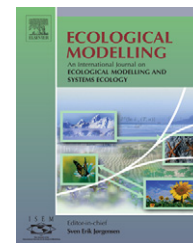




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How do forage availability and climate control sheep reproductive performance?

An analysis based on artificial neural networks and remotely sensed data

Marcos Texeira^{a,b,*}, José M. Paruelo^a, Esteban Jobbagy^c

^a Laboratorio de Análisis Regional y Teledetección, IFEVA, Facultad de Agronomía, Universidad de Buenos Aires and CONICET, Avenida San Martín, 4453 (CP 1417) Buenos Aires, Argentina

^b Cátedra de Métodos Cuantitativos Aplicados, Facultad de Agronomía, Universidad de Buenos Aires, Avenida San Martín, 4453 (CP 1417) Buenos Aires, Argentina

^c Grupo de Estudios Ambientales -IMASL, Universidad Nacional de San Luis and CONICET, Ejercito de los Andes 590 -Primer Piso (CP D5700) San Luis, Argentina

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ABSTRACT

Environmental variability affects life history and fitness of both animal and plant species. For herbivores in particular, climate can have strong direct and indirect effects on demography, which tend to exacerbate in arid and semiarid environments with highly seasonal weather. We studied the joint effect of forage conditions, plant phenology, and climate on the reproductive performance of a “model” population: domestic sheep in the Patagonian steppe of Argentina. In this region sheep behave as semi-natural populations and relatively good population records are available. Using linear models and artificial neural networks trained by second order back-propagation methods, we demonstrated that reproductive performance, characterized by the marking rate (number of lambs per ewe), was associated to the timing of growing season start and to the primary production (as estimated from remotely sensed data) at mating. An ANN model including these variables explained 73% of the variability of normalized marking rate, and predicted observed marking rates with an accuracy of 63%. Our results highlight the importance of forage availability as opposed to weather regulating the reproductive performance of sheep at Patagonia, suggesting that bottom-up controls are of dominant importance for these populations. Using artificial neural networks, satellite imagery, and historical productive and climatic records, we disentangled the controls of sheep reproductive performance in a region characterized by weak but consistent relationships between environment and sheep dynamics.

Our work aims to the development of quantitative tools for the management and planning of sheep herd structure from ranches to regions, especially for those situations in which classical methods (i.e. linear methods) fail.

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* Corresponding author at: Laboratorio de Análisis Regional y Teledetección, IFEVA, Facultad de Agronomía, Universidad de Buenos Aires and CONICET, Avenida San Martín, 4453 (CP 1417) Buenos Aires, Argentina. Tel.: +54 11 4524 8070x8114; fax: +54 11 4524 8730.

E-mail address: mtexeira@ifeva.edu.ar (M. Texeira).

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1. Introduction

Environmental variability affects life history and fitness of both animal and plant species (Tuljapurkar, 1989; Benton et al., 1995; Caswell, 2001). For herbivores in particular, climate can have strong direct and indirect effects on demography. The seasonal dynamics and interannual variability of forage quantity and quality affects body condition, which in turn correlates with growth, maturation, survival and fecundity of wild and domestic herbivores (Langvatn et al., 1996; Coté and Festa-Bianchet, 2001; Pettorelli et al., 2005a,b). Climate has been identified as a major determinant of forage production in rangelands across space and through time (Webb et al., 1978; Smoliak, 1986; Lauenroth and Sala, 1992; Epstein et al., 1997; Paruelo et al., 1999; Jobbagy et al., 2002).

Overimposed to the constraints on forage availability, climate exerts a direct control upon herbivore vital rates, specially in sites with harsh winters (Portier et al., 1998; Coronato, 1999; Catchpole et al., 2000, Pettorelli et al., 2005a,b). Studies related to the direct effects of climate on effective reproductive performance of mammalian herbivores are scarce. Langvatn et al. (1996) have showed that red deer (*Cervus elaphus*) calving rates in Norway and Scotland were negatively affected by spring temperature. Portier et al. (1998) found that perinatal mortality (a vital rate commonly “masked” in measures of reproductive performance) in Mountain goats (*Oreamnus americanus*) in Canada was higher when spring precipitation was higher, and lower in years with cooler spring and winter temperatures.

Extensive grazing with domestic herbivores is one of the most important uses of arid and semiarid ecosystems, and the relationships between herbivore demography, climate and vegetation are often a key aspect of their functioning and a critical determinant of their sustainability.

