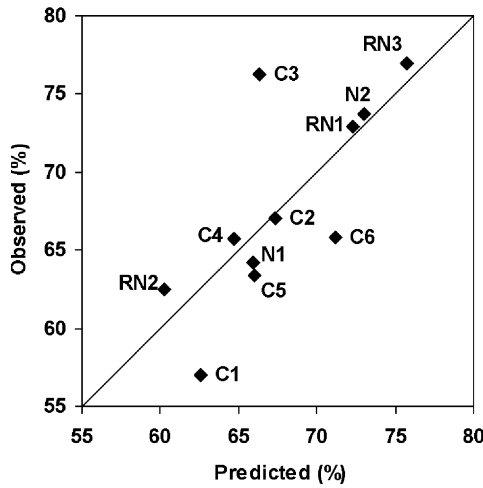


Fig. 1. Correlation between observed mean effective lambing rate (mELR, %) and mELR predicted using biophysical variables (Eq. (1)). The regression model explained 63.5% of the variability [$p = 0.02$, $N = 11$; r^2 (adjusted by the degrees of freedom) = 54.4%]. Each point represents a ranch, and the names of the ranches correspond to those in Table 1. Predicted values are equal to observed values along the solid diagonal line.

pixel (Fig. 2). This interpolation is based on the assumption that the management of the herds and the environmental controls of the ELR in NW Patagonia are the same as the ones we found with data from the 11 selected ranches. The general trend is of decreasing expected mELR from west to east, with the exception of the higher values in the central east (Fig. 2).

3.2. Inter-annual variability in effective lambing rate

The coefficients of variation (CV) of the effective lambing rate varied between ranches, from 6% (RN3) to 18% (C1). The relative variability of the effective lambing rate was lower than the relative variability of the climatic variables (Fig. 3a and b). This was most noticeable in the case of annual precipitation (Fig. 3a). There was only one ranch (C1) whose ELR was substantially more variable than its surface temperature (Fig. 3b). There was no clear difference between the relative variability of ELR and mean NDVI (Fig. 3c). This last metric, though, was clearly less variable than the climatic values, particularly precipitation (Fig. 3d and e). Seasonal values of the environmental variables showed similar patterns.

We analysed the probability that a given year's ELR is less than the equilibrium ELR. Lambing can be described as a binomial process, where each ewe is a trial, a success is having a live lamb, and the probability of success (p) is the lambing rate. This allowed us to calculate the standard deviation in lambing rate as $[(p(1-p))^{0.5}]$. By normalizing each value of ELR by the mean of its respective ranch, we determined that the distribution of these data were not significantly different from normal

