



Direct and indirect effects of climate and vegetation on sheep production across Patagonian rangelands (Argentina)

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ABSTRACT

Extensive sheep production is an important agricultural industry in the Patagonia region of Argentina, where the most important production metric is the effective lambing rate of the sheep (L%). Climate factors can affect sheep production in two ways: (i) directly on the survival of the lamb, and (ii) indirectly by determining the start of the growing season, aboveground net primary productivity (ANPP) and the availability of forage. The aim of this study was to determine the relationships between climatic variables and vegetation attributes as the major drivers of sheep productivity (ewe live weight pre-mating (ELW) and effective lambing rate (L%)), using structural equation modelling. We observed that precipitation in late autumn/winter and vegetation productivity in late spring/summer were the main drivers and were positively associated with ELW. The ELW was highly and positively correlated with L%. Additionally, the maximum temperature in late spring showed a strong direct and negative relationship with L%. These results indicated that ELW should be taken into account when modelling L%. Regional Patagonian climate change models predict, for the next century a decrease in precipitation and an increase in temperature. Thus, according to our findings, sheep production systems would be affected by a decrease in primary productivity, as well as ELW and L% since these variables are positively associated with precipitation and negatively with temperature. The use of strategic supplementation to meet nutrient requirements and protection from climatic stressors during physiologically demanding production stages of pregnancy and lactation through additional shelter and housing for the sheep could mitigate the effects of climate change by having a positive effect on L% and, therefore, on the total farm income.

1. Introduction

Patagonia is one of the most extensive rangelands in the world, where extensive sheep farming is a major agricultural industry (Gaitán et al., 2020). The above ground net productivity (ANPP) in Patagonia is subject to climatic variability in precipitation and temperature which ultimately influence productivity of the sheep enterprise. Consequently, climatic variability determines the availability of forage, and determines herbivore-carrying capacity (Oesterheld et al., 1992). Additionally, the ability of grazing ruminants to utilize these forage resources is affected by climatic variables and topography, in addition to temporal precipitation patterns, and type of vegetation among other factors which ultimately determine the selection of grazing sites (Texeira et al., 2012).

Due to water redistribution, induced by the topography, wet meadows, locally known as “mallines” occur in the drainage lines between hills and plateaus (Gaitán et al., 2011a). These meadows are characterized by their relatively high forage production potential in the spring and summer seasons that are highly valued grazing resources in sheep production systems (Villagra et al., 2013). The presence of mallines within these Patagonian sheep production systems has been positively correlated with the higher body condition of the sheep pre-lambing, as well as the daily weight gain of the lambs (Villagra, 2005).

Climatic factors exert a significant impact all aspects of sheep production in extensively managed sheep operations (Texeira et al., 2012). High temperatures in spring and summer in addition to low rainfall can directly affect the productivity of ewes and lambs. For example, high

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temperatures can affect both ewes and lambs due to the direct effects on growth, reproduction, wool production, lactational performance, animal health, and overall survival (Al-Dawood, 2017). Similarly, low rainfall can reduce the amount of drinking water available on these extensive landscapes (Teixeira et al., 2012). Specifically, climate can indirectly affect the sheep by determining the onset of the growing season (Jobbágy et al., 2002), the ANPP and the availability of forage (Jobbágy et al., 2002; Gaitán et al., 2014). These effects influence the body condition of the sheep at critical moments in their production cycle, affecting the effective lambing rate of the sheep (L%) (Teixeira et al., 2012), which reflects the productive success of the ranch (Villagra et al., 2015).

We recognize the difficulty of separating the direct and indirect effects of climate and vegetation that act as limitations on animal production. To this end, Structural Equation Modelling (SEM) has been used to identify direct and indirect effects with observational data (e.g. Teixeira et al., 2012; Gaitán et al., 2014). Structural Equation Modelling has been identified as a suitable approach to explore and test hypotheses about causal relationships of the environment, vegetation and animals (Pugesek et al., 2003). This analysis consists of the evaluation of a priori models, based on the knowledge generated in previous studies, developed to understand how multiple factors affect a variable of interest (Grace, 2006).