Patagonia is a vast arid to semiarid region located in the southernmost portion of South America (Soriano, 1983; Ares et al., 1990). Extensive grazing started there at the beginning of the 20th century, with the introduction of the first sheep (*Ovis aries*) flocks (Soriano, 1983). Since their introduction, sheep have relied on the native vegetation as the sole source of forage and their populations have been maintained by the internal replacement of ewes and wethers. Historical stocking rates across the region range from 0.2 sheep/ha to 2.4 sheep/ha, increasing with the net primary production of the steppe and the proportion of meadows in the landscape (Golluscio et al., 1998a). In Patagonia, sheep flocks behave as semi-natural populations both regionally and at the ranch scale, since they are maintained year long in large paddocks (usually larger than 2500 ha) with minimum control of the grazing regime, no forage or nutrient supplementation and minimal sanitary management. Flock records have been kept in some ranches since the beginning of the 20th century, and represent today a valuable source of information to explore how vegetation, climate and demography interplay in these systems. Sheep were then used as a “model” herbivore population to investigate the controls of herbivore reproductive performance.

Vegetation dynamics in Patagonia shows a highly seasonal pattern, with forage production concentrated in spring and

early summer. Peak productivity occurs in December–January (Jobbagy and Sala, 2000). The concentration of precipitation during winter makes soil water availability very reliable at the end of the cold season in spite of the overall aridity of the area. Consequently, primary production during early spring is not water limited but constrained by temperature (Paruelo et al., 2000b). Jobbagy et al. (2002) showed a negative relationship between winter temperature and the date of start of the growing season, as derived from the seasonal dynamics of the Normalized Difference Vegetation Index (NDVI). By controlling the onset of the growing season, winter temperatures also affect the timing of high quality forage availability, since new grown plant tissues have a high N and low lignin content (Somlo et al., 1985).

The analysis of the relationships between environmental factors and demographic rates raise big challenges that restrict the use of traditional linear statistical techniques: sparse data, correlated predictors, non-normal distributions, unknown interactions and weak and non-linear relationships among variables. Artificial neural networks (ANN, Smith, 1994; Anderson, 1995) then become a suitable alternative for studying this kind of problems. These models have been shown to outperform predictive capabilities of regression models (Paruelo and Tomasel, 1997; Lek and Guegan, 2000), but at the cost of a poorer explanatory power. However, recent advances in ANNs (Olden and Jackson, 2002; Olden et al., 2004) have provided methods to quantify and interpret the relative importance of independent variables, providing more mechanistic insight.

In this paper we studied the joint effect of climate and a key functional attribute of the ecosystem, the phenology of primary production, on the reproductive performance of domestic sheep (*Ovis aries*) at the Patagonian steppe by means of multiple linear regression and artificial neural networks (ANNs) trained by second order back-propagation methods. Using spectral-derived information, climate data, and correlative models relating vegetation onset and winter temperatures (Jobbagy et al., 2002), we investigated the relative importance of forage versus climate, looking for a ranking of importance of the factors controlling reproduction of our model herbivore population.

2. Materials and methods

2.1. Study area

The study area is located in northwestern Patagonia where the climate is temperate to cool-temperate, with mean annual temperatures decreasing from 12 °C to 3 °C in a NE–SW direction (Paruelo et al., 1998a). Mean temperature in the coldest month (July), is greater than 0 °C throughout the region, yet freezing temperatures are common with minimum absolute values of –20 °C recorded in the southwestern locations. The predominance of strong “westerly winds” is characteristic of the Patagonian climate with mean annual wind speeds ranging from 15 km h⁻¹ to 22 km h⁻¹ (Paruelo et al., 1998a). Maximum speeds occur between September and January and minimum speeds occur during winter (Beltrán et al., 1996). These winds reduce by ~4 °C on average the perception of tem-

peratures by endotherm animals over the whole region (i.e. chilling factor, Coronato, 1993).

Precipitation shows a strong seasonal pattern, with 70% of it occurring during winter and Fall. From the Andes mountains and 200 km eastward total annual precipitation decreases exponentially from 800 mm y⁻¹ to 150 mm y⁻¹ determining the structural and functional characteristics of the vegetation. Along this gradient aboveground net primary productivity (ANPP) decreases from 900 kg ha⁻¹ y⁻¹ to 390 kg ha⁻¹ y⁻¹ (Paruelo et al., 1998b). In the boundary with the sub-Antarctic forests (a strip covering the Andes mountains from 42°S to the South), *Festuca pallelescens* dominate the grass steppes. Toward the east, the cover of *F. pallelescens* decreases giving place to shrubs (*Mulinum spinosum*, *Adesmia campestris* and *Senecio filaginoides*) and more xerophytic grasses (*Stipa speciosa*, *S. humilis*) (Paruelo et al., 1991; León et al., 1998).

2.2. Data

The analysis of the reproductive performance of sheep was based on marking rates (number of lambs marked in December divided by the number of ewes in December). These are obtained concentrating sheep in very small paddocks or corals, and then counting them and marking (and counting) lambs with a cut in the ear. Depending on the area and the geographic location of the ranch, marking can take place from early to late December, and last up 2 weeks depending on the size of the flock. Several people count simultaneously ewe and lambs, in order to avoid counting errors. For this reason we expected only a minor effect of counting and counting date uncertainties. Marking rates were obtained from nine sheep ranches in northwestern Patagonia (Table 1, Fig. 1, Supplementary material) covering a total area of more than 500,000 ha. Data encompassed variable periods, from 1948 to the present. All ranches are located in a strip parallel to the Andes (within a 22,000 km² rectangle, extending between 39°35'S and 45°40'S and from 70°20'W to 71°25'W, Fig. 1) that include the major climatic gradients of the study area.