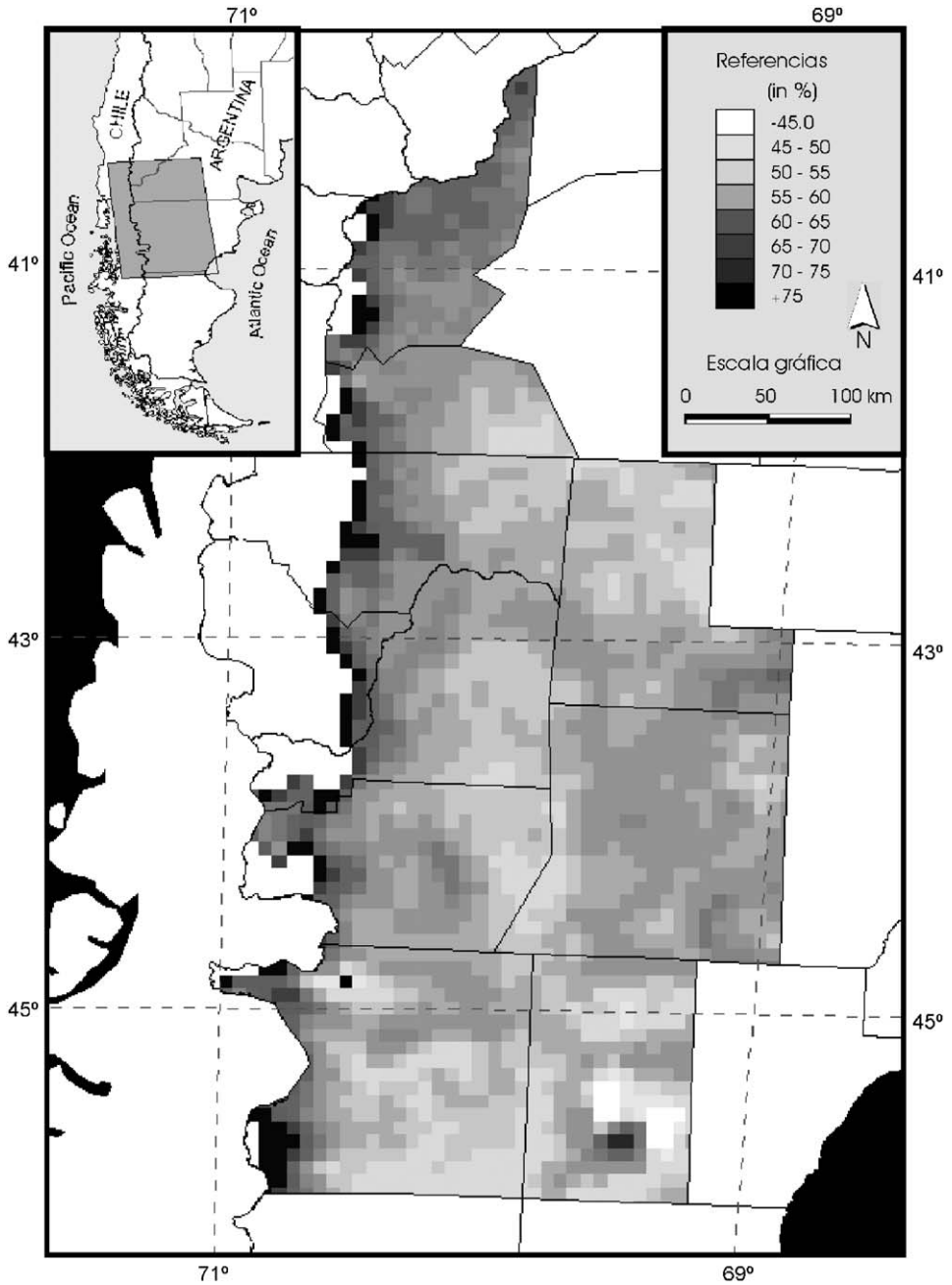
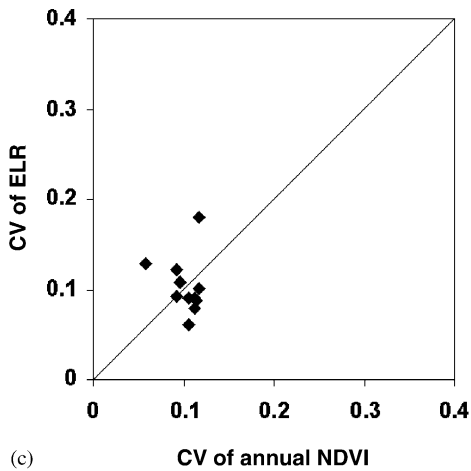
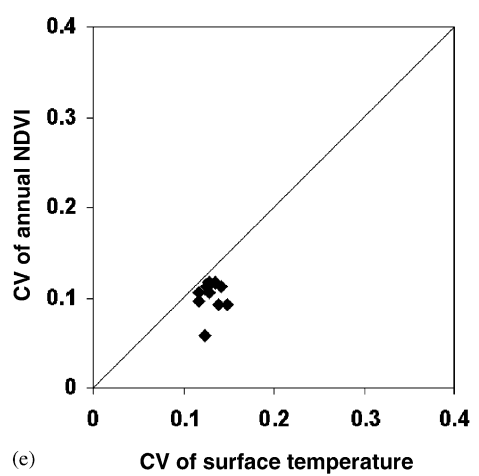
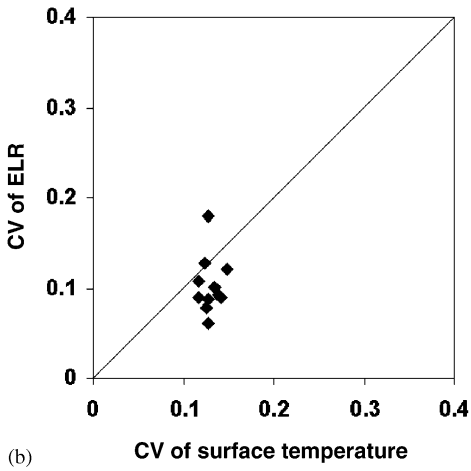
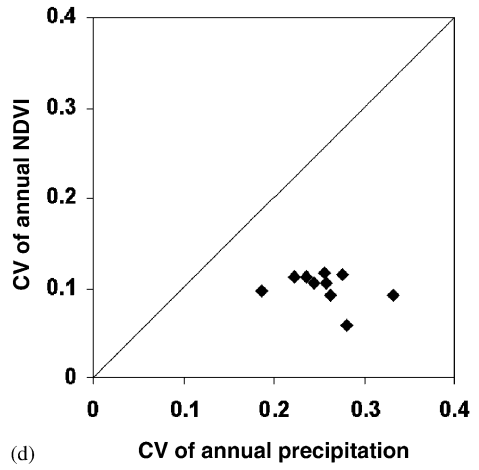
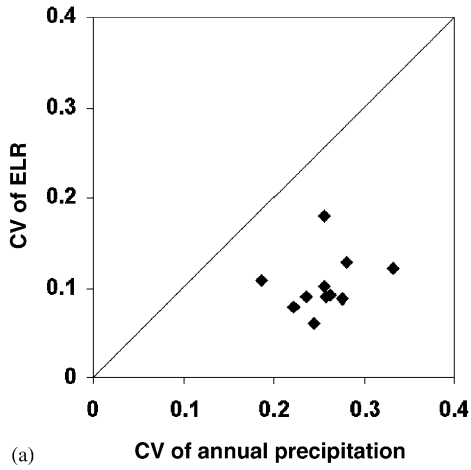