In order to promote a more sustainable use of Patagonian rangelands there is a need to elucidate how climate variables and vegetation attributes work together to directly and/or indirectly affect sheep production. We aimed to do so by evaluating the relative importance of climate and vegetation factors as drivers of animal related variables using a *a priori* causal model (Fig. 1) and structural equation modelling (SEM).

2. Materials and methods

2.1. Study area

Sheep ranches ($n = 23$) were studied in an area of nine million hectares in the province of Río Negro, in northern Patagonia (Fig. 2).

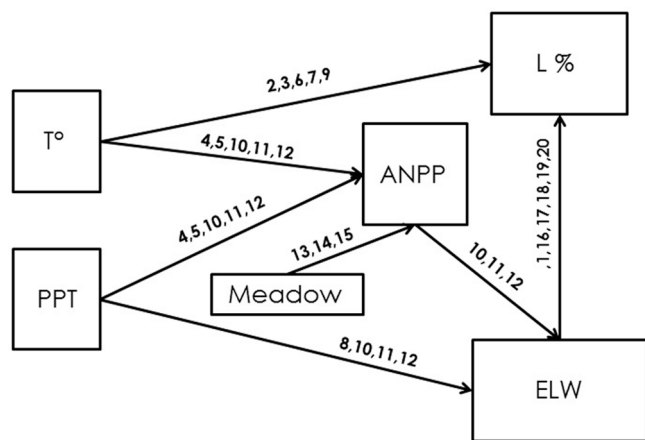


Fig. 1. A priori model that represents the way in which climate and vegetation variables can directly or indirectly influence sheep productivity. Arrows indicate a hypothetical causal relationship of one variable over another. Numbers above the arrows indicate studies that support our hypothetical relationships. T°: Temperature. PPT: precipitation. ANPP: aboveground net primary productivity. Meadow: percentage ranch surface area occupied by meadows. ELW: ewe live weight. L%: effective lambing rate. 1: Villagra, 2005; 2: Hall and Paruelo, 2006; 3: Coronato, 1999; 4: Jobbágy et al., 2002; 5: Gaitán et al., 2014; 6: Olaechea et al., 1981; 7: Bellati and von Thüngen, 1988; 8: Irazoqui, 1981; 9: Teixeira et al., 2012; 10: Pettorelli et al., 2005a, 2005b; 11: Côté and Festa-Bianchet, 2001; 12: Langvatn et al., 1996; 13: Ayesa et al., 1999; 14: Jouve, 2003; 15: Buono et al., 2010; 16: Giraudo and Villar, 2010; 17: Cueto et al., 2015; 18: Kelly, 1992; 19: Molina et al., 1994; 20: Vatankhah and Salehi, 2010.

The vegetation is dominated by grasslands, shrub steppes, scrublands and semi-deserts (León et al., 1998). The dominant soils have sandy and loamy textures and belong mainly to the Aridisols and Entisols orders (Del Valle, 1998). Average annual precipitation and temperature range from 100 to 800 mm and 8 to 13 °C, respectively. Sheep grazing is the most widespread agricultural use in the area (Villagra et al., 2013).

2.2. Climatic data

We obtained monthly precipitation maps for the entire study area from January 2012 to December 2015 by interpolating the monthly precipitation data from twelve weather stations using ordinary kriging (Goovaerts, 1997). From these maps, we extracted estimated monthly precipitation data for each ranch (Fig. 2).

The maximum, minimum and average temperatures of each ranch were estimated using the MODIS Land Surface Temperature (LST) and Emissivity Product (MOD11A2), which provide estimates of day and night temperatures with a spatial resolution of 1 km every eight days (Wan and Li, 1997). The temperature estimates derived from MOD11A2 have proven to be a very good predictor of the temperature recorded at weather stations in the study area ($R^2 = 0.93$) (Gaitán et al., 2011b).