Ranches in Patagonia may cover thousands or even hundreds of thousands of hectares. Livestock production is extensive and the ranches considered in this study are homogeneous relative to production structure and man-

agement (Golluscio et al., 1998a,b). The exclusive sheep breed is Merino. Both ewe and wethers are shorn once a year (September–November), mating takes place in late Fall (April–May) and lambing in early spring (October). Lambs are marked in December and marking rate represents the only available measurement of reproductive performance (Battro, 1992). As far as we know no other sources of long-term data on the reproductive performance of an herbivore are available in the region.

After exploring the existence of long-term temporal trends using linear regression, we analyzed the controls of inter-annual variation of marking rates. In order to remove the effect of spatial differences in long-term temporal trends, we normalized the data from each individual location and year by the site mean and the year prediction derived from the temporal linear regressions when they were significant.

We used the normalized difference vegetation index (NDVI) as a surrogate of aboveground net primary production (ANPP). ANPP is the main determinant of forage availability (Oesterheld et al., 1992, 1998; Paruelo et al., 1999). The relationship between NDVI and ANPP has been described for grasslands and shrublands across the world (Tucker et al., 1985; Diallo et al., 1991; Prince, 1991; Paruelo et al., 1997, 2000a; Piñeiro et al., 2006) and Paruelo et al. (2004) confirmed its validity in our study area.

Values of NDVI for each site 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: http://daac.gsfc.nasa.gov/data/avhrr/continent/south_america), and were processed using ERDAS Imagine software, Version 8.2 (Leica Geosystems, Atlanta, GA, USA). For each month the value used for a given site corresponded to the maximum of three consecutive images (composites of three 10 day intervals), in a rectangle of pixels that included the total area of the ranch.

Exploratory analyses and biological significance guided us in the selection of the independent variables. The final set of five independent variables (NDVI in Fall, i.e. average NDVI from march to may, NDVI in May, mean spring temperature, annual snowfall and month of growing season start, see Table 2 for codes) resulted from trying with different groupings of inde-

Table 1 – Description of the study sites: latitude/longitude, area (ha), mean marking rate (MMR) for the site, data points (years) used in the analyses involving models with the five independent variables considered (N_{full} , see Section 2) or involving growing season start as the only independent variable (N_{start}), mean precipitation (MAP, mm/year), mean annual temperatures (MAT, °C) and annual NDVI

	Coords Lat/Long	Area (ha)	MMR (CV)	N_{start} (N_{full})	MAP (mm) (CV)	MAT (°C) (CV)	NDVI (CV)
Site 1	–41°11'31", –70°32'20"	12000	0.680 (11%)	25 (14)	325 (33%)	8.4 (7%)	0.223 (7%)
Site 2	–41°12'28", –71°5'35"	48000	0.643 (12%)	20 (17)	613 (27%)	8.2 (7%)	0.29 (7%)
Site 3	–44°12'5", –71°3'29"	7500	0.630 (5%)	3 (0)	512 (26%)	7.3 (23%)	0.256 (8%)
Site 4	–42°19'31", –71°0'39"	108000	0.679 (9%)	23 (14)	459 (26%)	8.5 (6%)	0.273 (5%)
Site 5	–45°32'55", –71°27'30"	12000	0.762 (11%)	12 (0)	372 (19%)	5.0 (14%)	0.278 (8%)
Site 6	–42°41'12", –71°2'43"	81000	0.631 (10%)	13 (6)	326 (26%)	10.2 (6%)	0.225 (8%)
Site 7	–41°6'41", –70°40'12"	42000	0.626 (14%)	25 (12)	325 (33%)	7.5 (13%)	0.24 (7%)
Site 8	–39°42'21", –70°50'51"	23000	0.750 (8%)	16 (12)	414 (26%)	10.1 (5%)	0.27 (8%)
Site 9	–43°37'0", –71°12'17"	175000	0.672 (8%)	25 (21)	315 (22%)	8.3 (11%)	0.304 (10%)

Percentage coefficients of variation (CV) are included where meaningful.

