

An exploration of direct and indirect drivers of herbivore reproductive performance in arid and semi arid rangelands by means of structural equation models

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ABSTRACT

Climate variability affects both animal and plant populations. Understanding how this variability is modulated by topography, vegetation and population densities and how this impact on ungulate demography is an important step in order to forecast consequences of alternative management scenarios or the effects of climate change.

Structural equation modeling (SEMs) is a tool particularly suited to this kind of situations, and allowed us to study the direct and indirect effects of climate, topography, structural and functional aspects of vegetation and population density upon reproductive performance of Patagonian sheep flocks, measured at paddock scale. The application of SEMs in conjunction with information criteria and related techniques for model selection, model averaging and multi-model inference revealed that despite considerable model uncertainty, those paddocks towards the East, with a greater spatial variability in July temperatures and greater primary production during fall-winter (estimated by remote sensing) showed greater lambing rates. Paddocks with higher proportion of meadows and with more intense forage consumption, were also associated with a better reproductive performance. Our results not only provide quantitative hypothesis about the controls at the landscape level of herbivore performance but also provide the basis to devise better management alternatives.

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1. Introduction

Climate variability affects both animal populations and vegetation (Benton et al., 1995; Tuljapurkar, 1989). The effective impact of climate variability on herbivores is mediated by vegetation, topography and population densities, which in turn determine the environment experienced by individual animals. Understanding this “climatological downscaling” (Pettorelli et al., 2005a,b) is a fundamental step in order to understand the drivers of demography and population dynamics and to forecast the consequences of alternative management schemes or the effects of climate change.

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Climate can have strong direct and indirect effects on herbivore populations. On the one hand it exerts a direct control upon herbivore vital rates, specially in sites with harsh winters (Coronato, 1999; Catchpole et al., 2000; Pettorelli et al., 2005a,b; Portier et al., 1998). On the other hand, climate affects the seasonal dynamics and interannual variability of forage quantity and quality (del Grosso et al., 2008; Epstein et al., 1997; Jobbágy et al., 2002; Lauenroth and Sala, 1992; Paruelo et al., 1999; Smoliak, 1986; Webb et al., 1978), affecting indirectly body condition, growth, maturation, survival, fecundity and migration patterns of wild and domestic herbivores (Coté and Festa-Bianchet, 2001; Langvatn et al., 1996; Pettorelli et al., 2005a,b).

An approach specially suited to explore and contrast hypotheses on causal relationships among variables, and to identify direct and indirect effects with observational data are path analysis and structural equation models (“SEMs”, Kline, 2011; Pugsek et al., 2003). These approaches have received increased attention in ecological studies (Almaraz, 2005; Iriondo et al., 2003; Malaeb et al., 2000; Myrsterud et al., 2008). In its broadest sense, SEMs

translate a series of hypothesized cause–effect relationships among variables into a composite hypothesis concerning patterns of statistical dependencies and correlations (Shipley, 2000). These relationships are described by parameters that indicate the magnitude of the effect (direct or indirect) that independent variables have on dependent variables. These variables can be manifest (observed) or latent (unobserved, hypothetical or theoretical constructs). The construction of a SEM model, implies that the researcher has at least some knowledge about which variables are assumed to affect other variables, and the direction (positive or negative, unidirectional or bidirectional) of these effects. Depending on the amount and development of this prior knowledge, SEMs can be applied in at least three ways or contexts (Pugesek et al., 2003). First, in a strictly confirmatory application, the researcher has a single model that is accepted or rejected based on its correspondence to the data. Second, a somewhat less restrictive context, concerns the testing of alternative models, and it refers to situations in which more than one a priori model is available. The last way, is that of model generation. This is probably the most common use, and occurs when an initial model does not fit the data, and is subsequently modified until achieve an adequate fit. The modified model is tested again with the same data. The final goal of this search is to find an adequate model, i.e., one with theoretical sense, parsimony and correspondence to the observed data (Kline, 2011). Our use of SEMs falls somewhere between the second and third contexts described, and is intended to establish causal assumptions and generate a data grounded conceptual model of our study system, the Patagonian sheep flocks.

Patagonia is a vast arid to semiarid region located in the southernmost portion of South America (Ares et al., 1990; Soriano, 1983). Extensive grazing started there at the beginning of the 20th century, with the introduction of the first sheep (*Ovis aries*) flocks (Soriano, 1983), and now represent one of the most important activities in the region. Since their introduction, sheep have relied on the native vegetation as the sole source of forage and their populations have been maintained in large paddocks (usually larger than 2500 ha) by the internal replacement of ewes and weathers, without forage or nutrient supplementation and minimum sanitary and grazing regime management. The low management intervention on the system determines that sheep flocks behave, to a great extent, as semi-natural populations (Texeira and Paruelo, 2006). More than a hundred of years of grazing by sheep, hampered the ecological and economical sustainability of the Patagonian steppes (Golluscio et al., 1998).