Fig. 2. Spatial patterns of expected mean effective lambing rate (mELR) in non-forested areas of NW Patagonia. These patterns result from applying Eq. (1) to AVHRR/NOAA pixels within the departments of Pilcaniyeu and Ñorquinco (Province of Río Negro), Cushamen, Gastre, Futaleufú, Languiñeo, Tehuelches, Paso de Indios, Río Senguerr and Sarmiento (Province of Chubut). This equation predicts mELR based on remotely sensed mean annual NDVI and mean spring surface temperatures.



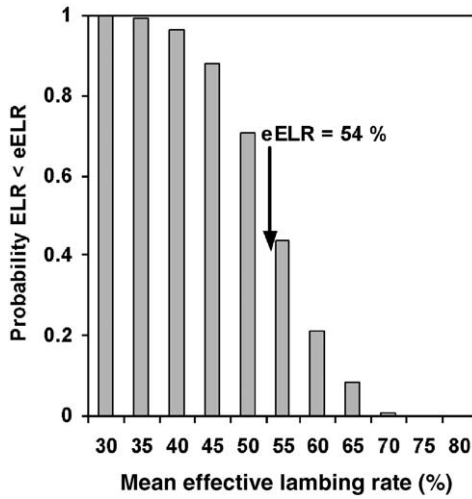


Fig. 4. Probability that a given year’s effective lambing rate (ELR) is lower than the equilibrium effective lambing rate (eELR), for different values of mean effective lambing rates (%). These probabilities are based on 1000 years of simulated ELR, assuming that ELR is normally distributed, with a fixed mean (varied from 30% to 80%, in 5% increments), and a standard deviation calculated assuming lambing is a binomial process, with the probability of success equal to the lambing rate.