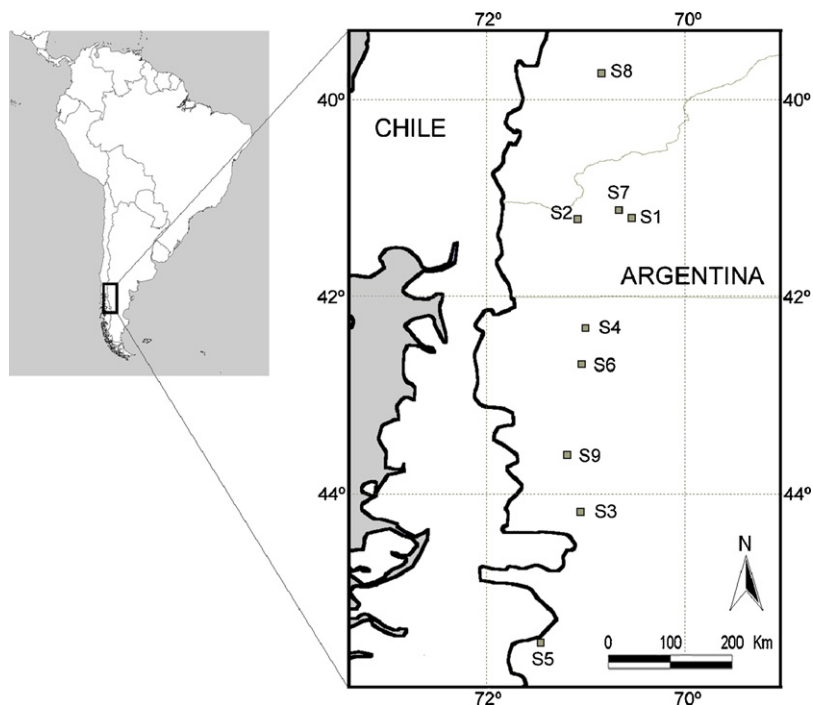


Fig. 1 – Localization of the study sites.

Table 2 – Independent variables considered in the models

Independent variable	Description numerar lineas	Codes
NDVI	Fall NDVI and May NDVI	VEG _{fall} , VEG _{May}
Snow	Logarithm (snow) accumulated yearly	Snow
Temperature	Mean spring temperatures	T _{spring}
Growing season start	July, August, September or October	START

pendent variables. Both NDVI in Fall and NDVI in May describe forage available at the time of sheep mating. It has been demonstrated that nutrition during this period has strong effects on ovulation and lambing rates (Russel, 1971; Gunn, 1983; Gonzalez et al., 1997; McDonald et al., 1997). We also considered the time of growing season start because lambing occurs close to it and lamb survival could be severely affected by its delay. An earlier beginning of growing season, could determine more forage available and of better quality during the end of gestation and during lactation. We estimated growing season start based on its close relationship to mean July temperature, mJ_T (Jobbagy et al., 2002) (Fig. 2). Julian day of growing season start, was then transformed in month of growing season start (July=7, August=8, September=9, October=10). Weather harshness could affect marking rate by increasing lamb mortality between birth and marking. We considered mean spring temperatures (September–December) and logarithm of accumulated snow during the year (i.e. in the previous winter) as indicators of weather harshness. These variables were obtained from weather records at the ranches, or from the nearest meteorological stations (Esquel airport, 42°43'S, 71°1'W and Bariloche airport, 41°22'S, 71°5'W). By considering these independent variables we ameliorated multicollinearity, which could flaw the results of both multiple regression and neural network analysis (Draper and Smith,

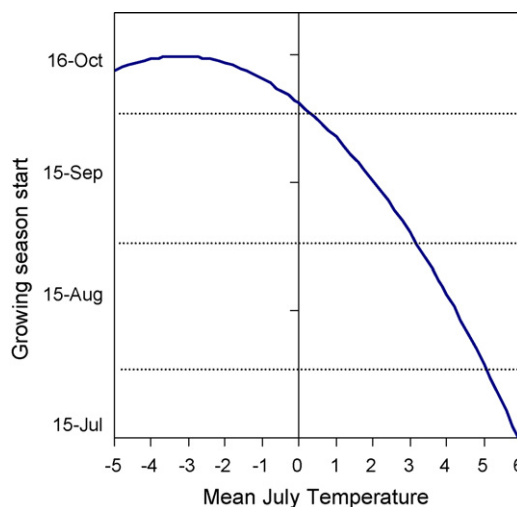


Fig. 2 – The relationship between growing season start, and mean July temperatures: $\text{Julian day of growing season start} = -1.1 (mJ_T)^2 - 7.1 (mJ_T) + 278$ ($R^2 = 0.57$, $p < 0.001$). Horizontal dashed lines represent month limits (from Jobbagy et al., 2002).

1981; Smith, 1994; Graham, 2003). The analyses that included NDVI, restricted the length of the time series of marking rates from 1981 to the present ($N = 96$). All the independent variables were normalized in order to standardize (i.e. make comparable) the measurement scales.

2.3. Regression models

We first analyzed the controls of the normalized marking rate (MARK), by means of multiple linear regression (Draper and Smith, 1981). We performed all subset regressions and selected the most parsimonious model by means of Mallor's C_p criterion (Draper and Smith, 1981; Faraway, 2004). This criterion estimates mean square error of prediction, and is calculated as

$$C_p = \frac{RSS_p}{MSE_{full}} + 2p - n$$

where p and RSS_p are the number of terms and residual sum of squares of the model under consideration, MSE_{full} is the mean square error of the model with all predictors included, and n is the number of observations. A small C_p value indicates that the model is relatively precise (has small variance) in estimating the true regression coefficients and predicting future responses. Biased models with poor predictive ability have C_p values much larger than p . We looked for the regression model with the lowest Mallor's C_p value. From this model we eliminated non-significant variables at $\alpha = 0.1$.