The lambing rate (percent of ewes giving birth to a live lamb) represents a key indicator of the herd sustainability and persistence. The actual lambing rate is not measured on ranches. In turn, the effective lambing rate, the number of lambs alive at marking (approximately 3 weeks after lambing) relative to the number of ewes at marking, is the only measure of reproductive performance of widespread use in Patagonia (Battro, 1992). This index summarizes the genetic and environmental constraints on sheep reproduction.

An understanding of the relationships among herbivore demography, climate, vegetation and landscape is crucial in order to provide basis for developing sustainable management alternatives for sheep husbandry in Patagonia. Moreover, the semi-natural behaviour of sheep flocks make them an ideal system to study how environmental factors interact in controlling critical demographic parameters of herbivore populations. In a previous work we showed that the temporal dynamics of reproductive performance of sheep at ranch scale in Patagonia, was associated to the onset of the growing season and the quality and quantity of forage at mating (Hall and Paruelo, 2006; Texeira et al., 2008).

In this article we aim to show the potential usefulness of structural equation models in observational studies in which the action of direct and indirect effects is very clear and the application of methods like multiple regression is inappropriate. The case study is the evaluation of the direct and indirect effects of climate, topography, vegetation structure and function, and population density on the reproductive performance of semi-natural sheep herds at paddock scale in northwest Patagonia, Argentina.

2. Methods

2.1. Study site

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

Precipitation shows a strong seasonal pattern, with most of the precipitation falling during winter. From the Andes mountains and eastward, total annual precipitation decreases exponentially from 800 mm y⁻¹ to 150 mm y⁻¹ (Jobbagy et al., 1995). This precipitation gradient determines profound changes in structural and functional characteristics of the vegetation (Jobbagy et al., 1995; Paruelo et al., 2004), e.g., aboveground net primary productivity (ANPP) decreases eastward from 900 kg y⁻¹ to 390 kg y⁻¹ (Paruelo et al., 1998b).

2.2. Effective lambing rates

The four ranches considered in this study are located in a strip parallel to the Andes mountains (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. These ranches cover thousands or even hundreds of thousands of hectares, and share the same production structure and management (Golluscio et al., 1998). These ranches were selected, given the availability of spatially detailed records of marking rates (i.e., at the scale of paddock).

The exclusive sheep breed is Merino. Both ewe and weathers are shorn once a year (September–November), mating takes place in late fall (April–May) and lambing in early spring (October). Lambs are weaned around February. Marking occurs in December and effective lambing rate is calculated as the number of lambs relative to the number of sheep at marking (Battro, 1992).

We selected paddocks with at least 3 years of effective lambing rates data for the period 2000–2005. Mean area of the sixty six paddocks that filled this criterion was 2840 ha, and ranged from 350 ha to 9800 ha. Effective lambing rate in each paddock and year was calculated as the ratio between lambs and ewes at marking (December). We then averaged these yearly marking rates, in order to obtain mean values for the paddocks and period considered.

2.3. Surrogates of climate

Latitude and longitude were used as surrogates of mean annual temperature (MAT) and mean annual precipitation (MAP), given