(Kolmogorov-Smirnov $D = 0.09$, $p \sim 0.15$). We therefore generated sets of 1000 random ELR values from normal distributions with means ranging from 30% to 80% (in 5% increments), and standard deviations calculated as described. We found that the probability that a given year’s ELR is lower than eELR can be greater than 47%, when the mean ELR is slightly greater than the equilibrium ELR (Fig. 4).

3.3. Temporal patterns of effective lambing rate

We computed the correlation in annual effective lambing rate and environmental variables for all pairwise combinations of the 11 ranches. We found that yearly lambing rates were significantly correlated between pairs of ranches in only 49% of the cases ($p < 0.05$). The number of significant correlations between pairs of ranches for environmental variables were substantially higher: up to 96% of the pairs showed a significant correlation for surface temperature attributes and up to 78% for NDVI attributes.

Fig. 3. Comparison of relative inter-annual variability of effective lambing rate (ELR, %) with the relative variability of environmental variables at the 11 ranches. In all graphs the solid line represents the 1:1 line, where both variables have equal relative variability. Left panel: Coefficient of variation (CV) of ELR versus (a) CV of annual precipitation (mm), (b) CV of mean annual surface temperature (°C) and (c) CV of annual NDVI. Right panel: CV of annual NDVI versus (d) CV of annual precipitation and (e) CV of mean annual surface temperature.

When we pooled the annual data of the 11 ranches, we found that none of the seven models selected based on AIC_c (sample size ranging from 91 to 161) explained more than 25.7% (adjusted r^2) of the variance in yearly effective lambing rates. As we could not rigorously compare these models based on AIC_c , we used the adjusted r^2 of each model (both of the original dataset, using all the effective lambing rate values, and the validation set, made up of the 46–60 independently predicted points), as well as the qualitative comparison of the ranges of predicted values, relative to the observed, to select the best model. Two models performed equally well. The best model ($r^2 = 0.23$, $N = 161$) was

$$\begin{aligned} \text{ELR} = & 27.3(\pm 11.3)\text{maxNDVI} \\ & + 34.5(\pm 7.8)\text{wNDVI} + 50.7(\pm 5.5), \end{aligned} \quad (2)$$

where ELR is the yearly effective lambing rate, maxNDVI is the maximum value of NDVI for that year ($p = 0.02$) and wNDVI is the mean winter NDVI (June, July and August; $p = 0.0001$). Almost indistinguishable from this model was the following ($r^2 = 0.26$, $N = 139$):

$$\begin{aligned} \text{ELR} = & 66.0(\pm 14.2)\text{laNDVI} \\ & + 0.3(\pm 0.1)\text{JyST} + 43.9(\pm 5.4), \end{aligned} \quad (3)$$

where laNDVI is the mean NDVI during lambing (October and November; $p = 0.0001$) and JyST is the July surface temperature ($p = 0.02$).

We evaluated the sensitivity of the parameters of both models to the actual sample used by eliminating 15 points and recalculating the coefficients (four repetitions). The recalculated coefficients did not differ in more than 1 standard error from the original coefficients. When we used the newly calculated regression coefficients to predict the (approximately) 15 data points that had been eliminated before fitting the model (four repetitions), the correlation between observed and predicted values of effective lambing rate was greater than that of the original dataset (Eq. (2): $r^2 = 0.30$, $N = 55$, Eq. (3): $r^2 = 0.55$, $N = 46$) (Fig. 5). The slope was significantly different to unity in both cases (1.1, $p = 0.0004$; and 1.3, $p < 10^{-5}$, respectively).

Despite the low proportion of the variance explained, Eqs. (2) and (3) were able to correctly predict the occurrence of better-than-average years (when the effective lambing rate was greater than the mean for the total dataset, 68%) and worse-than-average years (when the ELR was lower than 68%) 65% and 76% of the time respectively. These frequencies were significantly different from what would be expected with a random distribution of 4 classes [2 predicted classes \times 2 observed classes; $X^2 = 3239$, $p < 10^{-5}$ (Eq. (2)); $X^2 = 2653$, $p < 10^{-5}$ (Eq. (3))] or with a distribution proportional to the range of values in each class [$X^2 = 3369$, $p < 10^{-5}$ (Eq. (2)); $X^2 = 2695$, $p < 10^{-5}$ (Eq. (3))]. The range of predicted values in both cases was approximately half the range of the observed values, though the mean was approximately equal (Fig. 5).

