

Landscape heterogeneity influences on sheep habits under extensive grazing management in Southern Patagonia

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Abstract

In Southern Patagonia, continuous grazing with fixed stocking rates in large paddocks prevails over grazing systems subjected to regular evaluations and rotational rests. Because of this, sheep extensive systems need technologies to improve their production levels under sustainable management. In this context, the aim of this work was to provide knowledge of sheep habits (diet, daily activity and spatial distribution patterns) in seven paddocks at a production scale throughout the year in Southern Patagonia. The area is an extensive ecotone between forest and steppe, characterized by a rugged landscape with valleys and mountains.

Three vegetation types were distinguished in each paddock: forest, steppe and wetland. After a two years trial, sheep showed an important array of strategies for facing restrictions imposed by climate and low forage availability. A strong dietary selectivity, a high percentage of time allocated to grazing, large explored areas and opportunistic selection of vegetation types explained the capacity for reproduction under Southern Patagonia harsh conditions. The application of an intensified management involving paddock subdivision and separation of vegetation types should consider how sheep grazing strategies are limited.

Key words: *daily activities, diet, GPS tracking, vegetation types*

Introduction

Extensive livestock production systems in Southern Patagonia are dominant, with a marked seasonal grass production that is restricted to a 5 to 7 month growth period due to water stress and low winter temperatures (Andrade et al 2014). The prevailing activity in the area is sheep rearing for meat and wool production, with some important cattle production in sites of high grass availability, like valleys or Andean prairies. Sheep were introduced in Punta Arenas (Chile), Malvinas and Buenos Aires before the end of the 19th century (Correa Falcón and Klappenbach 1924), with no evidence of significant improvement in sheep management in the last 130 years (Quargnolo et al 2007; Andrade 2012). Currently, continuous grazing with fixed stocking rates in large paddocks (1000 to 5000 ha) prevails over grazing systems subjected to regular evaluations and rotational rests.

Lamb production implies a particular nutritional requirement curve, with higher demand before the start of winter to ensure both pregnancy (May mating) and resistance to winter conditions until spring resprout. The months before resprout are critical because it coincides with the last two-month period of sheep gestation, when nutritional requirements increase considerably. Ewes must recover after lambing and until May, but this coincides with the lactation period, which is generally interrupted due to weaning in January or February. In this scenario of high requirements and free grazing in large paddocks, sheep develop a strong selection for certain habitats, which sometimes may lead to overuse or underuse of some areas, leading to the degradation of natural grasslands (Lange 1985; Danckwerts 1989). Intensive management that considers flexibility in stocking rate and the time that animals spend in the paddock would help improve paddock use efficiency (Golluscio et al 1998). This system is advantageous for both sheep and natural grassland conservation, but requires knowledge of the habits of grazing animals in terms of diet, daily activities and spatial distribution.

Several biotic and abiotic factors influencing decisions made by grazing animals have been reported (Squires 1974; Arnold 1982; Bailey et al 1996; Howery et al 1998; Bailey and Provenza 2008). The interaction of these factors, however, determines a complex behaviour that requires studies under different environmental conditions (Dudzinski and Arnold 1979; Shinde et al 1997; Marijuán et al 1998). These factors, which condition the habits of domestic herbivores, operate at different scales (plant, patch, plant community, landscape, and region) and are related to the daily activities of the animals (grazing, resting, movement and search for food) (Bailey and Provenza 2008). Specifically, grazing activity and diet, as determinants of sheep body condition and reproductive response, are influenced by heterogeneity and diversity of the available vegetation (Laca 2008). Furthermore, studies on animal preferences for different vegetation types (*forest, wetland and steppe*) contributes to the analysis of grazing decisions at a larger ecological scale, which is rarely addressed in scientific studies (Senft et al 1987; Bóo et al 2002). For example, rangelands in the Andean region contain different proportions of ñire (*Nothofagus antarctica*) native forest, which occurs in patches interspersed with wetland and steppe vegetation types; and, to a lesser extent, in continuous stands (Peri and Ormaechea 2013). To date, no studies have addressed sheep behaviour and preference in paddocks with different vegetation types and for different stages of the production cycle in Patagonia. This information is very useful as a complement to the assignment of stocking rates and planning of grazing schemes (Barbari et al 2006; Bertiller and Ares 2008).

The aim of this study was to describe sheep habits (diet, daily activity and spatial distribution patterns) in seven paddocks at a production scale throughout the year, as a tool for improving grazing management in the forest-steppe ecotone of Southern Patagonia.

Materials and Methods

Study site and production system

The trial was conducted in Cancha Carreras ranch (51° 20' S - 72° 10' W) located in southwestern Santa Cruz province in Argentina. The area is an extensive ecotone between forest and steppe, characterized by a rugged landscape with valleys and mountains, located at 600-1,000 meters above sea level. Three vegetation types were distinguished in each paddock: forest, steppe and wetland. The ñire native forest is located in the area of valleys and mountain slopes, covering about 12600 ha, approximately 21% of the entire ranch area. Ñire forests develop in site class II (height of dominant trees between 7 and 12 m) and III (<7 m) (Peri 2009). The floristic composition of the understory herb layer is predominantly gramineous, with some herbs, including *Agrostis flavidula*, *Berberis buxifolia*, *Bromus setifolius*, *Carex macloviana*, *Deschampsia flexuosa*, *Festuca palllescens* and *Poa pratensis*. The steppe is dominated by tussock grasses (*Stipa* sp., *Festuca palllescens*, *F. gracillima*) and other gramineous species (*Hordeum* sp., *Poa dusenii*, *P. poecila*, *Deschampsia flexuosa*, *Rytidosperma virescens* and *Agropyron fuegianum*) and graminoids of the genus *Carex*, as well as shrubs and dwarf shrubs (*Chiliotrichium diffusum*, *Junellia tridens*, *Empetrum rubrum* and

Berberis sp.). Herbs include *Polygala darwiniana* and species of the genus *Acaena*. Wetlands are mostly associated with rivers and streams, but occasionally occur in landscape depressions. The prevailing species in this vegetation type are *Phleum alpinum*, *Dactylis glomerata*, *Juncus balticus*, *Eleocharis albibracteata*, *Azorella trifurcata* and species of the genera *Hordeum* and *Agrostis*.

Mean annual precipitation in the area during the study period was 502 ± 20 mm and was recorded with rainfall sensors (WatchDog 425, Serpac Spectrum Technologies Inc., Coviva, California, USA). Mean annual air temperature was 5.4 °C (July: -0.3 °C; January: 11.5 °C), measured with sensors (HOBO H8 Family, Onset Computer Corporation, USA) placed 1 m above the ground. The prevailing winds are south-west, with an average speed of 1.4 m/s in the ñire forest and 7.5 m/s in adjacent, treeless sectors (Bahamonde et al 2009).