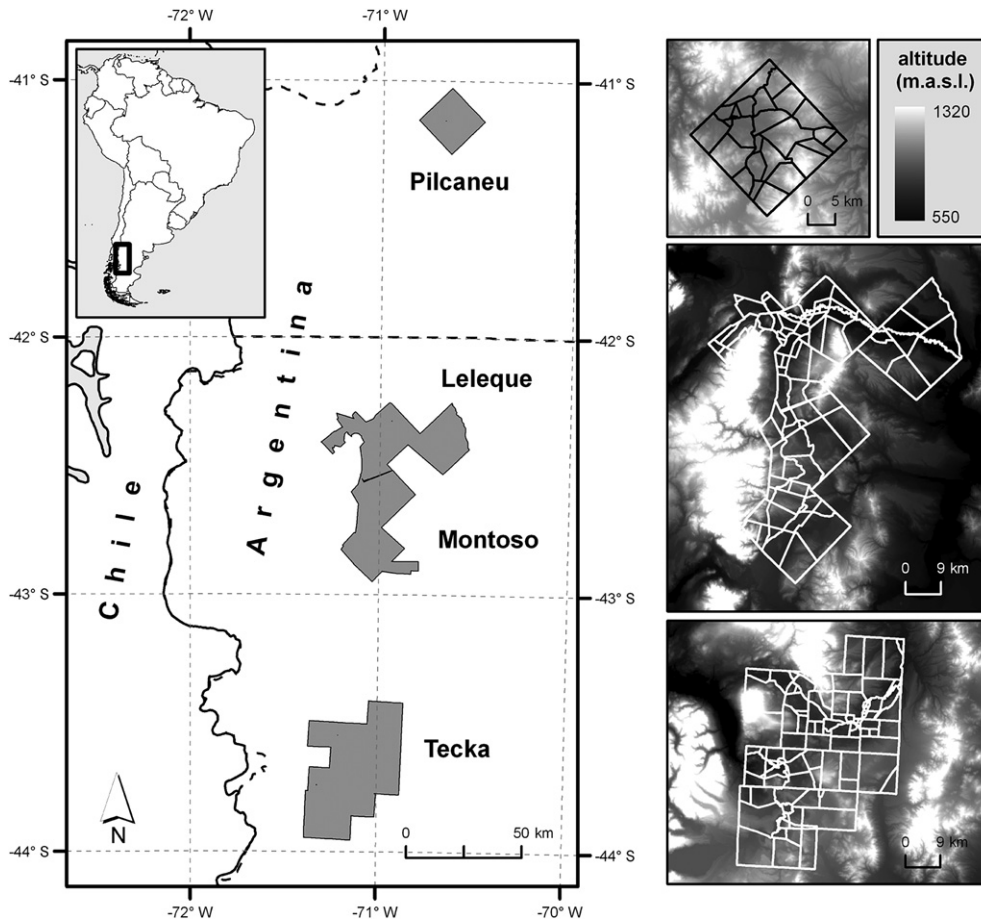


Fig. 1. Localization of study sites. The right panel show the maps of the ranches superimposed on a digital elevation model map (dem).

the known north–south temperature and west–east precipitation gradients (Jobbagy et al., 1995; Paruelo et al., 1998a).

2.4. Remotely sensed data

2.4.1. Topography

The topographic information was extracted from the “Shuttle Radar Topography Mission” (SRTM) digital elevation models (DEM), with a spatial resolution of 90 m (0.81 ha) (USGS, 2004). Three topographic variables were considered in this study. The first two, percentage of the paddock below 1000 m.a.s.l., and median paddock altitude, were used as surrogates of air temperature and snow cover. The last one, aspect, is related with air temperature and wind intensity. For this variable we defined four categories: Northwest (NW), Northeast (NE), Southwest (SW) and Southeast (SE). The best conditions for sheep correspond to the NE exposed hillsides which are “protected” from strong westerly winds and are more exposed to sunlight across the year. Intermediate situations are found in the NW and SE hillsides whereas the worst situations correspond to the SW (where the weather is windier and colder).

2.4.2. Vegetation structure and physiognomy

Land cover characterization data was extracted from Paruelo et al. (2004). These authors performed a supervised classification of a mosaic of four Landsat 5 TM scenes (WRS2 path 231, rows 88–91) corresponding to 30th December 1997. Nine physiognomic types were identified: forests, scrublands, prairies (meadows), grass steppes, grass-shrub steppes, shrub-grass steppes, shrub

steppes, semideserts and ‘low-covered’ grass steppes, plus two barren land covers: snow & rocks and water bodies. For each paddock, we quantified landscape composition through the calculation of three metrics: area of prairies, percentage of paddock covered by prairies and physiognomic type richness. For the first step in their quantification we slightly modified the classification with a 7×7 pixel moving window majority filter in order to eliminate the “salt and pepper” appearance. Then, we vectorized this map and intersected it with the paddock limits. Polygons smaller than 0.36 ha (four Landsat pixels) were eliminated because they would not represent pure grassland polygons.

The first metric was defined as the sum of the area of all the prairie polygons, and it is related to the main forage source (prairies). The second one was defined as the area of prairies relative to the total area of the paddock, and it represents the relative quality of the paddock in terms of forage. This variable was transformed to arcsin (\sqrt{x}), previous to all the analyses. The last metric was calculated as the sum of all the physiognomic types found in the paddock (minimum 1 and maximum 11), and was related to the diversity of different resources in space (food, protection, etc.).

2.4.3. Vegetation functioning and phenology

We characterized the vegetation functioning through the analysis of the “enhanced vegetation index” (EVI) temporal series for the period 2000–2005, obtained from the MODIS-TERRA imagery (MODIS 13Q1 product). The enhanced vegetation index (EVI) is a surrogate of aboveground net primary production (ANPP) which in turn is the main determinant of forage availability (Oosterheld

et al., 1992, 1998; Paruelo et al., 1999). This spectral index was developed to optimize the vegetation signal with improved sensitivity in high biomass regions and improved vegetation monitoring through a de-coupling of the canopy background signal and a reduction in atmosphere influences (Huete et al., 1994, 1997, 2002). The equation takes the form

$$EVI = G \cdot \frac{\rho_{NIR} - \rho_{red}}{\rho_{NIR} + C_1 \cdot \rho_{red} - C_2 \cdot \rho_{blue} + L}$$

where ρ are atmospherically corrected or partially atmosphere corrected (Rayleigh and ozone absorption) surface reflectances, L is the canopy background adjustment that addresses nonlinear, differential NIR and red radiant transfer through a canopy, and C_1 and C_2 are the coefficients of the aerosol resistance term, which uses the blue band to correct for aerosol influences in the red band (Huete et al., 1994, 1997, 2002). MODIS spectral information was filtered based on the quality flags of each pixel. We considered four factors to perform the filtering: 1) low quantity of aerosols, 2) no cloud cover, 3) no ice or snow cover and 4) no shadows.

For each paddock, we calculated the average EVI for the most relevant periods of the reproductive cycle of Patagonian sheep: around mating (from April to June) and around the onset of growing season and lambing (from July to November). Because we had several monthly EVI values, we also performed a principal component analysis to obtain a synthetic measure of vegetation functioning for each key period.