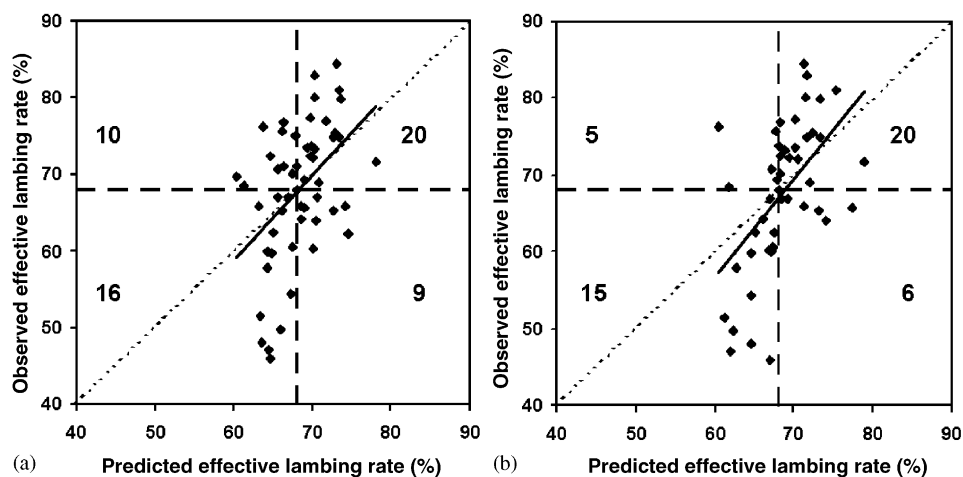


Fig. 5. Correlation between the observed effective lambing rate and the effective lambing rate (ELR) predicted by (a) Eq. (2) and (b) Eq. (3). The data points presented were eliminated in four repetitions of 15 randomly selected points each, and the regression coefficients were recalculated without them. The solid line represents the correlation between observed and predicted; the thin, dashed line represents the 1:1 relationship; the bold dashed lines identify average observed and predicted values of ELR (68%). The four numbers in each panel refer to the number of points in each of the four quadrants determined by the average observed and predicted values.

4. Discussion

4.1. Spatial patterns of mean effective lambing rate

The environmental variables most strongly correlated with the effective lambing rate are consistent with what we expected, given the available knowledge on the constraints on sheep reproduction. The importance of our results lies in the identification of the main variables, the quantification of their relative importance, and the generation of a descriptive regression model that could be interpolated to all NW Patagonia.

The most highly correlated variable was the mean annual NDVI, which is a good surrogate for annual ANPP (Prince, 1991; Paruelo et al., 1997). Its positive relationship with the effective lambing rate quantifies the importance of nutrition throughout the year for sheep reproductive efficiency (Gunn, 1983; Robinson, 1983; McDonald et al., 1997). This effect could be due both to the amount of forage available and to its quality, which are positively correlated in this region (Golluscio et al., 1998b). The relationship between forage availability and reproductive efficiency is mediated, among other things, by the stocking rate, which determines individual forage availability (Rattray and Jagusch, 1978; Penning et al., 1986) and each animal's capacity to select its diet, affecting the effective quality of the diet. This last effect could be particularly important in semi-arid regions, due to the low mean

quality of the vegetation. We were unable to include stocking rate in this analysis, despite its importance, due to the impossibility of adequately quantifying this variable at a scale compatible with our objectives. Therefore, the effect of stocking rate on the ELR remains as part of the unexplained residuals of the regression model, as do other management aspects.