The ranch is mostly devoted to extensive sheep production, with about 35000 head, mostly Corriedale breed, and a small proportion of Merino. Throughout the year, the animals use different paddocks from May to September (mating and gestation), September to January (lambing and lactation) and January to May (from weaning to mating moments). Paddock changes are associated with specific activities, such as eye-shearing (May), pre-lambing shearing (September) and marking (January). Paddocks situated above 700 meters above sea level are mostly used in summer, because they are covered with snow during the winter season and are very extensive (4000-6000 ha), with steppe and wetland vegetation types. The remaining paddocks, located below 700 m, are more protected from snow and wind and are divided into smaller paddocks (35 to 2500 ha), with steppe, wetland and forest vegetation types.

Mating takes place in the field after eye shearing in May and includes 1 ram for every 25 ewes. Forestry practices to promote livestock production are almost non-existent, but the presence of ñire forest is considered beneficial because it provides shelter for animals.

Paddock characteristics

Sheep habits variables were evaluated in seven paddocks of different areas and proportions of vegetation types throughout the 2008-2009 and 2009-2010 production cycles (Table 1). Paddock shape and distribution of vegetation types are shown in Figure 1. Grassland availability was evaluated before the animals were introduced, using the Santa Cruz Method for the steppe (Borrelli and Oliva 2001), the Botanal method for the wetland (Suárez 2007) and the Ñirantal Sur method for the forest (Peri 2009). Three-year old Corriedale sheep were assigned to each paddock, according to grassland carrying capacity (550 to 6000 ewes). The animals were handled by specialized personnel taking into consideration animal welfare in accordance with the IPCVA recommendations (2006).

Forage sampling

Forage availability was determined before the animals were introduced by sampling biomass clippings from the seven paddocks used in the trial, using 0.2 m^2 ($0.2 \times 1 \text{ m}$) quadrats for the steppe and 0.1 m^2 quadrats for wetland and forest. Sampling effort was proportional to the area of the different vegetation types in the landscape, following Peri et al (2013) ($n=479$ in the steppe, $n=73$ in wetland and $n=174$ in forest). Each sample was divided into green and senescent fractions. Each fraction was ground and sent to the laboratory for in vitro determination of dry matter digestibility and crude protein (CP) content. Total N content was obtained by whole combustion of the sample in ultrapure oxygen atmosphere using a Leco FP528 (USA) analyzer. The CP value was calculated by multiplying total N by 6.25 (McDonald et al 1986). Digestibility of dry matter (DMD) was determined using an ANKOM Daisy^{II} incubator and the filter bag procedure.

GPS collar schedule and data processing

Animal distribution patterns in the paddocks were evaluated using collars equipped with satellite GPS devices, Trackstick II and Supertrackstick models (TrackstickTM, USA) attached to six randomly selected animals per paddock. Data from collars gave location information (Latitude, Longitude, Time) recorded at fixed intervals (8-min). Total recording time was subjected to battery performance, and an average of 5 days per collar was obtained from the moment the sheep entered each paddock. Measurements were recorded in each paddock and repeated during the two evaluated productive cycles. An average of 5400 locations was recorded per paddock (6 collars x 5 days x 180 records/day). A location corresponds to the geographic location of an animal every 8 minutes, measured through the global positioning coordinate system. Initial locations were considered 12 hours after the animals had been introduced to the paddocks.

Table 1. Main characteristics of paddocks used for sheep grazing and climate in Southern Patagonia during the evaluated period.

Paddock	Area (ha)	Vegetation types (%)			Use period	Animal physiological stage	Forage allowance (kg DM/ha)	Stocking rate (SE/ha)	Average medium air temperature (°C)	Average minimum air temperature (°C)
		Forest	Wetland	Steppe						
Large steppe paddock (LSP)	5078	0	11	89	From late summer to early autumn (Feb - Apr)	Recovery period from weaning to mating	257 ±24	0.8 ±0.10	8.2 ±0.7	3.9 ±0.5
Medium-sized steppe paddock (MSP)	650	0	11	89	From late autumn to winter (May - Sep)	Mating and Pregnancy	323 ±25	1.2 ±0.09	1.4 ±1.2	-2.9 ±2.0
Small steppe paddock (SSP)	158	0	7	93	May	Mating	544 ±245	7.4 ±3.9	3.7 ±2.3	-1.0 ±1.6
Medium-sized forest paddock (MFP)	318	88	4	8	Winter (May - Sep)	Pregnancy	439 ±59	5.0 ±0.63	1.4 ±1.1	-2.6 ±1.4
Large multihabitat paddock (LMP)	2012	26	10	64	From spring to early summer (Oct - Jan)	Lambing and Lactation	551 ±33	1.1 ±0.16	7.3 ±1.3	2.2 ±1.2
Medium-sized multihabitat paddock (MMP)	314	41	10	49	Spring (Oct - Dec)	Lambing and Lactation	489 ±45	4.4 ±1.36	7.3 ±1.6	1.8 ±1.4
Small wetland paddock (SWP)	37	0	60	40	January	Lactation	1432 ±95	18.1 ±7.92	10.2 ±1.0	5.2 ±0.4

Data were recorded using the following protocol: Watertight boxes were prepared to store the GPS receiver and a set of alkaline D batteries, and were lined with red tape to facilitate their location. The interior of the box was adapted to the shape of the GPS receiver and batteries using rigid polyurethane foam. Thus, some degree of temperature isolation was achieved to optimize battery performance. The boxes were fixed with screws to harnesses especially prepared for sheep. The design allowed box placement on the sheep's back in order to obtain good capture of the satellite signal. GPS devices were previously set up on the computer to establish their identification, record interval and to establish the minimum radio of location differentiation. For collar placement, animals were confined in corrals near the paddocks where they would later graze. The collars remained attached to the animals for at least 20 days until they were recovered for data transfer by gathering the animal group. After recovering the collars, the data stored were transferred to a computer for analysis.

Home range, vegetation type preference, mean and maximum distance traveled, and mean and maximum explored area were determined for each paddock using the shapefile (.shp) of locations. The parameter home range is used to determine the area most frequently used by animals during their daily activities (Powell 2000). Home ranges were estimated using Crimestat® 3.3 software and the Kernel density estimator, which determines highly used areas by means of probability density functions (Barbari et al 2006). All the locations of all the collars for a single day and paddock were considered for each estimation. In all cases, a Normal interpolation method, a fixed band width (25 m) and a probability contour of 95% were used. Graphical representation was performed via QGIS 2.0.1 Dufour.

Environmental preference was calculated using the program Havistat v2 beta 2.1 (Montenegro and Acosta 2008) and Ivlev's electivity index (Equation 1) (Ivlev 1961 in Lechowicz 1982). This index considers several characteristics, such as equidistance between positive and negative values, and specific limits; it is widely used in preference studies due to its easy interpretation (Lechowicz 1982). Non-random use of vegetation types was tested using Havistat v2 beta 2.1 (Levins's niche breadth index, 1968) and whether the sample size was appropriate (Dixon and Massey 1969; Cherry 1996).

$$IV_i = (f_{loc_i} - pa_i) / (f_{loc_i} + pa_i)$$

Where: IV_i : Ivlev Index of vegetation type i ; f_{loc_i} : frequency of locations in a vegetation type i ; pa_i : participation of the vegetation type i .

For IV, a value of 1 indicates total preference for a given vegetation type, a value of -1 indicates total avoidance and a value of 0 represent indifference for the vegetation type.