2.4.4. Surface temperatures

As air temperature was not available, we characterized land surface temperature (LST) through the MODIS 11A2 product (<http://edcdaac.usgs.gov/modis/mod11a2v4.asp>) (Wan and Li, 1997; Wan et al., 2002, 2004). LST is defined by the radiation emitted by the land surface observed by MODIS at instant viewing angles (Wan et al., 2004). Mean monthly values for the coldest months (from June to November) were calculated for each 1×1 km pixel ignoring pixels contaminated by clouds or LST average error >1 °K, using the quality control flags. We also characterized the temporal variability in the mean monthly LST in two different ways. First, we calculated the inter-annual standard deviation of the monthly means. Second, we calculated the mean of the inter-pixel standard deviation for each month and paddock. In order to obtain a measure that synthesized thermal environment, we performed principal component analysis with mean monthly temperatures and variability measures.

2.4.5. Harvest index

As an indirect measure of density dependent effects on reproductive performance, we estimated the mean harvest index (Golluscio et al., 1998) during the period for each paddock. Harvest index was calculated as the quotient between consumption and forage availability, assumed to be equal to aboveground net primary production (ANPP):

$$HI = \frac{\text{Consumption}}{\text{ANPP}}$$

Consumption was estimated as

$$\text{Consumption} = \frac{S \times Do \times InI}{\text{area}}$$

where S means stocking (number of animals), Do number of days of paddock occupation and InI individual daily forage intake. We assumed an individual daily dry matter intake of 3% of sheep live weight. We assumed live weights between 25 kg and 50 kg,

depending on the sex, age and physiological status of sheep occupying the paddocks.

Forage availability was assumed equal to aboveground net primary production (ANPP), and was estimated from Monteith model (Monteith, 1981)

$$ANPP = \varepsilon_a \times \int APAR$$

where ε_a is the energy conversion coefficient (in g/MJ month) and APAR is the absorbed photosynthetically active radiation. The integral was calculated over the year and considering monthly intervals. APAR was obtained multiplying the fraction of photosynthetically active radiation absorbed by green vegetation ($FPAR_g$) by the incoming photosynthetically active radiation (PAR). In order to estimate ANPP, we assumed a linear relationship between EVI and $FPAR_g$ (Piñeiro et al., 2006). Energy conversion coefficient values were obtained from Paruelo et al. (2004) and Irisarri et al. (2012). Mean monthly values of PAR were obtained from Esquel airport (-42.91° S, -71.15° W), for the period 1995–2005.

2.5. Statistical analyses

Structural equation modeling (SEM) is a powerful set of tools specially suited to study hypothesized causal relationships among variables when using observational data. This fact makes SEMs particularly relevant for ecology and natural resource management, disciplines in which experimental control and manipulation are not always feasible or ethical. Another feature of SEMs is the capability to model direct and indirect effects acting upon a focal variable or group of focal variables. Graham (2003) recommended the use of SEMs as one of the best alternatives for overcoming the problem of multicollinearity in multiple regression. In our case the use of multiple regression is not appropriate given the presence of strong correlations among the independent variables and the presence of direct and indirect effects acting upon the dependent variables.

In this kind of statistical model the user generates a path diagram that represents the causal relationships and correlations among the variables presumed to be important for the system or phenomenon under study. These relationships should be based on prior knowledge, generally grounded on theory, previous experience, or a combination of both (Iriondo et al., 2003; Malaeb et al., 2000). Our conceptual diagram is depicted in Fig. 2, and arose from previous studies and knowledge acquired from more than a century of sheep husbandry in Patagonia (Golluscio et al., 1998; Hall and Paruelo 2006; Olaechea et al., 1981, 1983; Teixeira and Paruelo, 2006; Teixeira et al., 2008).

The fundamental null hypothesis to be tested in SEMs is that the covariance (or correlation) matrix of the observed variables is consistent with the covariance (or correlation) matrix associated with the model's path diagram. Thus, SEM fitting methods minimize the differences between the observed covariances and the covariances predicted by the model (Pugesek et al., 2003).

Because we had different indicators of thermal environment, topography, and vegetation variables we tested the model structure in Fig. 2, but with different indicator variables in each box (Table 1). We applied this methodology instead of structural equation models with latent variables given the low sample size ($n = 66$). Previous to the analyses all continuous variables were standardised.