The selection of spring surface temperature as the second variable related to the spatial variability of effective lambing rate indicates that sites with warmer springs (i.e. lambing period) have higher ELRs. Two complementary hypotheses could explain this relationship. The negative effects of extreme climatic conditions on perinatal mortality have been documented in the region (Olaechea et al., 1981; Bellati and von Thüngen, 1988). Temperature has also been shown to have an important impact on vegetation growth (Jobbágy et al., 2002). Higher temperatures are related to an earlier start to the growing season (Jobbágy et al., 2002), which would provide higher forage availability during the last portion of gestation and during lactation, which would positively influence reproductive efficiency (Alexander and Peterson, 1961; Mukasa-Mugerwa et al., 1994; McDonald et al., 1997).

The spatial patterns of expected mean effective lambing rate are consistent with the biophysical variables defined above. The importance of the NDVI dominates across the region, as shown by the decreasing west-to-east trend in mELR. The region in the central east with values higher than 50% is characterized by grass-shrub steppes, as opposed to the central area of low expected mELR, where there are semideserts (Paruelo et al., 2004), which have the lowest ANPP of the region. In the northwest, high values of mELR are expected further east than in the rest of the region (Fig. 2). This seems to indicate a shift in dominance over mELR from vegetation characteristics to spring temperatures.

The model represented in Eq. (1) explained close to two thirds of the spatial variability of the effective lambing rate (63.5%). The unexplained variance (36.5%) could be related to the existence of biophysical variables not considered in our model that affect sheep reproductive efficiency, such as wind or predation. Both factors are known to affect the ELR by increasing lamb mortality (Olaechea et al., 1981; Bellati and von Thüngen, 1988; Coronato, 1999). Management practices, such as stocking rate, mating time, supplementary feeding and shearing time, are also known to affect ELR (Rattray and Jagusch, 1978; Husain et al., 1997; Golluscio et al., 1998b). There are also methodological constraints that could account for the unexplained residual. Multiple regression analysis can only identify linear relationships between variables. Non-linear relationships have been found between ANPP and temperature (Jobbágy et al., 2002). Reproductive processes are not continuous (McDonald et al., 1997), so threshold relationships could be expected between reproductive and environmental variables. Paruelo and Tomasel (1997) showed the deficiencies of regression models in capturing non-linear and threshold relationships by comparing their performance with that of neural networks, using a totally deterministic simulated system. However, our analyses showed that the contributions of all these factors (other environmental variables, management, methodological problems) are less important than NDVI and sST.

4.2. *Inter-annual variability in effective lambing rate*

The observed inter-annual variability in effective lambing rate was not correlated to environmental variability. The magnitude of the relative variance of ELR was generally smaller than that of climatic variables. This suggests that the ecosystem has the capacity to buffer environmental variations. Transfer of resources from periods of abundance to times of scarcity could explain this buffering capacity. These transfers include resources for plants (e.g. soil water storage, carbon storage in plants, resistance organs, etc.; Paruelo et al., 1999) or for the animals (forage kept from past growing seasons, sheep's weight change, a foetus' priority as an energy sink; McDonald et al., 1997).

The existence of buffering mechanisms at each trophic level suggests that the ecosystem's buffering capacity would increase with the number of trophic levels considered. Our results do not show this, as the effective lambing rate is approximately as variable as NDVI (Fig. 3c). This could be due to the fact that plants have a dormant period, in winter, where climatic variations would not have a significant effect of vegetation functioning. Sheep herds, meanwhile, are active all year round. This could mean that the herbivores are subject to greater environmental variability (climatic and forage availability), confounding the comparison of their buffering capacity with that of the vegetation. However, the ecosystem's buffering capacity became evident when we compared the variability of climatic conditions versus ELR (Fig. 3a and b). This inherent buffer, likely dominated by the vegetation, could have important consequences for the sustainability of these herds, reducing inter-annual variation in lambing rates.