The obtained locations of each GPS receiver were reprojected and transformed from geographical coordinates to Transverse Mercator using the program Global Mapper v6.07® in order to determine $f loc_i$. Locations corresponding to each paddock (6 collars for 5 days) were separated into night or day records, since the greatest proportion of hours devoted to grazing are concentrated during the day (Bueno and Ruckebusch 1979). For this purpose, the Computersimulation program of Dr. Erhard Regener 8.0 (www.geodesta.com) was used to determine sunrise and sunset on each of the days evaluated, considering the geographical location of each studied paddock.

Vegetation types were digitally delimited within each paddock using the program ArcView 3.2® and a satellite image (ASTER-9 bands of 15 m resolution, Transverse Mercator projection, Datum WGS84 dated October 2007). Finally, locations and vegetation types were overlapped using the Geoprocessing extension, using the Assign data by location option in ArcView 3.2®. With this tool, .dbf files (compatible with Excel) were generated containing the information of the number of total locations per collar and the vegetation type corresponding to each location. Furthermore, to determine pa_i the area of each vegetation type (*forest*, *steppe* and *wetland*) was calculated as well as the total paddock area, using the program ArcView 3.2®.

Data of daily distances traveled by sheep were obtained using the extension *Animal Movement Analysis*, using Create polyline from point file, which calculates distances between locations (http://alaska.usgs.gov/science/biology/spatial/gistools/index.php/animal_mvmt.htm). *Animal Movement Analysis* is an extension of Arcview that allows integration of GIS data and analysis of animal movements. The daily explored area was also calculated with the extension *Animal Movement Analysis* but with the tool MCP (Minimum Convex Polygon). This method has been internationally accepted for estimating the area traveled by animals over a given period (Black Rubio et al 2008; Burgman and Fox 2003). Values of traveled distances and explored area were obtained for each animal with a GPS collar in the separate paddocks. Then, the mean and maximum daily traveled distances and explored areas were calculated for both production cycles.

Sheep activity

Daily activity was estimated in all paddocks in both productive cycles (2008-2009 and 2009-2010). Each measurement was performed during one day from sunrise to sunset. Activity observations were made every 15 minutes, with a rest period of 1 hour every 5 observations (Marijuán et al 1998). Activity was observed with binoculars using the “scan sampling” method, which consists of a general sampling of the herd (a minimum of 20 sheep), detecting the activity of each animal at the moment of observation (Altman 1974). The type of activity was determined classified as follows (Dumont and Boissy 2000; Marijuán et al 1998): (i) grazing (sheep are standing, with head down), (ii) walking (walking or running with head up), (iii) resting (lying down or standing with head up) and (iv) searching (walking with head down).

This observation method allowed us to estimate the time sheep allocated to each activity and to establish the percentage of animals grazing, resting, walking or searching for food (Altman 1974). The observations of both production cycles were averaged per paddock and time of the day to determine important variations in animal behaviour over the day. Thus, animal behaviour was evaluated taking into account paddock characteristics and season of the year, which is associated with different climatic conditions that influence forage offer and access, and, therefore, time devoted to each activity (Owen Smith 2008).

Sheep diet

After each daily activity observation, fresh feces were randomly collected from the field and subjected to microhistological analyses to identify plant species included in the diet. On each occasion, three pools of samples were collected per treatment, each with a minimum of 30 feces. Samples were placed at 60 °C for 72 hours, ground, placed in labeled containers and sent to the laboratory. Botanical composition of sheep diet was determined at the Laboratorio de Microhistología, INTA EEA Bariloche. Dietary items were identified to genus or species level, depending on the histological characteristics of epidermal (Sparks and Malechek 1968) and non-epidermal tissues (Sepúlveda et al 2004). Items were determined and quantified following Holechek and Vavra (1981), and the relative frequency percentage of each plant species consumed by these herbivores was obtained (Holechek and Gross 1982). The data obtained from sample pools was averaged to obtain a value per paddock and season of the proportion of each genus or species in the diet. Similarity indices between dietary pairs (Equation 2) were then calculated to compare sheep diet among paddocks, using the Czekanowsky similarity Index (Feinsinger et al 1981).

$$ISim=100-0.5 \sum [p_{ij} - p_{ik}]$$

Where: ISim= Similarity Index, p_{ij} : proportion of genus or genus + species i in the diet j , p_{ik} : proportion of genus or genus + species i in the diet k .

The dietary items obtained for each paddock were grouped into grasses, graminoids, herbs, dwarf shrubs, shrubs, trees and others. A Principal Component Analysis was then performed using the software INFOSTAT 1.1. Information of food items consumed in each paddock is included in Appendix 1.

Results

Forage quality varied among vegetation types within each paddock, with a range of CP values between 2.8 and 12.7%, and of DMD between 44.5 and 68.2% (Table 2). In general, forage quality in the forest was high. The highest DMD percentages were found in the paddock used in January, which is strongly related to the high G/S relationship (>1).

Sheep distribution pattern

As expected, daily home range of sheep covered a greater proportion of the area of the smallest paddocks (Figure 1). There was a clear association between home range and wetland vegetation type in large paddocks (LSP, MSP and LMP). Forest areas were clearly included in home range estimation, indicating no avoidance of this vegetation type.

Daily distances traveled by sheep tended to be shorter in smaller paddocks (2.5±0.8 km/day in SWP, with an area of 37 ha) than in larger paddocks (4.8 ±1.7 km/day in LSP, with 5078 ha) (Table 3). Maximum distance was 6.4±2.2 km/day in LSP. Similarly, mean explored area was detected in large paddocks (213±145 ha/day in LSP). However, MMP (73 ha/day) was the exception because it exceeded values of LMP (51 ha/day), despite its smaller area. The maximum area explored by sheep was detected in LSP, with 399±259 ha/day.

Table 2. Forage allowance and forage quality (±standard deviation) in seven different paddocks and vegetation types. LSP (large steppe paddock), MSP (medium-sized steppe paddock), SSP (small steppe paddock), (MFP) medium-sized forest paddock, LMP (large multi-habitat paddock), MMP (medium-sized multi-habitat paddock) and SWP (small wetland paddock)

	Vegetation type	Forage allowance (Kg DM/ha)	CP ^a (%)	DMD ^b (%)	G/S ^c
LSP	Wetland	756 ±119	5.7±1.0	51.1±2.9	1.0
	Steppe	196 ±12	5.6±1.6	53.4±7.4	1.0
MSP	Wetland	1526 ±189	6.0±0.3	47.5±0.6	0.2
	Steppe	175 ±5	12.7±5.9	62.2±8.1	0.8
SSP	Wetland	2104 ±37	5.1±0.9	44.9±0.6	0.4
	Steppe	427 ±261	11.7±1.4	57.7±1.5	0.9
MFP	Wetland	1528 ±858	7.1±1.0	46.1±0.7	0.6
	Steppe	360 ±76	8.9±1.3	54.7±1.6	0.6
LMP	Forest	397 ±21	11.1±0.7	54.5±5.8	1.5
	Wetland	1201 ±85	10.7±0.4	58.4±2.7	0.3
	Steppe	604 ±37	2.8±1.1	44.9±3.3	0.4
MMP	Forest	170 ±4	13.1±3.4	65.1±3.5	1.9
	Wetland	1256 ±232	5.1±1.0	52.6±2.8	0.3
	Steppe	567 ±39	5.1±2.1	60.2±5.4	0.5
SWP	Forest	209 ±8	4.1±0.3	44.5±1.3	0.3
	Wetland	2053 ±3	8.9±2.6	66.8±2.4	5.7
	Steppe	500 ±234	5.6±0.6	68.2±1.4	3.3

^a CP: crude protein; ^bDMD: digestibility of dry matter; ^cG/S: green-senescent forage ratio.