2.3. Estimating ANPP

The Normalized Difference Vegetation Index (NDVI) was used as a surrogate of ANPP. This variable has been shown to be a good estimator of ANPP because it is directly related to the photosynthetically active radiation absorbed by plant canopies (Tucker and Sellers, 1986). Gaitán et al. (2013) found that NDVI was positively related to vegetation cover in the Patagonian steppe. In sparsely vegetated ecosystems, like those we studied, vegetation cover is closely related to ANPP (Flombaum and Sala, 2009). Furthermore, previous studies have shown a positive linear relationship between NDVI and ANPP in this region (Paruelo et al., 2004; Paredes, 2011).

The NDVI data for each ranch was acquired using the MODIS sensor product MOD13Q1, which provides 23 captures per year, with a pixel size of 250 × 250 m. These data are geometrically and atmospherically corrected for each ranch, and we calculated the average NDVI between 2012 and 2015.

2.4. Percentage of meadows

High-resolution images taken from the Google Earth platform were used. Meadow polygons were drawn to calculate their area and proportion to the total area of each ranch with the Qgis 2.8.1 software.

2.5. Ewe live weight (ELW) and percentage of effective lambing rate (L%)

From 2013 to 2015 we recorded the ELW of 2–5 year old between 5 and 15 days before mating (pre-mating) on 23 ranches located in the study area. The ELW was measured individually with a cage on a digital scale. The percentage of ewes evaluated on each ranch was between 20% and 100% of the flock at the time of measurement. A total of 2511 ewes were recorded and the average live weight was analyzed on each ranch.

We calculated the percentage of lambing using the following equation:

$$L\% = n^{\circ} \text{ lamb} / n^{\circ} \text{ EM} * 100 \quad (1)$$

Where L%: Percentage of the effective lambing rate measured about three weeks after the end of the lambing period. n° lamb: number of lambs alive about three weeks after the end of the lambing period. n° EM: number of ewes present at mating.

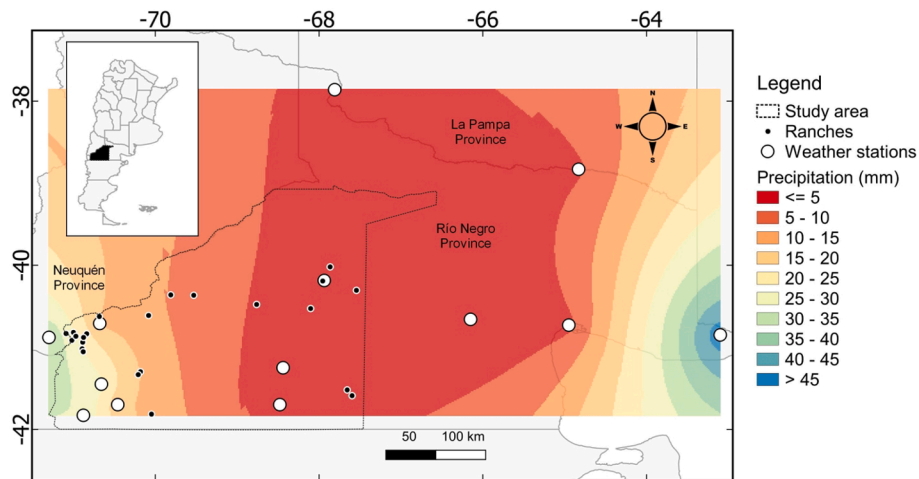


Fig. 2. Map of the distribution of weather stations from which monthly precipitation data estimates were made for each ranch. As an example, the figure shows the precipitation map obtained with the Ordinary Kriging interpolation method for May 2015.

2.6. Statistical analysis

We use SEM with observable variables to assess the relative importance of climate and vegetation attributes as drivers (direct and indirect) of sheep productivity. Previously, we carried out an exploratory analysis of the data by means of a correlation analysis in which we analysed the relationship between the predictor variables (climate and NDVI), in different periods of the year, and the response variables (ELW and L%). According to the results of the exploratory analysis, the variables that formed the SEM were selected.