We used three criteria for model selection (Fox, 2006; Malaeb et al., 2000). First, we used the probability associated to model Chi square statistic. This probability indicates the strength of the evidence in favour of the null hypothesis, i.e., that the observed covariance structure is consistent with the one assumed in the model. Thus, we looked for models with non significant Chi square

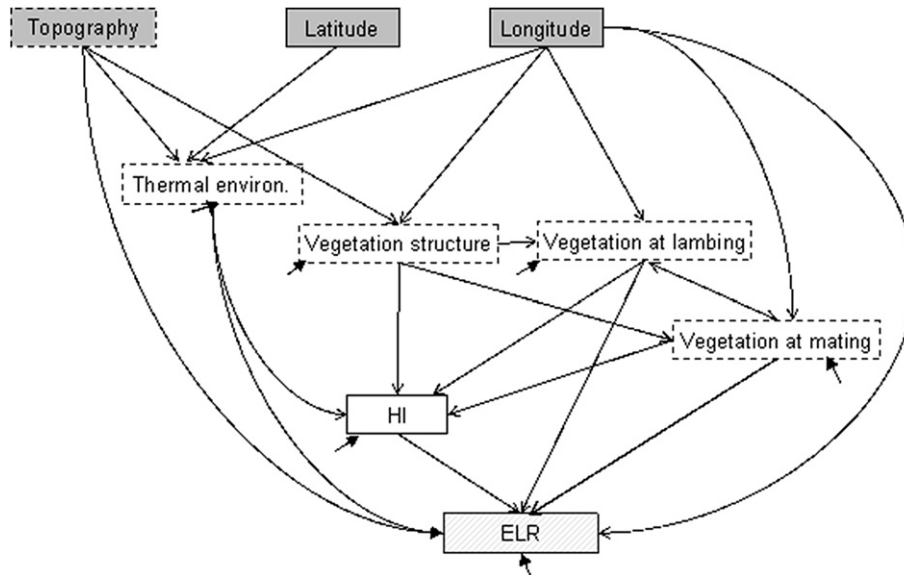


Fig. 2. Conceptual model of the controls of effective lambing rate (ELR). Dashed boxes represent constructs where different indicator variables were tried. Gray boxes represent external variables (analogous to independent variables in multiple regression). "HI" means harvest index.

p -values. Once we identified the set of models with non significant Chi square p -values, we inspected the second criterium, the Bayesian information criterion (BIC). BIC penalizes the likelihood-ratio chi-square statistic for the number of parameters in the model, the number of observed variables, and the sample size. Models with greater support from the data have in general more negative values of BIC. Based on BIC we compared the models adjusted, in order to measure how much better the best approximating model is compared with the next best models. The simplest way of doing this is to calculate the difference (ΔBIC_i) between the BIC value of the best model and the BIC value for each of the other models. Values of $\Delta BIC_i < 2$, represents a substantial level of empirical support of model i (Burnham and Anderson, 2002). Increasing differences in ΔBIC_i represents decreasing levels of empirical support of the models. ΔBIC_i can be used to calculate

Table 1
Construct variables and indicators used in the structural equation models of effective lambing rate.

Construct	Indicators
Topography	- Median altitude - Aspect - % of paddock below 1000 m.a.s.l.
Thermal environment	- Mean monthly land surface temperature (from June to November) - Inter annual variability (SD) of monthly mean temperatures - Mean of inter-pixel monthly temperature variability (SD)
Vegetation structure	- First two axis of PCA of mean monthly temperatures and variability measures - Functional Type richness - area covered by prairies
Vegetation at mating	- percentage of paddock area covered by prairies - Monthly EVI from April to June - Mean of monthly EVI values from April to June (EVI Fall-Winter) - First axis of PCA of EVI values from April to June - Mean integral of EVI in mating paddocks
Vegetation at lambing	- Mean of monthly EVI from July to December - Mean of monthly EVI values from July to December - First axis of PCA of EVI values from July to December - Mean integral of EVI in lambing paddocks

two additional measures to assess the relative strengths of each candidate model. The first of these is the evidence ratio (Burnham and Anderson, 2002) which provides a measure of how much more likely the best model is than model i . The second measure is the BIC weight w_i . BIC weights take values between 0 and 1, with the sum of weights of all models in the candidate set equal to 1. This measure could be interpreted as the probability that a given model is the best approximating model. BIC weights can also be used to estimate the relative importance (RI) of variables under consideration across all the models in the candidate set. This is done by summing the BIC weight for each model in which the focal variable appears (Johnson and Omland, 2004).

The third criterion was the root mean square error approximation (RMSEA), which is an estimate of goodness of fit, relative to the saturated model. In general values of $RMSEA \leq 0.05$ are indicating a good fit to the model. Given the small sample size and the fact that some variables exhibited skewed distributions, the significance of the estimators in the final model selected, was assessed by means of non-parametric bias corrected bootstrap with 2000 bootstrap replicates (Almaraz, 2005).

All analyses were performed in R v 2.8.1 (R Development Core Team, 2008) using the package sem (Fox, 2006).