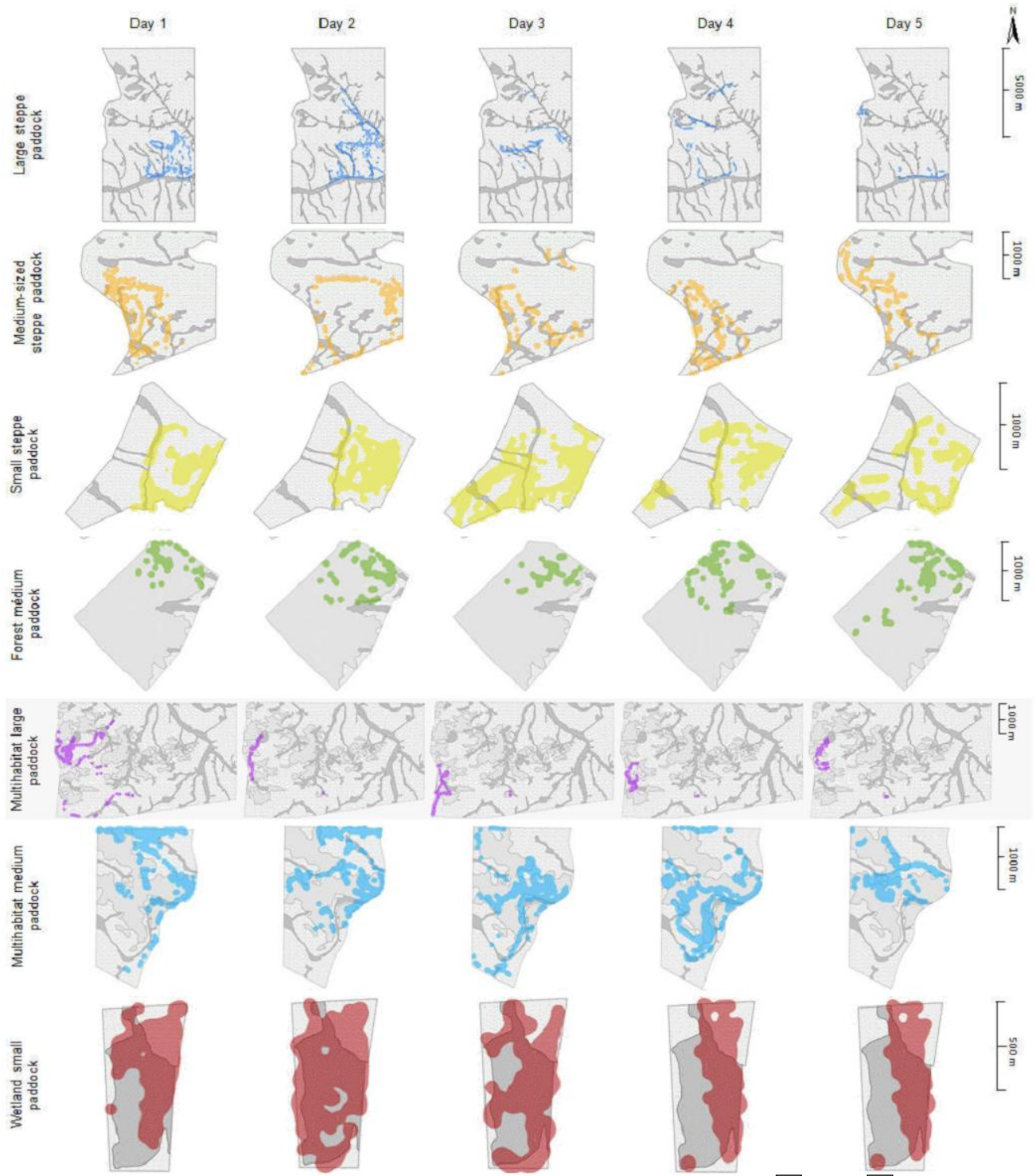





Figure 1. Spatial distribution of vegetation types in the seven different paddocks evaluated. Wetland ; Forest  and Steppe . Colored areas show Kernel Home range estimations for different days

Table 3. Mean values (\pm standard deviation) of distance traveled and mean and maximum area explored by sheep in seven paddocks evaluated. LSP (large steppe paddock), MSP (medium-sized steppe paddock), SSP (small steppe paddock), (MFP) medium-sized forest paddock, LMP (large multi-habitat paddock), MMP (medium multi-habitat paddock) and SWP (small wetland paddock).

	Mean traveled distance (km/day)	Maximum traveled distance (km/day)	Mean explored area (ha/day)	Maximum explored area (ha/day)
LSP	4.8 \pm 1.7	6.4 \pm 2.2	213 \pm 145	399 \pm 259
MSP	3.8 \pm 1.2	5.6 \pm 2.1	99 \pm 45	212 \pm 79
SSP	3.1 \pm 0.8	4.2 \pm 1.2	33 \pm 13	51 \pm 23
MFP	2.6 \pm 0.3	4.1 \pm 1.1	34 \pm 12	78 \pm 35
LMP	3.4 \pm 1.6	4.3 \pm 0.9	51 \pm 21	158 \pm 157
MMP	3.7 \pm 0.4	5.9 \pm 0.6	73 \pm 10	176 \pm 33
SWP	2.5 \pm 0.8	4.1 \pm 2.0	9 \pm 5	16 \pm 10

Preference analysis showed that sheep clearly avoided the wetland vegetation type during the night in all paddocks, whereas during the day, they showed preference or indifference (Table 4). Sheep used the steppe in proportion to the area in most of the paddocks in both periods of the day. However, in paddocks used in spring (LMP and MMP), sheep avoided the steppe during the day and night. The forest was the preferred vegetation type by sheep in the paddocks used in spring, both during the day and night. In the remaining paddock (MFP), sheep were indifferent (night) or slightly avoided (day) the forest.

Table 4. Preference of vegetation types by sheep. LSP (large steppe paddock), MSP (medium-sized steppe paddock), SSP (small steppe paddock), MFP (medium-sized forest paddock), LMP (large multi-habitat paddock), MMP (medium-sized multi-habitat paddock) and SWP (small wetland paddock).