The evaluation of the predictive power of the final regression model was tested Jackknifing data. We eliminated the first year from the series and used the remainder of the series to estimate the final regression parameters. With these parameters we predicted the normalized marking rate for the eliminated year, repeating the procedure for all years and locations ($n = 96$). The coefficient of determination of observed versus Jackknife-predicted marking rate (R^2_{pred}) indicates the predictive capacity of the model. We also calculated the percentage of correctly predicted years (above, below or within $\pm 5\%$ of the mean normalized marking rate), and tested if this was different from the percentage expected by chance using contingency tables (Everitt, 1992).

2.4. Artificial neural networks

We also analyzed our data set by means of artificial neural networks (Smith, 1994; Anderson, 1995; Lek and Guegan, 2000). We selected the most common architecture for generalized regression problems, the multi-layer perceptron (MLP) and trained it by second order methods of back-propagation (Levenberg-Marquardt training algorithm, Demuth and Beale, 2001). In this kind of networks the processing units ("neurons") are organized in layers: an input layer, a hidden layer (or several hidden layers) and an output layer (Fig. 3). We considered fully connected networks, in which all neurons in a given layer are connected to all neurons in adjacent layers. The input layer contains 5 neurons, one for each independent or predictor variable. The output layer consists of only one neuron, representing the dependent variable (the normalized marking rate). The number of hidden layer neurons is selected by training networks with different numbers of neurons in the

hidden layer, and testing the performance on a validation set. We selected the network that performed the best in terms of R^2_{pred} .

The connection between any two neurons is related to a weight that determines the intensity of the signal they transmit. The state or activity of each neuron is determined by the input received from the neurons connected (upstream) to it. The values of the input neurons are defined by the values of the independent variables. The values of the hidden layer neurons are determined by calculating the weighted sum of the incoming signals from the input neurons. The weighted sum is then subjected to a differentiable activation function (a logistic transfer function), to produce the state or output of the hidden neuron. The same process is repeated for the neurons in the output layer, but with a linear transfer function. The output produced by the network is then compared with the target (the observed normalized marking rate) associated with the independent variables in the training example. The most common measure of discrepancy between target and network output is the mean square error (Smith, 1994). The training process adjusts the connection weights, in order to minimize the mean square error. We used batch training, in which weights are adjusted after all the training examples are used at each epoch. Training is then stopped when the maximum epoch or the error goal is reached or when the risk of overfitting data starts to grow. This risk is evaluated with the validation sample. When the network is trained the error in the validation sample falls (as in the training sample). When the error starts to grow in the validation sample, whereas continues falling in the training sample, overfitting is occurring and the network "learns" the training data, but it cannot generalize to new examples.

We considered networks with 1–30 neurons in the hidden layer, and partitioned the data set into training and validation subsets using the following alternative proportions for each one, respectively: 3/4 to 1/4, 9/10 to 1/10, 19/20 to 1/20, and $(n-1)/n$ to $1/n$ (Jackknife validation). We trained these networks 300 times in each case and then averaged the prediction determination coefficient (R^2_{pred}) between the targets (observed MARK values) and predicted outputs in each run, selecting the network with greater R^2_{pred} and minimum number of hidden layer neurons. All connection weights in all networks were initialized randomly between -0.5 and $+0.5$, in order to fasten the learning processes during the training phase (Smith, 1994). Initially, we considered all the independent variables (as in the full multiple regression model).

The importance of the independent variables was assessed by means of the permutation approach proposed by Olden and Jackson (2002) and Olden et al. (2004). This technique permutes the dependent variable and re-trains the network (9999 replicates in our study) with the same initial connection weights. In this way we obtained an empirical distribution of final overall connection weights under the null hypothesis of randomly connected networks. Overall connection weights represent the effect of the input variables on the target via all hidden neurons. From these we can extract empirical p -values associated with the observed overall connection weights. This technique has been showed to be the best to evaluate the importance of variables in neural networks (Olden et al.,