3. Results

Neither of the models that included topography as an external construct showed adequate fits, and consequently, we removed it. Moreover, only models considering percentage of meadows as indicator of vegetation structure were adequate in terms of Chi square statistic probabilities. The best five models, in terms of the criteria considered, all contained percentage of meadows as indicator of vegetation structure and EVI in July as indicator of vegetation functioning around lambing (Table 2). Thermal environment was characterized in these models by means of mean inter pixel variability in July or interannual variability of mean monthly temperature in June. Vegetation around mating was characterized by EVI in April, EVI in June or EVI during Fall-Winter. As none of the first four models in Table 2 showed differences in BIC greater than two, neither of them could be considered superior in terms of fit to

Table 2

The best five models fitted. The first four columns represents the model rank and the indicators and the last six columns represents the fitting criteria: *p*-value stands for Chi square statistic *p*-value, RMSEA is the root mean square error approximation, BIC is the Bayesian information criterion, ΔBIC_i is the difference between the BIC of model *i* and the best fitting model. ER represents de evidence ratio, and BIC_w is the BIC weight. IaV stands for interannual variability of mean monthly temperature, IpV is the mean of inter pixel variability in each month and paddock.

Model rank	Thermal environment	Vegetation at mating	Vegetation at lambing	<i>p</i> -value	RMSEA	BIC	ΔBIC_i	ER	BIC_w
(1)	IpV July	EVI Fall-Winter	EVI July	0.816	0	-46.054	0	1	0.124
(2)	IpV July	EVI April	EVI July	0.808	0	-45.946	0.108	1.056	0.118
(3)	June IaV	EVI Fall-Winter	EVI July	0.783	0	-45.594	0.460	1.259	0.099
(4)	June IaV	EVI April	EVI July	0.783	0	-45.594	0.461	1.259	0.099
(5)	IpV July	EVI June	EVI July	0.652	0	-43.96	2094	2.848	0.044

the data. Additionally evidence ratios and BIC weights, show that the second, third and fourth models are almost equally likely that the “best” model (ER values around 1 and BIC weights around 0.1 for these models, Table 2). These results imply a considerable model uncertainty. However, when we inspected the relative importance of variables across all models, mean inter pixel temperature variability in July, EVI in July and EVI in Fall-Winter, were the most important indicator variables of thermal environment, vegetation around lambing and vegetation around mating respectively (Fig. 3).

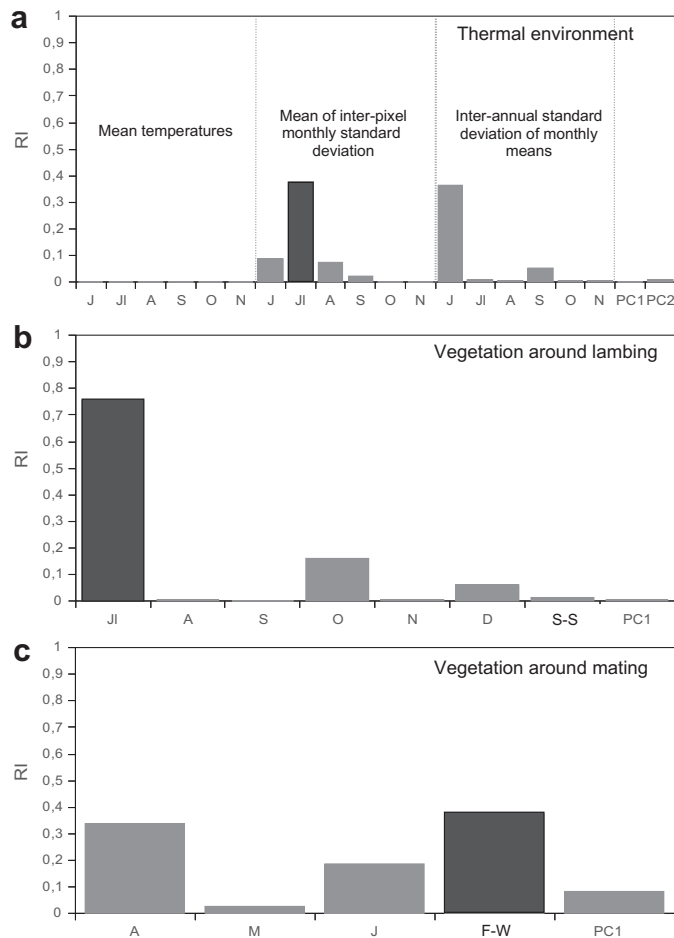


Fig. 3. Relative importance (RI, see methods) of the indicator variables of (a) thermal environment, (b) vegetation around lambing and (c) vegetation around mating. The dark bar in each graph, represent the most important indicator variable. The x axis represents months: from June (J) to November (N) and first two principal components (see methods) for (a), from July (JI) to December (D), Spring-Summer means (S–S) and first principal component for (b) and from April (A) to June (J), Fall – Winter mean (F–W) and first principal component for (c).