	Day			Night		
	Forest	Wetland	Steppe	Forest	Wetland	Steppe
LSP		0.4	-0.1		-0.6	0
MSP		0.3	0		-0.3	0
SSP		-0.1	0		-0.4	0
MFP	-0.1	0.5	0.2	0	-0.7	0.1
LMP	0.4	0	-0.5	0.5	-0.6	-0.7
MMP	0.2	0.2	-0.3	0.3	-0.4	-0.5
SWP		0	0		-0.1	0.1

Sheep activity

Daily habits of sheep varied among paddocks, with a clear prevalence of grazing being observed (a mean of 60-80% of all daily activities). The highest time percentage allocated to grazing was detected in paddocks used in winter and spring (Figure 2). The analysis of sheep activity throughout the day showed a tendency to concentrate resting activity during the hours with highest sun radiation. Movement, however, was concentrated in the early and late hours of the day. Search activity did not show a definite pattern among paddocks and seasons of the year.

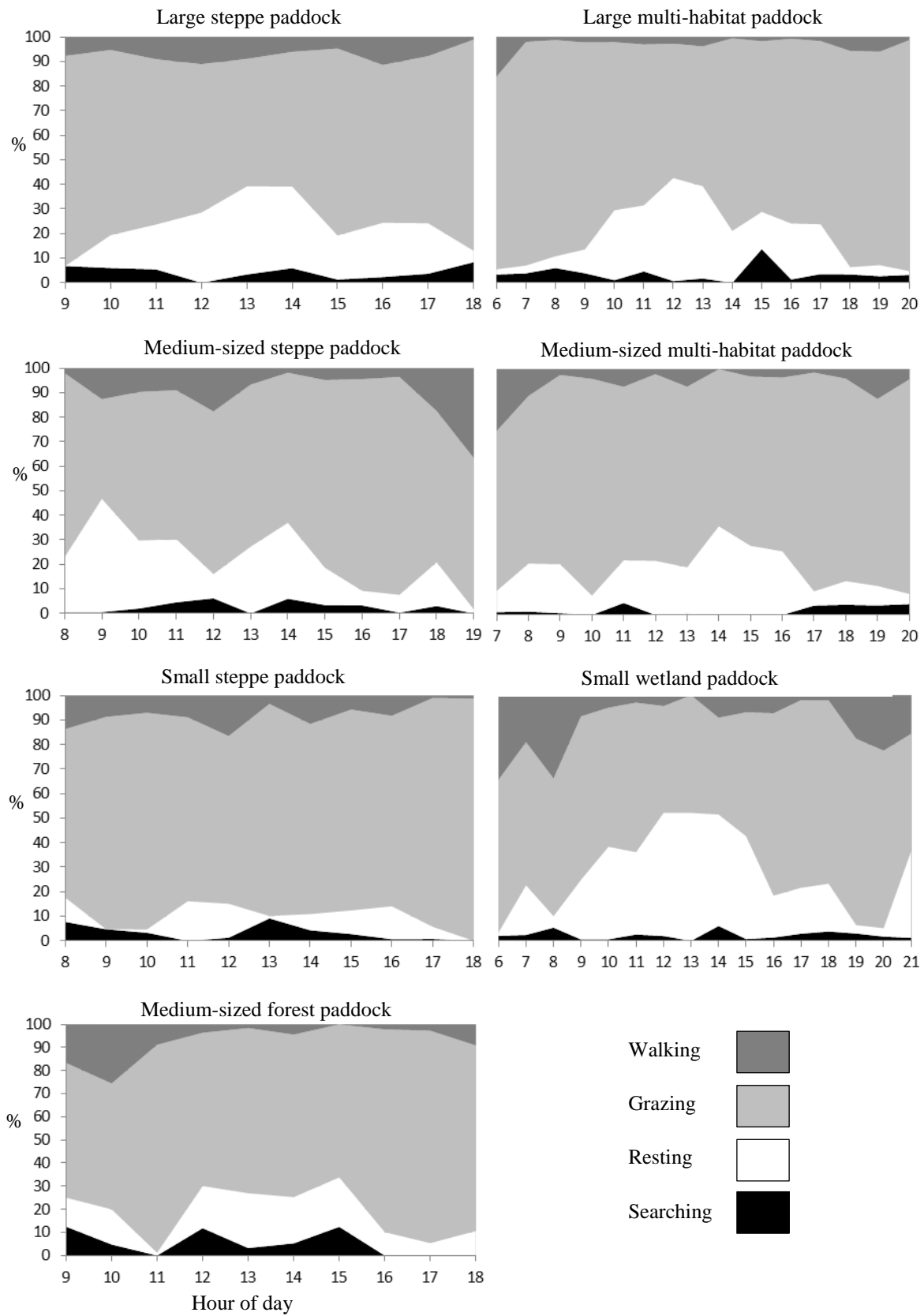


Figure 2. Daily activities of sheep in seven different paddocks in Southern Patagonia

Sheep diet

The most important functional group in the diet of sheep was grasses, with values exceeding 40% in all paddocks (Appendix 1), followed by graminoids and herbs, but with contrasting values among paddocks. The remaining groups (dwarf shrubs, shrubs, trees and others) were of low importance in the general diet of sheep, except for shrubs in LSP, with 11.8%. The species with highest general presence in the diet, with at least 5 % to 26%, were *Festuca gracillima*, *Agropyron* sp., *Poa* sp., and *Carex* sp. Other species, such as *Alopecurus* sp., *Rytidosperma virescens*, and *Deschampsia* sp., reached important values (22.2, 14.5 and 8.4%, respectively), but only in some paddocks.

The Principal Component Analysis of the diet data showed a gradient according to paddock size for LSP, MSP and SSP, with a great importance of shrubs in large paddocks and of grasses in small paddocks. Herbs were important only in LMP. The category “others” (mosses, ferns and hemiparasites, associated with trees), showed an important biodiversity component in ñire forests with respect to the other vegetation types in the sheep diet.