We tested the fit of the *a priori* model (Fig. 1) to our data. The analyses were performed with R software version 3.3.3 and the SEM piecewise package (Lefcheck, 2016), assuming normal distributions for the variables.

3. Results

The *a priori* SEM model explained 72% of the variation in late spring and during summer NDVI (NDVI_SS), as well as 55% and 52% of the variation found in the ewe live weight pre-mating (ELW) and L%, respectively. The stepwise SEM based on mixed models reproduced well the data based on the comparison of the Fisher C statistic with a distribution of χ^2 (Fig. 3).

3.1. Relationship of the climate and the percentage of meadows with vegetation productivity

Late autumn and during winter precipitation (PPT_AW, May to September is the period with the most accumulated precipitation) and the percentage of Meadow were directly and positively related to the NDVI_SS (December to February is the period with the most accumulated forage). Meanwhile, the maximum temperature in January of year $n + 1$ (TJ1) was directly and negatively related to the NDVI_SS (Figs. 3–4).

3.2. Direct, indirect and total effects of climate and vegetation on the ewe live weight pre-mating and the effective lambing rate

The total standardized effect obtained from the SEM showed that PPT_AW and NDVI_SS were the main effects responsible for variations in the ewe live weight pre-mating (ELW) (0.52 and 0.36 respectively). The maximum temperature in November of year $n + 1$ (TN1) and the ELW had the greatest overall effect on the effective lambing rate (L%) (−0.45 and 0.37 respectively). PPT_AW (0.19) and NDVI_SS (0.14) had somewhat lower values with L% (Figs. 3–4).

Approximately 78% of the effect that the PPT_AW had on the ELW was direct, and 22% was indirect. Meadow presented a positive and

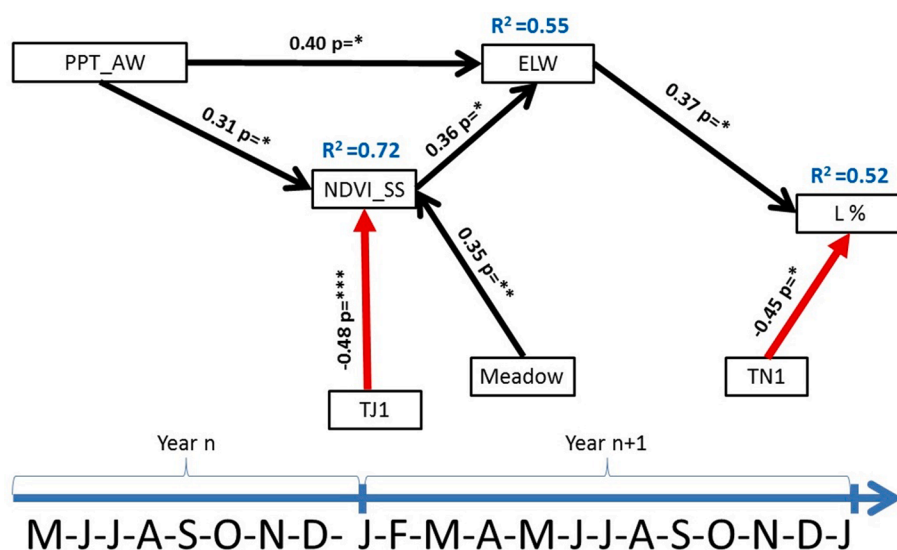


Fig. 3. Stepwise SEM. Arrows indicate a hypothesized causal influence of one variable on another. The numbers on the arrows indicate the weight of the standardized regressions and their p-values. Black arrows indicate positive and significant relationships and red arrows indicate negative and significant relationships. The R² over the response variables indicates the proportion of variance explained. The light blue arrow indicates the months of the year. PPT_AW: Accumulated precipitation from May-September; NDVI_SS: Average normalized difference vegetation index from December year n to February year $n + 1$; TJ1: Average maximum temperature for January of year $n + 1$; Meadow: percentage of ranch area occupied by meadows; ELW: Average ewe live weight pre-mating; L%: Effective lambing rate measured about three weeks after the end of the lambing period.; TN1: Average maximum temperature for November of year $n + 1$. C (Fisher's C statistic) = 14.71, P = 0.55. * P < 0.05; ** P < 0.01; *** P < 0.001. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