For this reason and given the similarities among the best five models, we discuss the results referring to the first model in Table 2. This model included as significant explanatory variables, longitude, the spatial variability of mean July temperature, percentage of paddock covered by prairies, harvest index, EVI in July and mean EVI in Fall-Winter. (Fig. 4, Table 3) (BIC = -46.054, *p* = 0.816, RMSEA = 0). Longitude, a surrogate of mean annual precipitation, exhibited a double effect on effective lambing rate: a direct positive effect and indirect negative effect mediated by the spatial variability of mean July temperature. The spatial variability of mean July temperature was correlated positively with ELR. Percentage of the paddock covered by prairies, had an indirect positive effect through harvest index. This means that forage consumption was greater in paddocks with greater percentage of meadows. On the other hand, ELR was greater in paddocks in which forage consumption (as estimated by HI) was intense. The positive relationship between harvest index and effective lambing rates, seems to contradict the expected density dependent pattern, i.e., a negative relation between harvest index and lambing rates. However, if we consider the relationship between harvest index and above-ground net primary production derived by Golluscio et al. (1998) from the findings of Oesterheld et al. (1992) for grassland ecosystems, this apparent contradiction could be in part explained. This relationship show that the rate of increase of the HI with ANPP, decreases with ANPP. As the ANPP gradient is associated with a precipitation gradient (Sala et al., 1988), the increase in HI with ANPP, reflect an increase in precipitation that would be associated to changes in drinking water availability and/or forage quality

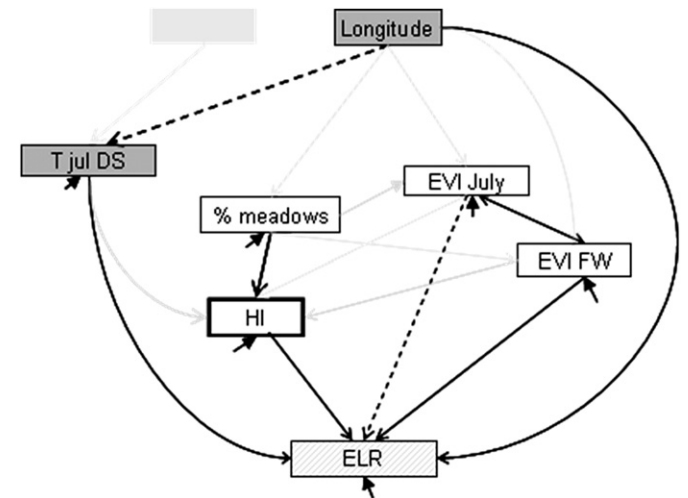


Fig. 4. Best model fitted. Filled arrows represent positive effects and dashed arrows represent negative effects. Light gray arrows and boxes represent non-significant terms and variables. Little arrows from nowhere represent error terms. “ELR” stands for effective lambing rate, “T jul DS” means spatial variability of mean July temperature, “HI” means harvest index, “EVI FW” represents mean EVI during fall-winter.

Table 3

Estimates of the best model fitted. Significant terms are highlighted in bold. S.E. stands for standard error, Lower and Upper are the lower limit and the upper limit of the 95% bias corrected bootstrap confidence interval.

Coefficient	Estimate	S.E.	Lower	Upper
Latitude → temperature	-0.1675	0.1616	-0.4693	0.1462
Longitude → temperature	-0.4089	0.1616	-0.6955	-0.1349
Longitude → % meadows	-0.1630	0.1224	-0.4311	0.0703
Longitude → EVI July	0.0056	0.1245	-0.3631	0.3334
Longitude → EVI fall-winter	0.2068	0.1227	-0.5547	0.1346
Longitude → E.L.R.	0.5962	0.1306	0.3695	0.8392
Temperature → harvest index	0.0547	0.0961	-0.1299	0.2898
Temperature → E.L.R.	0.3688	0.1243	0.1589	0.5692
% meadows → EVI July	0.1397	0.1245	-0.1220	0.3717
% meadows → EVI fall-winter	0.0412	0.1227	-0.2432	0.3166
% meadows → harvest index	0.5756	0.0947	0.2156	0.8514
EVI July ↔ EVI fall-winter	0.7540	0.1520	0.5531	0.8713
EVI July → harvest index	0.0882	0.1464	-0.3133	0.4580
EVI July → E.L.R.	-0.4007	0.1692	-0.7732	-0.0410
EVI fall-winter → harvest index	-0.4201	0.1476	-0.8057	0.0074
EVI fall-winter → E.L.R.	0.5464	0.1823	0.1132	0.9917
Harvest index → E.L.R.	0.2741	0.1142	0.0387	0.5251

(Milchunas et al., 1988). The change of both drinking water and forage nutritive quality is greater in the arid extreme of the gradient than on the humid one. Fig. 5 shows the harvest index predicted by the ANPP model and the harvest index observed in the paddocks considered in this study. According to the differences between observed and model predicted HI, we can infer that most of the paddocks have experienced harvest intensities below those expected according to the paddock's ANPP. This could explain why density dependent effects on effective lambing rates were not found, and could point to a sub-utilization of these paddocks.

The quantity and quality of forage around mating (represented by mean EVI during fall-winter, EVI FW) had a direct positive effect, whereas forage around growing season onset – lambing (EVI July) had a negative direct effect. As expected these two variables exhibited a strong positive correlation. Fig. 6 show the observed ELR vs model predicted ELR for the harvest index and for the effective lambing rate. The regression lines showed in the graphs are not statistically different from the 1:1 line.