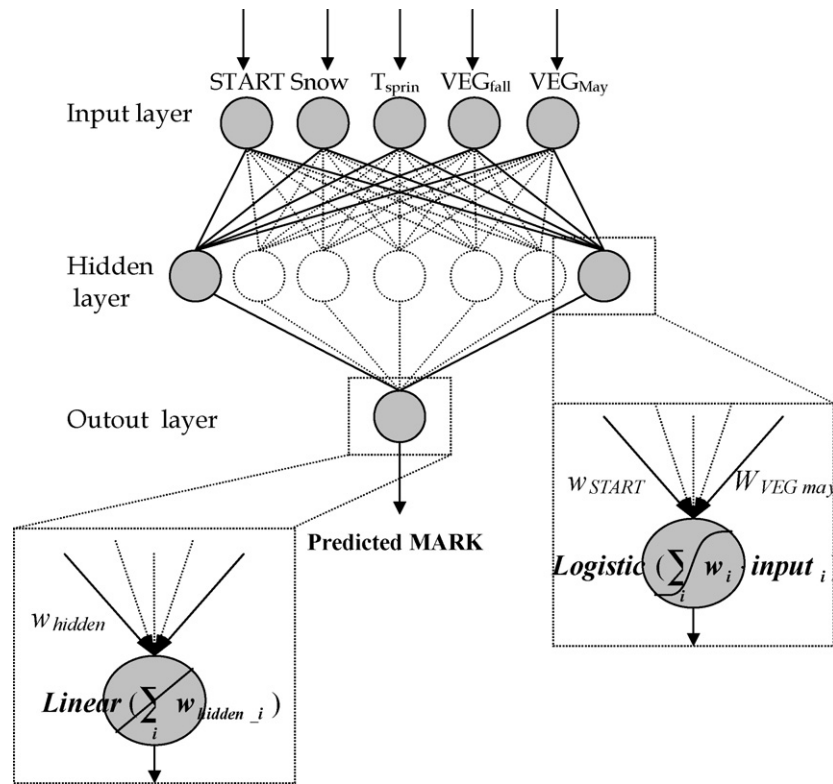


Fig. 3 – Schematic representation of the artificial neural network used in our analyses. Dashed lines and neurons are showed for illustrative purposes. Variables in the input layer are those described in Table 1.

2004), and can be used as an objective variable selection technique. We did not apply the permutation technique to study input-hidden and hidden-output connection weights for two reasons: first, linear regression models showed no evidence of interaction among variables, and second, it is extremely difficult to interpret $5 \times 20 + 20$ connections arising from the full network.

3. Results

Reproductive performance showed a slight, yet consistent improvement during years in which the growing season started earlier and had higher NDVI values in the month of May (mid Fall). An analysis of variance considering the complete series of marking rates ($N = 162$), and the month of start of the growing season as a classification factor was significant (Fig. 4, $F_{3,158} = 4.659$, $p = 0.004$, $R^2 = 0.081$). All regression models had low predictive power (Table 3a). The best model, according to Mallows C_p , included month of growing season start and May NDVI ($p < 0.001$, Table 3b).

$$\text{MARK} = 1.012 - 0.034 \times \text{START} + 0.015 \times \text{VEG}_{\text{May}}$$

When we analyzed the percentage of correctly predicted years (above, below or around $\pm 5\%$ of the mean) resulting from the Jackknife predictions, this value (40.6% of correct predictions) was not different than those expected from the null model of random predictions ($X^2_2 = 3.067$, $p = 0.547$). Although the prediction determination coefficient was low, the regression of observed versus Jackknife predictions was significant,

and not different from the 1:1 line (intercept $p = 0.593$, slope $p = 0.592$, Fig. 5a).

Neural networks showed a much higher predictive power than multiple linear regressions. The neural network with best performance had 20 neurons in the hidden layer and Jackknife validation ($R^2_{\text{pred}} = 0.728$). The permutation approach showed that growing season start and May NDVI, were the only variables that had a significant effect (at an $\alpha = 0.1$) on the reproductive performance of sheep (Table 4), in agreement with the regression analyses. The overall connection weight of normalized marking rate was negative with time of growing season start and positive with May NDVI. The reduced neural network constructed considering only these independent variables showed a high predictive performance (Table 4, Fig. 5b). Regression of observed versus Jackknife predictions

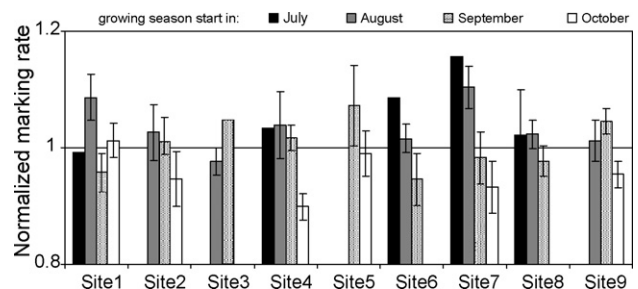


Fig. 4 – Mean normalized marking rate ($\pm 1\text{S.E.}$) as a function of the month of growing season start for the nine sites considered.