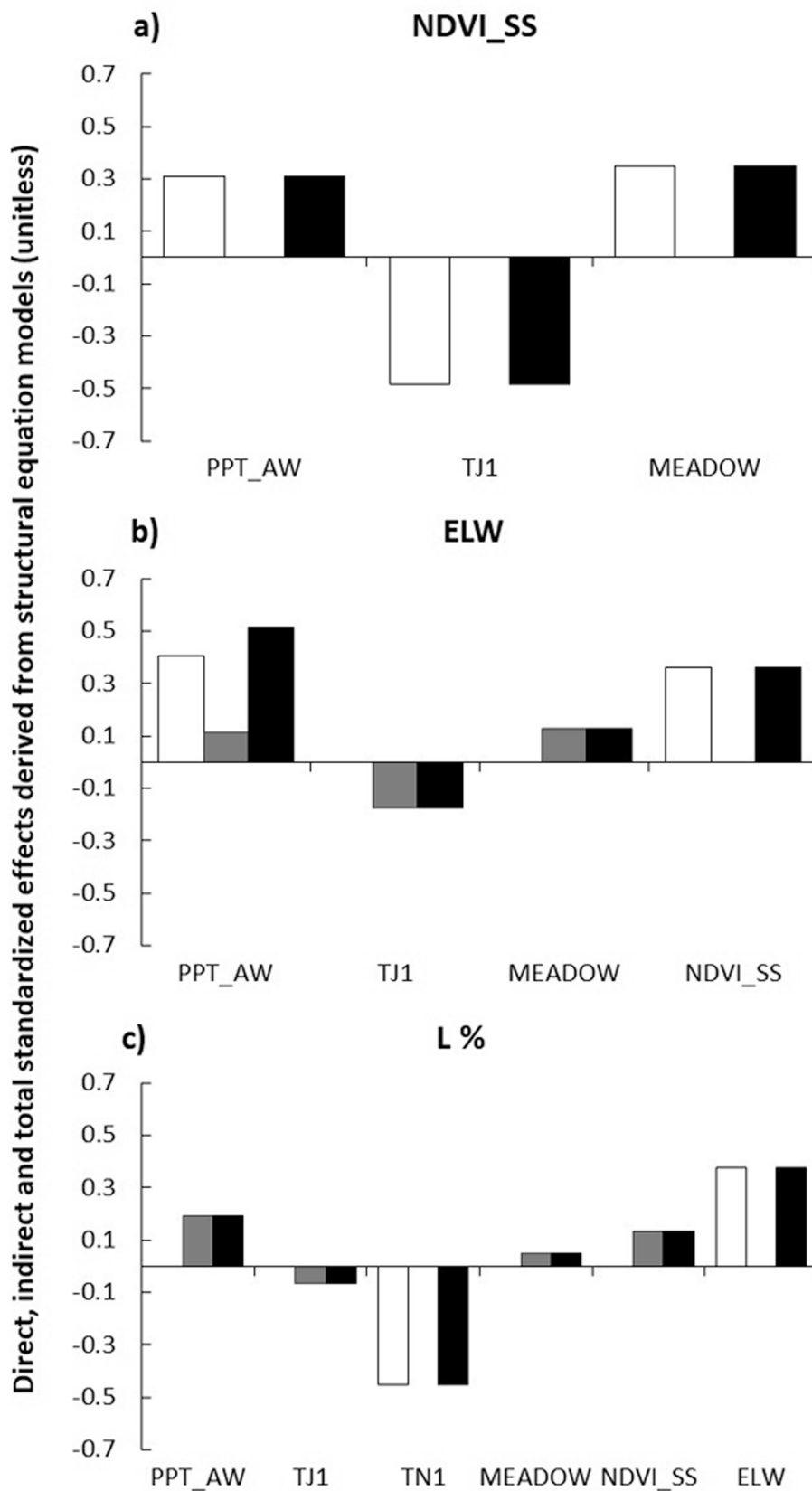


Fig. 4. Standardized direct (white), indirect (gray), and total (black) effects of PPT_AW (accumulated precipitation from May-September), TJ1 (Average maximum temperature for January of year n + 1), TN1 (Average maximum temperature of November of year n + 1), Meadow (percentage of ranch area occupied by meadow), NDVI_SS (average normalized difference vegetation index from December year n to February year n + 1), ELW (Average ewe live weight pre-mating) over a) NDVI_SS b) ELW and c) L% (effective lambing rate).

indirect effect on ELW (0.13), while T_{J1} had a negative and indirect effect (−0.18). The three variables (PPT_{AW}, Meadow and T_{J1}) that presented an indirect effect with the ELW were mediated by its relationship with NDVI_{SS} (Figs. 3–4).

Both TN₁ and T_{J1} had a negative effect on L%, whereas the effect of T_{J1} was low and indirect, and that of TN₁ was high and direct (−0.45). The ELW showed a direct and positive effect with the L%, being the second most important in value (0.37). As for PPT_{AW}, NDVI_{SS} and Meadow, they had a small positive and indirect effect on L%, mediated through ELW (Fig. 4).

4. Discussion

Our results provide novel insights in regards to the relationships between climate, vegetation attributes, and sheep production parameters, which is otherwise difficult to obtain through small-scale factorial experiments or bivariate empirical studies. According to our hypotheses, we found that the ELW explained a significant and unique portion of the variability found in L% at the regional scale, independent of that explained by climate and vegetation and almost as important as climate. These results indicated that the ELW should be taken into account when modeling the L%.