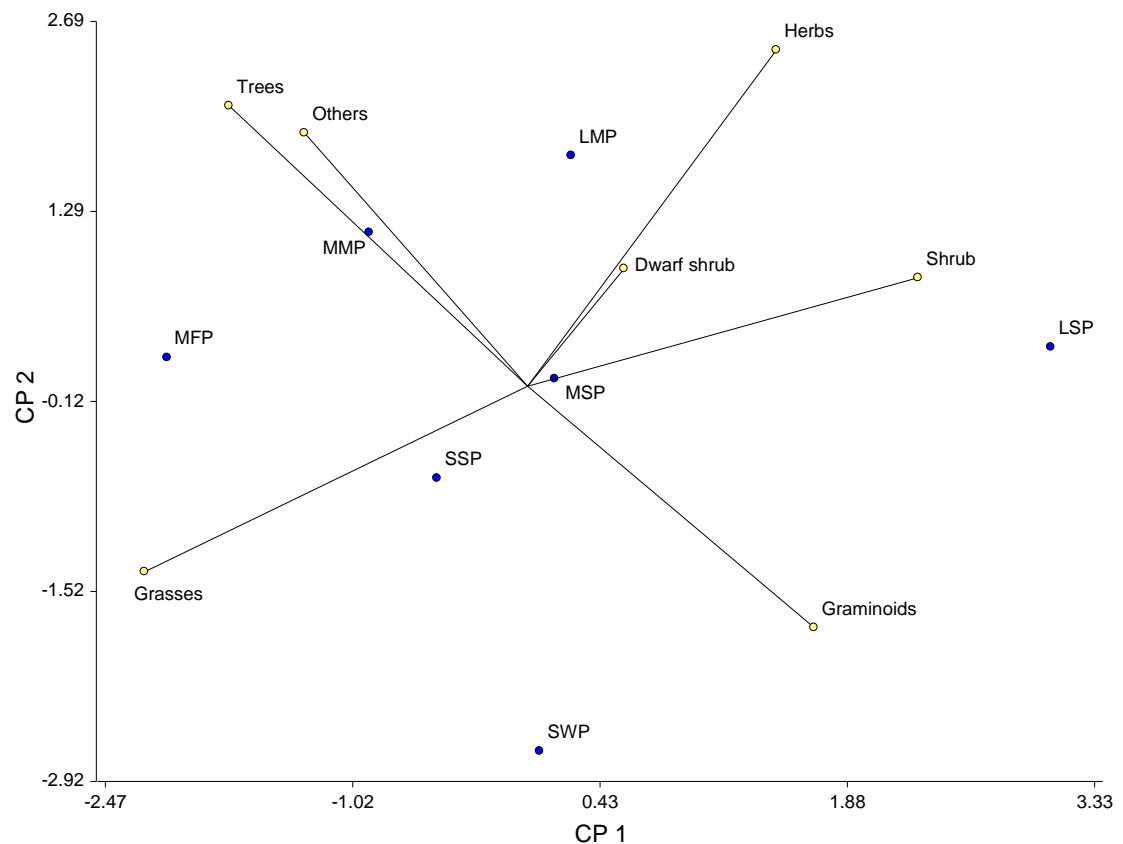


Figure 3. Principal Component Analysis of sheep diet in seven paddocks and identified functional groups. LSP (large steppe paddock), MSP (medium-sized steppe paddock), SSP (small steppe paddock), MFP (medium-sized forest paddock), LMP (large multi-habitat paddock), MMP (medium-sized multi-habitat paddock) and SWP (small wetland paddock).

Table 5. Diet similarity index among paddocks. LSP (large steppe paddock), MSP (medium-sized steppe paddock), SSP (small steppe paddock), MFP (medium-sized forest paddock), LMP (large multi-habitat paddock), MMP (medium-sized multi-habitat paddock), SWP (small wetland paddock)

	LSP	MSP	SSP	MFP	LMP	MMP	SWP
LSP	-	55.1	56.4	51.3	57.6	56.5	56.9
MSP		-	74.2	77.4	62.9	70.8	54.9
SSP			-	71.6	67.9	71.4	56.1
MFP				-	66.2	69.3	53.6
LMP					-	76.0	56.8
MMP						-	57.5
SWP							-

The analysis of diet similarity among paddocks showed contrasting values with respect to area. The largest paddock (LSP) and the smallest one (SWP) had lower similarity values than medium-sized paddocks (Table 5). Furthermore, diet similarity among paddocks with similar proportion of vegetation types was also noticeable (LMP-MMP: 76 and MSP-SSP 74.2), as well as the low similarity observed among paddocks with different vegetation types (MFP-LSP: 51.3 and MFP-SWP: 53.6).

Discussion

In this study, home range determination allowed us to make a rapid comparison of sheep distribution in the seven contrasting paddocks studied (Figure 1). This information, along with the distance traveled and area explored by animals (Table 3), revealed a great capacity of sheep to explore the area in search of the best grazing or resting sites when the paddock area was not restricted.

Defining the scale of analysis is important for interpreting sheep habits variables, because the scale determines the factors involved in decisions made by large herbivores (Senft et al 1987). According to Bailey et al (1996), spatial scales are functionally defined and related to herbivore's decisions (preference for grazing, resting, ruminating, refuge and water drinking sites) that are made at different temporal scales. Considering the area of the studied paddocks (40 to 5100 ha), sheep decisions would be included in categories from "daily range" to "lifetime range" (Bailey and Provenza 2008). Thus, sheep had the possibility of selecting different sites or vegetation types in relation to their needs. However, each evaluated paddock has at least three important characteristics that may have influenced grazing behaviour: spatial distribution and proportion of vegetation types, season of use and area.

Spatial distribution and proportion of *vegetation types*

In this study, sheep preference for the different vegetation types varied among paddocks and between times of the day. This response of sheep to resource heterogeneity has been observed both in controlled conditions (Hewitson et al 2005) and real-scale experiments (Putfarken et al 2008). The presence, absence or proportion of vegetation types in a paddocks conditioned preference behaviour by sheep. This result was also confirmed via diet similarity analyses, when comparing the different paddocks (Table 5 and Figure 3), which showed consistency among diets and species present in the vegetation types, considering local records (Peri and Ormaechea 2013, Roig et al 1985).

Wetlands are areas usually preferred for grazing by herbivores due to their forage quality and abundance characteristics (Somlo et al 1986; Anchorena et al 2001; Utrilla 2004). In addition, this vegetation type often represents a source of drinking water for animals, since they are associated with river courses and land depressions. However, these sites are colder than highland sites. Here, we observed a clear avoidance for this vegetation type in all paddocks during the night, possibly because sheep prefer drier and warmer sites for resting. Furthermore, no marked

preferences were observed for wetlands in several paddocks during the day, which could be related to seasonal variations in forage quality and availability (Table 2).

Availability of steppe in the grassland is usually lower than in the forest or wetland. In addition, the steppe is dry, and therefore sheep prefer these sites for resting. This vegetation type in general occupies the greatest proportion in paddocks and it is therefore difficult to observe high preference indices despite being highly used.

The forest often provides better quality forage than adjacent treeless sites (Wilson and Ludlow 1991; Lin et al 2001; Peri et al 2005), as well as shelter from wind and extreme temperatures. Measurements taken in the study area (Bahamonde et al 2009) indicate a reduction in wind speed inside the ñire native forest of between 77 and 84 %, which would strongly influence the animal's thermal perception, because wind limits thermal isolation with increasing area of heat exchange (Blaxter 1977). Accordingly, a slight increase in sheep preference for the forest during the night was observed in all paddocks containing forest, suggesting that animals might use these paddocks for resting and obtaining thermal comfort. The patchy disposition of the forest, surrounded by steppe or wetland prevails over continuous forest stands (Peri and Ormaechea 2013). The ñire forest is mostly open and of low height, allowing animal movement and light availability, which facilitates the occurrence of grassland understory.

Period of use

In the study area, changes in climatic conditions throughout the year are determinant of sheep habits. Mean lowest temperatures in winter (-3.7°C to 3.6°C) along with low grassland quality (Table 2) and, possibly, no access to grassland due to snow cover are severe limiting factors for sheep to meet nutritional requirements. Likewise, the few light hours (up to 8 hours less than in summer) influence the amount of time devoted to grazing. This is consistent with our findings, since animals were found to allocate great part of their time budget to grazing (Figure 2). There may be limitations in individual bite and intake rate due to low access to and availability of grasses and accumulation of ice or snow, which would lead to a trade-off in behaviour by devoting more time to grazing at the expense of other activities. In spring, the greater time allocated to grazing may have been associated with higher physiological requirements during the last three months of gestation. Finally, in summer, grazing activity percentages were somewhat lower, due to the increase in ingestion rate as a result of grass availability during the growth peak. In addition, relative grass quality is highest in summer (Table 2) because grasses reach a peak production in this season and quality is higher than in the remaining seasons.