Table 3 – (a) Multiple regression models fitted to the normalized marking rate (MARK)

MODEL	Mallow's C_p		R^2	R^2_{pred}
(a)				
Full model	6.000		0.2281	0.1362
START + T_{spring} + VEG_{May}	4.212		0.2091	0.1457
START + VEG_{May}	4.891		0.1861	0.1396
Final model	Estimate	Estimate's p -value	Partial R^2	Partial R^2 p -value
(b)				
Intercept	1.0123	0.0000		
START	-0.0338	0.0002	0.1363	0.0002
VEG_{May}	0.0153	0.0873	0.0311	0.0856

Mallows C_p , fit determination coefficient (R^2) and prediction determination coefficient (R^2_{pred}) are showed. (b) Parameter estimates, partial determination coefficients (Partial R^2) and significance levels associated to the final regression model. Codes of the variables are provided in Table 2.

was significant, and not different from the 1:1 line (intercept $p=0.535$, slope $p=0.494$, Fig. 5b). This model predicted correctly 84.4% of the years ($X^2_1 = 61.324$, $p=4 \times 10^{-15}$).

4. Discussion

Our results show that the most important controls of reproductive performance of sheep at Patagonia were foraging conditions in two critical times: mating and late pregnancy, confirming the trends presented by Hall and Paruelo (2006). However, our results reveal patterns with more clear interpretability and consistency among sites. Moreover such understanding allowed us to build prospective models of a critical variable for the sheep production system of Patagonia: the marking rate. Guided by previous evidence on the potential controls (i.e. forage resources at mating, phenological variability and climate harshness, Olaechea et al., 1981, 1983; Coronato, 1993, 1999; Langvatn et al., 1996; Pettorelli et al., 2005a) we identified two vegetation variables that seem to

exert a strong control of marking rate, probably through their link to sheep nutrition at the beginning (i.e. NDVI in May) and at the end of gestation (onset of growing season start) (Russel, 1971; Gunn et al., 1969; Gunn, 1983; McDonald et al., 1997). The vegetation variables that we identified can be derived from spectral information and forecasted with some anticipation based on climatic data, opening a new pathway for the development of tools to manage both sheep flocks and pastures.

In the system studied, forage condition had a prime importance controlling the reproductive performance of sheep while the analyzed weather variables, which could potentially affect marking rate through perinatal survival, were not significant in our analyses. Neural network models suggest that about three fourths of the variation in the reproductive performance of the studied herds could be attributed to forage condition, leaving a secondary role to climatic and top-down controls, at least at the spatial scale of our study. The small number of sheep removed from the flocks in the ranches included in our study (old and senescent sheep) would not have a significant effect on herd's reproductive performance. Since this practice

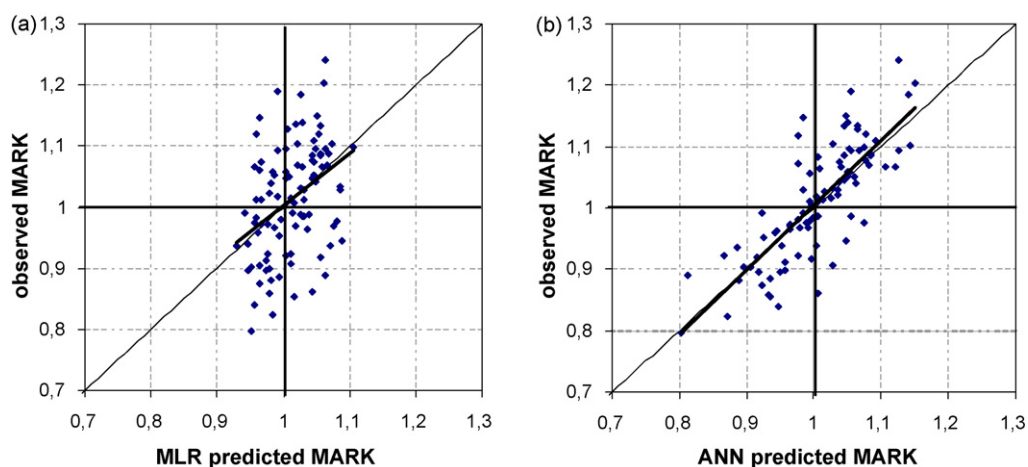


Fig. 5 – (a) Normalized marking rate observed (observed MARK) versus normalized marking rate predicted by Jackknifing the final regression model (MLR predicted MARK). The thick line represents the predicted versus observed regression line ($MARK_{obs} = 0.122 + 0.879 \times MARK_{MLR\ pred}$) and (b) normalized marking rate observed (observed MARK) versus normalized marking rate predicted by Jackknifing the final neural network model (ANN predicted MARK). The thick line represents the predicted versus observed regression line ($MARK_{obs} = -0.052 + 1.057 \times MARK_{ANN\ pred}$).

Table 4 – Overall connection weights (OW), associated with the variables included in the full and in the reduced neural network models (Full ANN and Reduced ANN)

Variable	Full ANN		Reduced ANN
	OW	P	OW
START	-0.3213	0.033	-0.2926
SNOW	0.1031	0.756	-
T _{spring}	-0.0601	0.584	-
VEG _{fall}	0.0100	0.630	-
VEG _{May}	0.5121	0.018	0.5424
	R ² = 1, R ² _{pred} = 0.7276		R ² = 0.73, R ² _{pred} = 0.6337

The p-values were based on 9999 randomizations. Codes of variables are the same as in Table 1.

is common throughout the region, we think that our results can be generalized to the whole region. Moreover, given the extremely extensive management of flocks, sheep reproductive behavior would be a good proxy for large herbivores in similar environments.