4. Discussion

Our analysis shows that paddocks towards the East, with a greater spatial variability of July or interannual variability of June temperature and greenness index during fall-winter showed greater mean effective lambing rates. Moreover, paddocks in which forage consumption have been intense (with higher HI), lambing have been greater. Moreover, harvest index, measured as

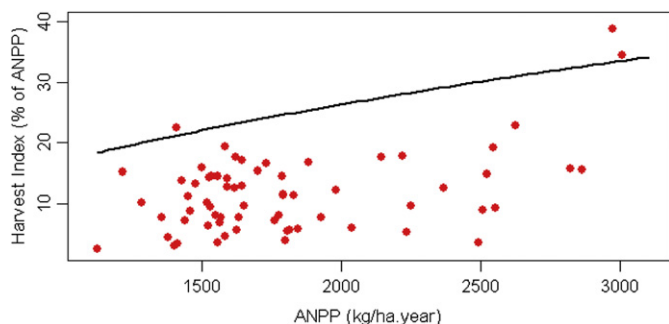


Fig. 5. Observed harvest indexes (dots) and harvest indexes predicted from ANPP (line). This model states that $HI = -5.71 + 0.7154 \cdot (PPNA)^{0.5}$. (Oesterheld et al., 1992; Golluscio et al., 1998).

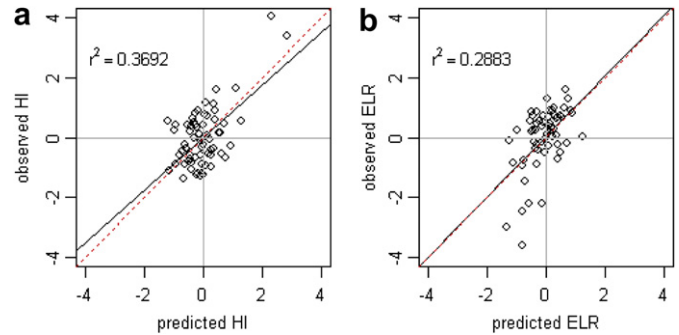


Fig. 6. Observed vs. model predicted graphs of standardised harvest index (a) and standardised effective lambing rate (b). Coefficients of determination between observed values and model predicted ones are shown in each graph. Filled lines represents observed versus predicted regressions whereas dashed lines represent 1:1 line. “ELR” stands for effective lambing rate and “HI” means harvest index.

a percentage of ANPP, was greater in paddocks with greater percentage of the area covered with prairies.

The direct positive effect of longitude could be interpreted at least in two ways. First as a negative effect of annual ANPP, given the strong east-west ANPP precipitation driven gradient (Jobbágy et al., 1995; Paruelo et al., 1998a). The second interpretation could be associated to the effects of mean annual temperatures, as paddocks towards the West are higher and thus exhibit lower mean annual temperatures, and are more prone to snowfall during winter. The spatial variability of mean July temperature was correlated positively with ELR; this could be associated to the availability of “thermal refuges” for sheep in the coldest month. Jobbágy et al. (2002), found that the beginning of the growing season was associated to mean July temperature and can occur in July. Then a more spatially variable July temperature, could be associated with a spatially heterogeneous growing season start, and thus an heterogeneous forage source, offer and availability. Spatially heterogeneous plant phenology leads to a prolonged period with high quality forage, as young plants have higher nutritional value and N concentrations and low lignin contents (Demment and van Soest, 1985). Somlo et al. (1985) have showed this for Patagonian grass and shrub steppe species.

The positive effect of vegetation greenness during fall-winter, points to the importance of foraging conditions around mating. Several authors have shown an association between nutritional status and ovulation rates in sheep and red deer (Gonzalez et al., 1997; Gunn et al., 1969; Langvatn et al., 1996; Russel, 1971). Higher EVI during fall – winter, could be thus associated to better nutritional status of ewe at mating and thus higher probabilities of ovulation and conception.

According to our results, mean EVI in July is associated to lower mean effective lambing rates. Although higher EVI in July could have a positive effect on nutritional status of pregnant ewe, it could determine an earlier growing season end, and as a consequence lower quality forage during lactation. This line or reasoning stems from the fact that the length of the growing season is constant, in particular in sites with mean annual temperatures above 3–4 °C (Jobbágy et al. 2002). This is the case for the northwest portion of Patagonia, the region in which the ranches of our study are located. This could translate into higher lamb mortality in November–December, and thus in lower effective lambing rates.

Our results have two important implications. On the one hand, provide quantitative hypothesis about the controls at the landscape level of herbivore reproductive performance, by relating by means of appropriate techniques (i.e., SEMs), topography, climate and vegetation. The application of multiple regression models to this

situation could be misleading, and could not allow us to establish causal assumptions (those associated to the diagram in Fig. 4), as a consequence of incorrect estimation of standard errors and significance levels (Graham 2003; Kline, 2011). In spite of the low predictive ability of the fitted model, we consider that the approximation could serve as a guide for further, refined explorations. Consideration of model uncertainty (by means of BIC weights and relative importance of variables across the entire candidate models set) showed that certain variables consistently appear in the “best” fit models. It also provides statistically sound evidences and thus potential advice for a better management of sheep flocks in arid and semi-arid rangelands.

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