4.1. Effects of climate and percentage of meadows on NDVI

We found that climate, inclusive of precipitation in late fall and during winter (PPT_{AW}), and maximum temperature in January (T_{J1}), was an important driver of late spring and during summer NDVI (NDVI_{SS}, our proxy of vegetation productivity). The importance of the percentage of meadows with respect to the NDVI_{SS} was similar to that of the PPT_{AW}. Climate (precipitation and temperature) and vegetation structure (percentage of meadows) influenced NDVI_{SS}, explained 72% of its variation.

The PPT_{AW} had a direct and positive effect on the NDVI_{SS}. This supports the findings of several authors who analyzed, in Patagonia between the NDVI of a given period, and the precipitation that had fallen months earlier in Patagonia (Jobbágy et al., 2002; Fabricante et al., 2009; Gaitán et al., 2014). In this region of Patagonia, precipitation falls mainly in autumn and winter (Godagnone and Bran, 2008) in agreement with, previous studies have found a positive relationship between precipitation during autumn and winter, and NDVI at the time of maximum biomass accumulation (spring and summer) (Fabricante et al., 2009).

The T_{J1} had an important direct and negative effect on the NDVI_{SS}. Epstein et al. (1996) also found a negative relationship between temperature and primary productivity in arid landscapes, attributing it to increased water losses due to direct soil evaporation with increasing temperature, which would reduce the ANPP. Evapotranspiration and drought stress increase with increasing temperature in water-limited ecosystems, which could explain the negative relationship we found between temperature and NDVI.