The inter-annual variability in lambing rate would be most limiting in areas where expected mean effective lambing rate is high enough not to constrain sustainability per se, but its variability determines that a high proportion of years the ELR could fall below the equilibrium ELR (Fig. 4), causing a fall in the number of reproductive ewes, or an increase in the mean age of the herd. A string of bad years, with ELR lower than the mean, could cause the population to crash. Such dynamics have been observed when environmental stochasticity is incorporated into simple population models (Gotelli, 1995). Teixeira and Paruelo (2005), using Markov chain models fit to ewe time-series data from one of the ranches used in this study, found that only an environmental scenario that allowed for long strings of "good" years would ensure positive population growth rates. Management practices should therefore be designed to reduce the variability in lambing and survival rates, and to obtain more productive population parameters, thereby increasing herd sustainability.

4.3. *Temporal patterns of effective lambing rate*

The environmental controls over the temporal patterns in effective lambing rate were different than over the spatial patterns. The relatively low proportion of pairs of ranches showing a positive correlation in their ELR anticipated this result. It would seem there are no better-than- and worse-than-average years, in terms of ELR, that can be generalized for the whole study area. Environmental variables were

more highly correlated between pairs of ranches. This lack of consistency could be due to the existence of spatial variability in the main controls over ELR, or to the existence of other control variables that were not quantified in this study and which varied between ranches. As mentioned above, these could be other biophysical factors (e.g. wind or snow), management practices (e.g. stocking rate) or local factors such as predation. Interactions between environmental variables, both those quantified in this study and those that were not, could also determine differences between ranches, and thereby explain the differences between spatial and temporal patterns.

It was possible to explain a small, if significant, proportion of the inter-annual variability in effective lambing rate when data from all ranches were pooled. Though we were unable to distinguish between the two selected models, both provide very similar insights into the relative importance of the variables associated with the yearly ELR. Both independent variables in Eq. (2) and one variable in Eq. (3) (maxNDVI, wNDVI and laNDVI) are related to the herds' nutrition. Their relative significance is in agreement with factors known to constrain reproduction in sheep. These variables are related to the ewes' nutrition during the last portion of gestation (wNDVI) and lambing (laNDVI). The effect of nutrition during said periods on lamb survival would explain this relationship (Alexander and Peterson, 1961; Irazoqui, 1981; McDonald et al., 1997). July surface temperatures are strongly related to the beginning of the growing season (Jóbbagy et al., 2002), so JyST is also an indication of forage availability during lambing, which overlaps the period when the vegetation becomes active. It could also be correlated with higher temperatures during lambing, decreasing lamb mortality before marking (Olaechea et al., 1981; Bellati and von Thüngen, 1988). MaxNDVI is a more integrative measure of forage availability, as a higher maximum is likely related to higher forage availability during the whole growing season.

Non-linearities, threshold responses and interactions among variables not accounted for by the regression models may have restricted our capacity to define a general linear model of the environmental controls over temporal variations in effective lambing rate. Further research on the environmental controls of reproductive efficiency is needed to discriminate the relative importance of other biophysical factors, interactions between variables, and management practices as constraints to ELR. This is necessary to define how manageable reproductive efficiency is in this system, relative to the strength of environmental constraints.

Climatic variables (excepting JyST, whose importance has been discussed) were not associated with the inter-annual variability in effective lambing rate. This could be because these variables, particularly precipitation, would affect vegetation functioning, which would be reflected in NDVI (Tucker and Sellers, 1986; Box et al., 1989). The vegetation acts as a buffer to climatic variations (Paruelo and Lauenroth, 1998; Paruelo et al., 2000), which would again determine that variations in NDVI would be more representative of the environmental effects on ELR.

Our results suggest that the environmental controls on the effective lambing rate differ in space and time. Similar methodology allowed us to explain a substantially smaller proportion of the inter-annual variability in ELR than for the spatial

variability of ELR. Such differences have also been observed in grassland systems, in the relationship between precipitation and ANPP (Lauenroth and Sala, 1992; Paruelo et al., 1999). In this study we added a further trophic level. An animal population, under human manipulation, would also have structural characteristics that limit its response to changing environmental variables. This added level could be expected to emphasize the difference between spatial and temporal controls on a functional characteristic, such as ELR.