We found that the timing of growing season start was the most important control of sheep reproductive performance in the sites analyzed, likely as a result of its impact on the nutrition of mothers in a critical period for reproduction, the end of gestation (Kruuk et al., 1999). Our results were similar to those found by Posse and Cingolani (2000, 2004) in the Magellanic, steppe where lamb production was strongly related with NDVI in September.

Warmer winters induce an earlier growing season start in the Patagonian steppe (Jobbagy et al., 2002), which in turn determines more and better forage available during the highly energy-demanding periods of gestation and lactation. Hence, an earlier vegetation onset could determine greater weight and better body condition of mothers giving birth to heavier lambs. A positive relationship between pregnancy (proportion of pregnant ewe in August) and ewe weight ($p < 0.01$, unpublished material) in a small subset of our data (and for only one ranch) supports this link. Although we have no direct information on the relationship between mothers weight and lambs weight (see Golluscio et al., 1998b), a positive association could be expected as it has been shown for Mountain goats (*Oreamnus americanus*) (Coté and Festa-Bianchet, 2001). Heavier lambs are better suited to afford climate harshness. We do not know, given our data set if the interaction between climate and foraging conditions, translate into an effect on marking rate. However we did not find significant interaction effects among climate and forage variables in our linear regression models. Even though climate have been recognized as the most important cause of lamb mortality in the perinatal period (a week after birth, Olaechea et al., 1981, 1983), according to our results, this seems to cause only a minor effect on marking rate (a marginal significant effect of spring temperature on the first reduced linear regression model). Of course we cannot discard that the use of better descriptors of weather harshness (i.e. wind chill factor or minimum temperatures) may identify a signal associated to perinatal mortality. Similar results have been described for herbivore populations from Europe. Warmer springs in Norway, have induced an earlier growing season start and thus have favored an earlier migration of

red deer (*Cervus elaphus*) from winter range to summer range, leading to increases in individual body mass (Pettorelli et al., 2005a). An earlier vegetation onset, positively affected body mass of reindeer calves (*Rangifer tarandus*) born the following autumn (Pettorelli et al., 2005b).

May NDVI, the second most important variable affecting marking rates is related to the forage availability at the time of mating. This link is consistent with previous evidences relating nutrition to ovulation rates in sheep (Russel, 1971; Gunn, 1983; Gonzalez et al., 1997; McDonald et al., 1997) and red deer (Langvatn et al., 1996). Moreover reproductive maturity is associated with a critical body weight above which females have an increasing probability of ovulation and conception (Gunn et al., 1969).

Our results could help to project the possible impacts of global warming on the sheep production systems of the Patagonian steppe. During 1959–1998, winter temperatures and the number of warm days and nights in winter have been increasing in the region (Rusticucci and Barrucand, 2004). This climatic shift would likely promote and earlier growing season start, potentially favoring sheep reproduction. Such simplistic reasoning should be taken with caveats, though, since global warming would be also associated to rising evapotranspiration rates which could curtail the overall annual primary production of the steppe causing a premature growing season end (Jobbagy et al., 2002). This could have an adverse effect in the nutritional status of ewe, previous to next year mating, lessening the probabilities of successful conception. Another important source of uncertainty regarding global warming effects is their possible interaction with long-term shifts in precipitation. We did not find any significant relationships between winter temperatures and annual and winter precipitations in the climatological series for each of the nine sites in our study however we found slight long-term increases in annual and winter precipitation at two of them. These findings add uncertainty to the expected effects of global warming upon vegetation and sheep flock dynamics.

5. Conclusions

Beyond the ranking of environmental variables according to their importance as reproductive controls in Patagonian sheep populations, our neural network model provides a valuable forecasting tool. Based on weather and NDVI data, we were able to forecast the reproductive output of flocks with an accuracy of approximately 60% and an anticipation of 3–5 months given that growing season start is strongly correlated to July temperatures (Jobbagy et al., 2002). If we decrease the resolution of our prospecting, focusing on the estimation of years that would have marking rates that are above, below or around the historic mean, prediction accuracy raises up to 80%.

Our findings contribute to the understanding of the joint effects of climate and vegetation on the reproductive performance of ungulates and provide one of the first contributions based on South American rangelands. A confirmation of the importance of bottom-up controls on the reproductive performance of Patagonian sheep populations would require population density records. Although these records are available at the whole ranch level, the interpretation of density

effects at this scale in meaningless. In turn, information at the paddock level is needed to correctly assess density patterns and trends and their link with reproductive performance. Paddock level information is scarce but available in a few ranches and we are currently compiling and analyzing paddock data to tackle this problem at a finer spatial scale, including information on local predation risks, landscape heterogeneity, plant functional type composition, among others.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2008.06.027.

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