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Cattle landscape selectivity is influenced by ecological and management factors in a heterogeneous mountain rangeland

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Abstract. Few studies addressing drivers of cattle selectivity focus on the combination of ecological (biotic and abiotic) and management factors such as rotational systems, paddock sizes and paddock shapes. As a consequence, it is difficult to prioritise management practices integrating information of different driving factors. In a heterogeneous mountain rangeland in Central Argentina we established a total of 419 square study plots of 1 ha located in 18 paddocks with differing sizes, shapes and cattle grazing management. Plots were small samples of landscapes, covering all existing variability in vegetation and physiography. For each plot we estimated the annual cattle use, average seasonal cattle density, forage types and abiotic characteristics. We used general linear models to show that selectivity was mainly driven by biotic variables. Cattle selected landscapes dominated by short palatable plants, but the strength of this influence differed among paddocks. Selectivity was strongest in paddocks with low abundance of lawns dominated by short palatable plants and low annual stocking rate. As stocking rate and the availability of lawns increased, selectivity strength decreased. Abiotic variables had far less influence than biotic variables, showing that cattle tended to avoid rough landscapes with steep terrain in the wet-warm season; and to be attracted by permanent water sources during the dry-cold season. Seasonal stocking density and paddock size had no detectable influence on cattle selectivity and distribution. Paddock shape influenced distribution but not the strength of forage selectivity. We conclude that in our system, cattle selectivity is mainly driven by biotic factors, and the most effective methods of changing the consequent distribution pattern is by manipulating forage types and paddock shape. The role of stocking rate remains controversial as it was correlated with the proportion of lawns in the paddock.

Additional keywords: distribution patterns, domestic herbivores, grazing lawns, paddock characteristics, stocking rate.

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Introduction

Livestock distribution in heterogeneous landscapes such as mountain rangelands is often uneven, particularly in large paddocks (Teague and Dowhower 2003; Bailey *et al*. 2004, 2015; Barnes *et al*. 2008). As a consequence, standing biomass is accumulated in certain areas of the paddock, due to their light use; whereas other areas are overgrazed (Adler *et al*. 2001; Fuhlendorf and Engle 2001; Castellano and Valone 2007; Cingolani *et al*. 2013). Uneven grazing combined with the fragility of mountain systems could reduce livestock performance (Bailey *et al*. 2001) and threaten soil and biodiversity conservation (Landsberg *et al*. 2003; Chartier and Rostagno 2006; Cingolani *et al*. 2013). Thus, understanding drivers of livestock habitat selection in mountain areas and the consequent distributional patterns is a useful contribution to better inform managers interested in sustainable livestock production and conservation issues (Kemp and Michalk 2007).

Ecological factors, which can be either biotic or abiotic, influence livestock selectivity in a multiple-scale hierarchy (Senft *et al*. 1987). The relative importance of biotic factors (related to forage quantity and quality) on livestock selectivity is greatest at smaller scales, such as individual plants or micro-patches. Whereas, the relative importance of abiotic factors increases at the landscape scale because herbivores tend to perceive other factors from the environment, which can limit their spatial distribution within paddocks (Bailey *et al*. 1996). This aspect is particularly evident in arid or semiarid rangelands where livestock tend to forage on all types of vegetation near water sources and only on good forage away from water sources. In more mesic and temperate heterogeneous rangelands, livestock tend to occupy flatter terrain or warmer sites (Cingolani *et al*. 2002; Bailey *et al*. 2004, 2015; Kohler *et al*. 2006). However, Gross *et al*. (1995) suggested that, although abiotic factors are important in mesic and temperate ecosystems to determine livestock selectivity at the landscape scale, biotic factors have more influence in these ecosystems than in arid systems, due to high spatial heterogeneity in forage quality and availability.

Besides ecological factors, management decisions such as stocking rate, timing of grazing, and paddock size and shape also play an important role in large domestic herbivores selectivity and distribution patterns (Vallentine 2001). For example, Teague and Dowhower (2003) suggest that selectivity can be decreased by pasture subdivision and increasing stocking density, but other research suggests that stocking density *per se*, may not decrease selectivity if stocking rate is held constant (Bailey and Brown 2011). Seasonality also has its own influence on livestock selectivity. In paddocks used during the growing season, with higher forage availability and a lower grazing pressure (i.e. more available biomass per animal unit), livestock tend to select habitats dominated by high-quality species (McNaughton 1986; Fuhlendorf and Engle 2001). Conversely, out of the growing season when forage is scarce (and the pressure over resources increases), livestock tend to decrease selectivity, foraging on all available plants and patches, independently of their quality (Vallentine 2001). In the same line of thinking, ranchers often assume that seasonal selectivity can be reduced by increasing stocking densities during the growing season, including animals in rotational grazing systems (Bailey *et al*. 1996; Bailey 2004).