The temporal models described in Eqs. (2) and (3), though they explained a relatively low proportion of the inter-annual variability, were able to predict, with reasonable accuracy (between 65% and 76%), the occurrence of better-than-average and worse-than-average years. Actual anticipation of a year's biophysical quality will only be possible if laNDVI or maxNDVI can be predicted, since they would only be measured very close to, or after, marking. The other two variables, wNDVI and JyST, can be measured beforehand. Tomasel and Paruelo (2000) have shown that it is possible to predict 10-day composite NDVI of grasslands in northern Patagonia 6 months into the future, using neural networks. It would be possible, therefore, to predict ELR (based on laNDVI and JyST) by the end of May. This prediction would allow management decisions to be implemented with sufficient time to either take advantage of a better than average year, or counteract the limitations of a worse than average year.

Our capacity to understand any system, and therefore predict its dynamics, is dependent on the correct identification of the hierarchical level and the scale at which the processes of interest and their controls are operating (O'Neill et al., 1986). The identification of the hierarchical level is not a trivial matter, and its definition is one of ecology's greatest challenges (Allen and Hoekstra, 1992). The importance of scale has been exemplified in this study: the change from a continuous range of values for effective lambing rate to a classification of better-than-average and worse-than-average years (coarser temporal scale) determined a substantial increase in the predictive capacity of the temporal models. The lack of data to discriminate lambing rate from perinatal mortality may have limited our capacity to explain the effects of environmental variables on the reproductive efficiency of Merino herds in NW Patagonia. Predicted values of ELR covered a range substantially smaller than that of the observed values, which is a key limitation to the temporal models presented here. The change of temporal scale at which the problem was analysed reduced the impact of this limitation. Even given these constraints, we have been able to identify and quantify the main environmental controls on ELR.

4.4. Applications and research needs

This study has allowed us to select the subset of environmental variables that control the spatial and temporal variations in effective lambing rate, and generate hypotheses to explain the functional relationships between these environmental controls and the ELR. Even though more research is needed, our results and the available knowledge on the climatic controls on vegetation dynamics (see Tomasel and Paruelo, 2000; Jobbágy et al., 2002) form the foundations for the development

of tools to generate projections of forage availability and/or lambing rates before the beginning of the growing season. This would help decrease the uncertainties in sheep production, reducing the risk and thereby increasing the economic sustainability of the ranches. It would also allow managers to plan for subsidies (e.g. extra forage) when needed, reducing overutilization of resources in unproductive years.

To improve the performance and predictive capacity of such tools, efforts should be concentrated on the evaluation of the effect of management practices, particularly stocking rate and grazing systems, on the effective lambing rate, and through it, the sustainability of sheep production in the region. The second critical need is the generation of more accurate predictive models of the inter-annual variations in effective lambing rate based on environmental variables. The availability of these models will allow spatially and temporally explicit predictions of ELR, at scales smaller than a ranch. Since in many ranches each herd will graze a single paddock year round, independently of other herds, this finer scale of analysis could benefit managers' decision-making for the different portions of the system.

Our results suggest that the environmental gradients that characterize NW Patagonia determine spatial differences in effective lambing rate, and potentially in the sustainability of Merino sheep herds. It is of critical importance that regional policies directed towards ranchers in this region, such as subsidies to rebuild herds after extreme winter mortality, take into account this heterogeneity. In areas where the environmental conditions constrain herd sustainability, these catastrophic events only cover up a more gradual decline in herd numbers. Therefore, subsidies to buy new ewes do not solve the reason for herds' decline, but rather exacerbate the overutilization of resources by helping maintain herds in areas where the populations are not sustainable.

The constantly growing availability of remotely sensed data and the increasing interest and research in climate modelling and prediction should allow many of the variables used in this study to be predicted in the near future. This, coupled with accurate temporal models for each area, would allow early predictions of effective lambing rates, which would constitute a powerful decision-making tool for managers. Growing Internet access makes it possible to keep managers constantly informed about effective lambing rate, forage availability and weather predictions. This would allow them to plan ahead and use available resources more efficiently and effectively, increasing productive and economic sustainability of Merino sheep production in Patagonia.

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