A general analysis of the daily activities of sheep showed agreement with other studies (Marijuán et al 1998; Mazorra et al 2003), in which grazing prevailed (60 to 80% of daily activities) over other activities, and the number of animals resting increased particularly at midday, with increased temperature. Furthermore, movement activity shows a tendency to be concentrated around sunrise and sunset. Tomkins and O'Reagain (2007) also found that animals increased movement activity at the beginning and end of the day. This was clearly observed in the study area, since sheep tended to move to low sectors at sunrise, in search of more palatable and abundant wetland grasses. At sunset, they moved back to higher sectors, which are drier and warmer and therefore more suitable for resting at night.

Preference for the different vegetation types also depended on the season. Among paddocks used in winter (SSP and MSP), forage quality was much lower than in the steppe, both in CP, DMD and G/S (Table 2). Similarly to other herbivores, sheep prefer plant communities of highest quality in the absence of other strong conditioning factors (Bailey and Provenza 2008). Other common limiting factors for this season are frosts and floods that make wetlands inaccessible. For these reasons, wetlands are unlikely to be used in winter and may be occasionally used for drinking if there is no water available in other sites.

Before sheep were introduced to the paddocks (LMP and MMP), in the spring, they were sheared, and therefore lose the thermal isolation provided by wool. Hence, cold temperatures recorded in October in both years (minimum values between -0.6 and 0.7 °C) were determinant for sheep avoidance of a vegetation type that provides low thermal comfort. Finally, sheep exhibited indifference for vegetation types in the paddock used in winter (SWP), allocating the least time to grazing (Figure 2) and traveling the shortest distances (Table 3) because, as previously indicated, grass quality and availability are high during this season, both in the wetland and in the adjacent steppe. This is consistent with findings reported by Roguet et al (1998), who indicated that domestic animals walk shorter distances when intake rate increases, and reduce their preference for specific sites when the nutritional value is similar.

After shearing, the isolating wool layer is reduced, and animals would reach a minimum critical temperature. Under this condition, sheep would start to require heat production to achieve thermal homeostasis, resorting to its body

reserves and therefore undergoing a reduction in productive efficiency (Blaxter 1977; Berge 1997). This fact explains the strong preference of sheep for the forest in the paddocks used after shearing (LMP and MMP).

Finally, it should be noted that sheep showed slight or no preference for the steppe in winter, which coincides with good quality short grasses (Table 2). Accordingly, in an ecosystem similar to Southern Patagonia, Anchorena et al (2001) reported an increase in sheep stocking rate on the steppe tussock grasses in winter. Here, after shearing at the beginning of spring, with the strong cold winds occurring in September and October, sheep avoided the steppe and preferred the shelter provided by the forest in paddocks LMP and MMP. It can therefore be assumed that in the evaluated area of Southern Patagonia, sheep distribution in the paddocks is conditioned by availability of shelter in winter-spring due to adverse climatic conditions and to high-quality forage availability in spring-summer.

Paddock area

Paddock area determined differences in sheep habits in terms of traveled distance, explored area and consumed diet. The relationship between paddock area and sheep habits variables showed associations for traveled distance and explored area (Figure 4), i.e., mean traveled distance by sheep ranged from 2.5 to 4.8 km/day and the explored area ranged from 9 to 213 ha/day in paddocks of 37 to 5078 ha, respectively. Squires (1974) reported distances traveled by Merino sheep between 7.4 and 10.4 km/day in heterogeneous paddocks of 1,400 ha in area, whereas Roux and Schlebusch (1987) and Roux (1992) found distances of 5 and 2.1 km/day in paddocks of 31 and 5 ha, respectively, also for Merino. Considering the existence of an association between traveled distance and explored area, paddock size might impose limitations in the use of strategies by sheep to reach nutritional and thermoregulation requirements, or other conditioning factors inherent to the landscape scale (Bailey and Provenza 2008).

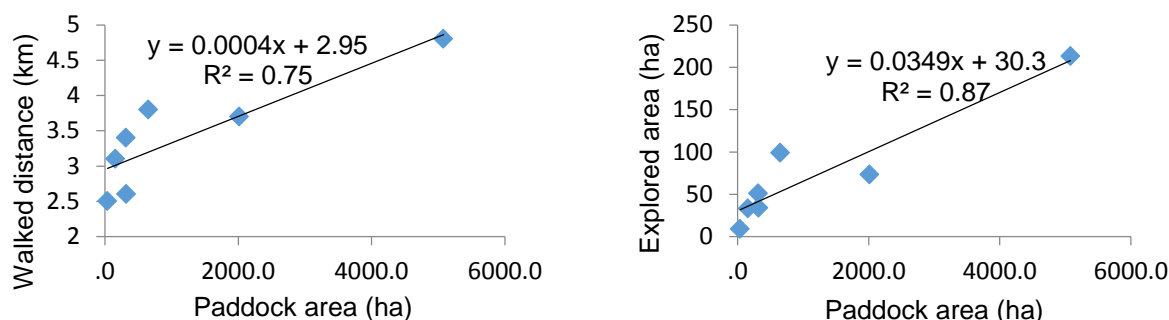


Figure 4: Regressions between paddock areas and sheep behavior variables (walked distance and explored area) in Southern Patagonia

Furthermore, the relationship between habits variables and paddock area was also reported in other works. For example, Barnes et al (2008) and Ormaechea et al (2012) studied the influence of different paddock sizes on sheep distribution and found more homogeneous grazing in smaller paddocks than in larger ones. Likewise, Hunt et al (2007) indicated that a proper distribution of water holes helped to improve livestock distribution in small paddocks. However, the authors highlighted the importance of considering use homogeneity at different scales, because despite a good animal distribution at landscape level, plant communities or areas may be under- or overused.

Sheep diet also showed a clear contrast among paddock sizes, since LSP (5078 ha) and SWP (37 ha) exhibited the lowest diet similarities of all paddocks. Likewise, a diet gradient was observed in LSP, MSP and SSP (Figure 3) in relation to paddock size, with a marked importance of shrubs in large paddocks and of grasses in small ones. Sheep diet studied in paddocks similar to LSP in summer also revealed an increase in shrub consumption (Posse et al 1996), which may be related to the season of use. However, large paddocks provide greater plant community diversity and lower competition among sheep than small paddocks, favoring the expression of their selective habit.

According to Bóo et al (2002), in order to define an association between plant species as a hierarchical scale in defining conditioning factors of animal distribution, it must be perceived as such by the herbivore and determine its selection. Vegetation types not only have clearly defined limits given by their physiognomy and species composition, but also, as observed in this work, seem to be sites selected by sheep for specific daily activities. Physical limits to sheep movement imposed by humans have conditioned sheep capacity to adapt to climate severity and grassland seasonality (Boone and Hobbs 2004). Thus, Patagonian extensive systems, with low or nil grassland management, confine animals to paddocks where they can only make decisions at community or lower scales. However, sheep

demonstrate an important array of strategies for facing restrictions imposed by the local climate and low forage availability. A strong dietary selectivity, a high percentage of time allocated to grazing, large explored areas and opportunistic selection of vegetation types explain the capacity for reproduction even under these harsh conditions.