The percentage of meadows land-mass in the ranches had a direct and positive effect on the NDVI_{SS}. This means that there would be higher forage productivity on the ranch with a higher percentage of meadows. This is consistent with other studies in the region that reported that meadows produce about 40–50% of available forage, even though they only occupy about 3% of the area (López et al., 2005) attributable to increased availability of water in the meadows leads to the development of azonal plant communities whose ANPP is 10–20 times greater than that of the surrounding steppes (Bonvissuto and Somlo, 1998; Ayesa et al., 1999). In the study area, Gaitán et al. (2011a) described three plant communities associated with meadows, which respond primarily to moisture and salinity gradients. Forage production in these environments varies between 500 and 7000 kg of DM ha^{−1}. If we compare the forage production of these communities with the surrounding steppes, where forage production ranges from 50 to 400 kg of DM ha^{−1} (Bonvissuto and Somlo, 1997), we can appreciate the

fundamental importance of meadows for livestock production systems.

4.2. Effects of climate and NDVI_{SS} on the ELW

Climate and vegetation explained 55% of the ELW variation. The PPT_{AW} and the NDVI_{SS} were the main controls of the ELW variations. To a lesser extent, and mediated by the NDVI_{SS}, the PPT_{AW}, the percentage of meadows and T_{J1} had indirect effects: positive for the first two variables and negative for the last one.

The PPT_{AW} presented the strongest relationship (direct and positive) of all the variables on ELW, but also an indirect relationship. An increase in precipitation would be associated with changes in the availability of water for livestock consumption and/or in the quantity and quality of forage (Texeira et al., 2012). Therefore, the direct effect would be associated with the availability of drinking water and the indirect effect with the quantity and quality of forage. The indirect and negative relationship of the T_{J1} on ELW was mediated by the NDVI_{SS}. This could be due to higher temperatures in summer could affect the quantity and quality of forage consumed by the animals.

The NDVI_{SS} presented a direct and positive relationship with ELW. This would indicate that a higher ANPP, and therefore a higher availability of forage, would be associated with a higher ELW. This is consistent with another study conducted in the area, where a significant relationship was found between forage production (measured through field surveys) and the ewe live weight (Villagra, 2005). This relationship was verified by Irisarri et al. (2014) at the national level for semi-arid and sub-humid regions, where a positive relationship was found between NDVI and herbivore biomass.

4.3. Effects of climate and ELW on L%

Climate and ELW explained 52% of the L% variation. The L%, a key factor determining the economic success of the Patagonian ranches, is highly and positively correlated with ELW. The current findings are similar to those of Molina et al. (1994) and Vatankhah and Salehi (2010), where L% was affected by an increase in ELW in mating. Molina et al. (1994) found that prolificacy was significantly affected by ELW. The increase in the percentage of lambs may be influenced by an increase in ewe prolificacy. A more recent study of Merino sheep in arid and cold areas of Turkey, similar to conditions in Patagonia (Aktas and Dogan, 2014), determined that the lamb twin rate was proportionally affected by pre-mating ELW, and the heavier ewes had 53.1% twins. The increase in prolificacy can be explained by the positive relationship between the ELW and the ovulation rate, as demonstrated in the first studies. Morley et al. (1978) found prolificacy increases of 1.7–4.1% for each kg of ELW increase at mating and Smith (1985) showed that the ovulation rate increased by 2% for each kg of ELW increase at mating. Therefore, the increase in L% observed in our study can be partially explained by the increased prolificacy of the heavier sheep. It is also known that both fertility and fecundity of ewes increase with increasing ELW, and that they must have a minimum of 40 kg at mating to be successful in reproduction (Kenyon et al., 2014). The presence of ewes weighing more than 40 kg may also have been a factor in increasing L%.

Additionally, another factor that influences the survival rate of lambs is their birth weight where several studies show that higher birth weight improves the survival rate of lambs (Assan, 2013). There are also numerous studies showing that an increase in the ELW has resulted in a proportional increase in both the birth weight and weaning weight of lambs (Gaskins et al., 2005; Aliyari et al., 2012; Aktas and Dogan, 2014). The reason for this phenomenon is that the degradation of the ewe's adipose reserves serves an important source of metabolic substrate for the ewe and ultimately helps decrease the metabolic demands of the fetus. Furthermore, in the case of a lighter ewe at first birth: young and inexperienced ewe, this can lead to poor maternal behavior compared to mature ewe (Corner et al., 2013). Therefore, in areas such as Patagonia, where supplementation during pregnancy is rare, the adipose reserves of

ewe during mating (e.g. a heavier ewe) will directly influence the birth weight of the lamb and therefore its survival rate.