It should be noted that the information obtained using GPS collars corresponded to a short period within the paddock use period; hence, it was not possible to know the effective space use throughout the entire period. However, the marked preference for certain vegetation types during the study period shows that a heterogeneous use of space, at least at this scale. Accordingly, other authors indicated that some sites in heterogeneous fields are overused with respect to others within a single paddock (Squires 1981; Lange 1985; Golluscio et al 1998; Owen Smith 2002). An intensified management involving paddock subdivision and separation of vegetation types might sensitively help improve grazing homogeneity and production efficiency, also reducing the limitations involved in the evaluation of grasslands. However, any management intensification should consider how sheep grazing strategies are limited.

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Appendix 1: Botanical composition of diet consumed by sheep grazing in seven paddocks evaluated in Southern Patagonia

	LSP	MSP	SSP	MFP	LMP	MMP	SWP
Total Grasses	44.6	62.6	61.9	67.8	48.0	55.2	60.4
<i>Agropyron patagonicum</i>	8.3	9.3	5.4	7.8	7.0	6.9	7.7
<i>Agrostis capillaris</i>	+	+	+	-	-	-	-
<i>Alopecurus magellanicus</i>	7.0	4.1	3.8	4.6	5.0	7.4	22.2
<i>Bromus setifolius</i>	+	-	-	-	-	-	-
<i>Bromus catharticus</i>	-	-	+	+	-	-	-
<i>Cortaderia sp.</i>	-	-	-	+	-	-	-
<i>Dactylis glomerata</i>	1.5	+	6.0	4.1	1.6	2.0	+
<i>Deschampsia sp.</i>	6.6	7.6	8.4	7.8	3.3	5.0	4.2
<i>Festuca gracillima</i>	10.4	16.6	11.3	17.0	9.5	6.7	12.0
<i>Holcus lanatus</i>	-	+	+	+	-	-	+
<i>Hordeum comosum</i>	-	-	+	-	-	-	-
<i>Phleum alpinum</i>	+	2.4	3.2	2.7	3.2	2.4	-
<i>Poa sp.</i>	8.8	6.5	9.0	10.2	8.2	8.2	11.1
<i>Puccinellia pusilla</i>	-	-	+	1.7	+	+	-
<i>Rytidosperma virescens</i>	+	12.6	11.9	10.9	9.7	14.5	2.8
<i>Pappostipa chrysophylla</i>	+	1.6	-	-	+	+	-
<i>Trisetum spicatum</i>	-	+	-	+	-	+	-
Total Graminoids	23.4	12.8	16.8	8.8	19.4	14.7	30.2
<i>Carex andina</i>	10.9	8.0	9.3	5.3	9.4	8.4	26.1
<i>Eleocharis pseudoalbibracteata</i>	+	1.1	+	+	+	-	+
<i>Juncus stipulatus</i>	6.9	1.0	5.2	1.1	3.1	3.7	1.7
<i>Luzula alopecurus</i>	4.7	2.7	1.7	1.9	6.3	2.6	2.1
<i>Triglochin palustris</i>	+	-	+	+	+	-	-
Total Herbs	17.1	14.0	12.4	10.1	16.8	11.6	4.6
<i>Acaena sp.</i>	4.0	1.6	1.0	1.1	5.5	2.2	+
<i>Achillea millefolium</i>	-	-	+	-	-	-	-
<i>Adesmia lotoides</i>	+	2.5	2.6	+	+	+	-
<i>Anemone multifida</i>	-	-	-	-	+	-	-
<i>Arjona patagonica</i>	+	+	-	-	-	+	+
<i>Armeria maritima</i>	+	+	+	+	+	1.0	+
<i>Azorella trifurcata</i>	-	-	-	-	-	-	+
<i>Bolax gummifera</i>	3.3	+	+	+	+	+	-
<i>Myosotis discolor</i>	-	+	-	+	+	-	+
<i>Draba magellanica</i>	+	+	+	-	+	+	+
<i>Cerastium arvense</i>	3.8	2.7	4.9	3.5	3.2	2.4	1.1
<i>Colobanthus lycopodioides</i>	+	+	1.3	+	1.4	1.9	-
<i>Epilobium australe</i>	-	-	-	-	+	-	-
<i>Erigeron myosotis</i>	+	+	+	+	+	+	-
<i>Erodium cicutarium</i>	-	+	+	+	+	-	-
<i>Adesmia pumila</i>	+	-	-	+	+	1.0	-
<i>Galium aparine</i>	+	-	+	+	+	-	-
<i>Gunnera magellanica</i>	+	+	-	-	+	-	-
<i>Hypochoeris incana</i>	-	-	-	-	+	-	-
<i>Medicago lupulina</i>	-	+	-	-	+	+	-
<i>Nanodea muscosa</i>	-	-	-	-	-	-	+
<i>Perezia recurvata</i>	+	+	+	-	+	+	-
<i>Polygala sp.</i>	+	-	-	-	+	-	-
<i>Rumex acetosella</i>	+	-	-	-	+	-	-
<i>Senecio magellanicus</i>	4.4	4.2	+	1.8	2.4	1.8	1.2
<i>Sisyrinchium arenarium</i>	-	-	-	-	+	-	-
<i>Vicia magellanica</i>	-	-	-	1.5	+	-	+
Total Dwarf shrubs	1.7	2.8	0.9	1.4	2.7	2.0	2.1
<i>Baccharis patagonica</i>	-	-	-	-	+	-	-
<i>Empetrum rubrum</i>	1.3	2.6	+	+	2.4	1.5	+
<i>Mulguraea sp.</i>	+	+	+	+	+	+	-
<i>Nardophyllum bryoides</i>	-	-	-	-	-	-	1.1
<i>Nassauvia aculeata</i>	-	+	-	-	-	-	-

Total Shrubs	11.8	4.7	2.9	2.7	2.5	3.6	1.1
<i>Adesmia volckmannii</i>	+	+	-	-	+	-	+
<i>Baccharis magellanica</i>	-	+	-	-	-	+	-
<i>Berberis microphylla</i>	1.6	3.7	1.8	2.1	+	1.4	+
<i>Chilliolepis diffusum</i>	6.6	+	+	-	+	+	+
<i>Mulguraea sp.</i>	+	+	+	+	-	+	-
<i>Mulinum spinosum</i>	+	-	+	+	-	-	-
<i>Pernettya mucronata</i>	2.7	+	+	+	1.1	1.0	+
<i>Ribes magellanicum</i>	-	-	-	-	+	-	-
Total Trees	0.5	1.0	1.4	5.9	4.9	3.5	0.0
<i>Nothofagus antarctica</i>	+	+	1.4	5.9	4.9	3.5	-
Total Others	0.9	2.2	3.7	3.2	5.6	9.5	1.5
<i>Blechnum penna-marina</i>	+	-	-	+	-	-	-
<i>Misodendrum punctulatum</i>	-	1.4	+	2.1	2.1	+	-
Moss	+	+	3.7	1.1	3.6	8.5	1.5

+: Presence of less than 1% in the diet of sheep

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