The TN1 had a strong direct and negative relationship with L%. This would indicate that higher temperatures in that period would be negatively associated with L%. The effects of high temperatures on animals are known as heat stress (HS), and there are many studies that discuss these effects on sheep (Al-Dawood, 2017; Marai, 2000; Marai et al., 2007). The HS redistributes the body's resources, including protein and energy at the expense of reduced growth (Marai et al., 2007), reproduction (Naqvi et al., 2004), production and health of animals (Gupta et al., 2013). In addition, HS reduces feed intake (Marai, 2000), milk yield and quality (Salama et al., 2014), and increases water consumption (Gupta et al., 2013). Heat-stressed animals decrease feed intake in an attempt to create less metabolic heat which aids in thermo regulation (Kadzere et al., 2002). In addition, maintenance needs increase by 30 percent due to HS (NRC, 2007) and energy intake would not be sufficient to meet daily needs, resulting in apparent body weight loss (Hamzaoui et al., 2013). Among the harmful effects of HS mentioned above, the detrimental effects during month of November might be related to reduced feed intake and decreased milk production. This coincides with when Patagonian flocks are finishing lambing, are in early or mid lactation, and potentially more susceptible to negative energy balance aggravated by heat stress (Moore et al., 2005). Therefore, a decrease in feed intake of the sheep, as well as a decrease in milk production and quality due to HS would jeopardize the growth and survival of the lambs, resulting in lower L%. This agrees with Marai et al. (2007) who stated that birth weight, live body weight gain, as well as, total body solids and daily solids gain are impaired by exposure to elevated temperatures.

Unfortunately, we have limited information to link HS to the weaning rate. However, HS probably affects weaning rate of sheep more dramatically because flocks weaning coincides with late summer time-points (between February and March), passing through the months of January and February where the maximum temperatures of the year occur (Godagnone and Bran, 2008).

5. Conclusions and implications

We concluded that in the Patagonian sheep ranches, precipitation in late autumn and during winter, and vegetation productivity in late spring and during summer were the main drivers for variations in the ewe live weight pre-mating (ELW). The ELW was highly and positively correlated with the effective lambing rate of the ewes (L%), a key factor determining the economic success of the ranches (Villagra et al., 2015). In addition, the maximum temperature in November of year $n + 1$ showed a strong direct and negative relationship with L%. A novel aspect in this study was the use of ELW measured across the ranches. Previous multivariate studies relating climate and/or vegetation attributes to L% did not use ELW taken at a key point in the sheep reproductive cycle. In this case, we were able to observe that the effect of vegetation on L% would occur through the ELW.

Our results allow us to theorize the implications that climate change could have on livestock production in the region. Regional climate change models that include Patagonia predict a decrease in precipitation and an increase in temperature (Barros and Camilloni, 2016). The ovine systems in northern Patagonia would be affected by a decrease in primary productivity, as well as in the live weight of the animals and L% because they are positively associated with precipitation and negatively with temperature, according to our study.

Management measures needed to mitigate these effects could be the use of strategic supplements to increase the weight of the sheep or the protection of the sheep from high temperatures during the lactation season (TN1) through shade infrastructure such as sheds. These measures could have a positive effect on L% and thus on total ranch income.

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CRediT authorship contribution statement

D.A. Castillo: Conceptualization, Investigation, Data curation, Formal analysis, Writing - review & editing. **J.J. Gaitán:** Conceptualization, Methodology, Supervision, Writing - review & editing. **E.S. Villagra:** Methodology, Resources, Supervision, Project administration, Funding acquisition, Investigation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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