Despite the importance of animal selectivity to production and conservation issues (Adler *et al*. 2001; Fuhlendorf and Engle 2001), most studies have been focussed on either ecological drivers (Gross *et al*. 1995; Bailey *et al*. 1996) or, more recently, on management factors (Broweleit *et al*. 2000; Bailey *et al*. 2001; Sevi *et al*. 2001; Bailey 2004; Hunt *et al*. 2007; Barnes *et al*. 2008; Rinella *et al*. 2011). In turn, little research has addressed the combined effects of ecological and management factors.

Here we attempt to fill that gap, by studying the combined effects of biotic, abiotic and management factors on cattle selectivity. Specifically, our objectives were to: (1) analyse the effect of biotic and abiotic ecological factors on annual cattle landscape selectivity; (2) analyse the effects of management related factors on the strength of cattle selectivity and on animal distribution patterns; and finally, (3) analyse if factors which drive selectivity differ among seasons.

Methods

Study area

The study was carried out in the upper altitudinal belt of the Córdoba mountains, 2000–2200 m a.s.l. (31°34′S, 64°50′W, Fig. 1). The mean temperatures of the coldest and warmest month are 5.0°C and 11.4°C, respectively, and there is no frost-free period. Mean annual precipitation is ~900 mm, with most rainfall concentrated in the warmest months (Colladón 2010; Cingolani *et al*. 2015). Soils are derived from the weathering of the granitic substrate and fine-textured eolian deposits (Cabido *et al*. 1987). The landscape is a mosaic of different plant physiognomic types including tussocks grasslands, short grasslands (hereafter lawns, *sensu* McNaughton 1986) and granite outcrops. *Polylepis australis* woodlands and eroded areas with exposed rock surfaces (locally named 'pavements') are also widespread in the landscape (Cingolani *et al*. 2004, 2013). The area comprises different physiographic units, including valley bottoms and ravines, plateaus with different degrees of dissection, rocky hilly uplands and steep escarpments (Cabido *et al*. 1987). Most of these units are rough, with abundant rocky outcrops, steep slopes and high topographic variability within short distances. In general, the combination of vegetation physiognomy and landscape physiography results in a complex patchy environment (Cingolani *et al*. 2004, 2008*b*). The main economic activity is livestock rearing, which began in the 17th century (Díaz *et al*. 1994). At present, cattle dominate domestic livestock, but horses, sheep, goats and domestic camelids are also present in small numbers. The large size of the paddocks (up to 3000 ha) allows animals to select between different landforms and plant communities. A traditional practice applied by landowners is the use fire to promote grass resprouting and, combined with grazing, to prevent the advance of tussocks and woody species, maintaining lawns of high forage quality (Díaz *et al*. 1994; Cingolani *et al*. 2014).

The study area comprises part of the Quebrada del Condorito National Park, created in 1997, and a neighbouring private ranch. In the National Park, domestic herbivores are used in some paddocks as a management tool to preserve biodiversity and to control excessive biomass accumulation, as a way to replace the former role of native herbivores, mainly guanacos (*Lama guanicoe*), currently extinct from the area (Díaz *et al*. 1994; Cingolani *et al*. 2014). Recently, a population of this native species was re-introduced with the aim of controlling landscape homogenisation (Berberián and Roldán 2001; Flores *et al*. 2012), and at the same time avoiding soil erosion processes induced by livestock (Cingolani *et al*. 2013).

Sampling design

We used a total of 18 paddocks with different sizes and grazing managements (Table 1). Eight paddocks were located within the Quebrada del Condorito National Park and had continuous cattle grazing (named C1 to C8 with C standing for 'Continuous'). Another eight paddocks had seasonal grazing and were part of three rotational grazing management units. Two of these units were also within the National Park (R1 and R3, with R standing for 'Rotational') and consisted of three paddocks each (a, b and c), with very high seasonal stocking density combined with a resting period without livestock. The remaining rotational grazing management unit (R2) was located in a neighbouring private ranch, which is part of a National Reserve (buffer area for the National Park), and consisted of two paddocks (a and b), also with very high seasonal stocking density combined with a resting period without livestock. Finally, we included in the study two paddocks with seasonal grazing, used to separate bulls out of mating season (Rb1 and Rb2). The range of annual stocking rates of seasonally grazed paddocks (0.04–0.18 AUY ha^{-1}) was similar to that of

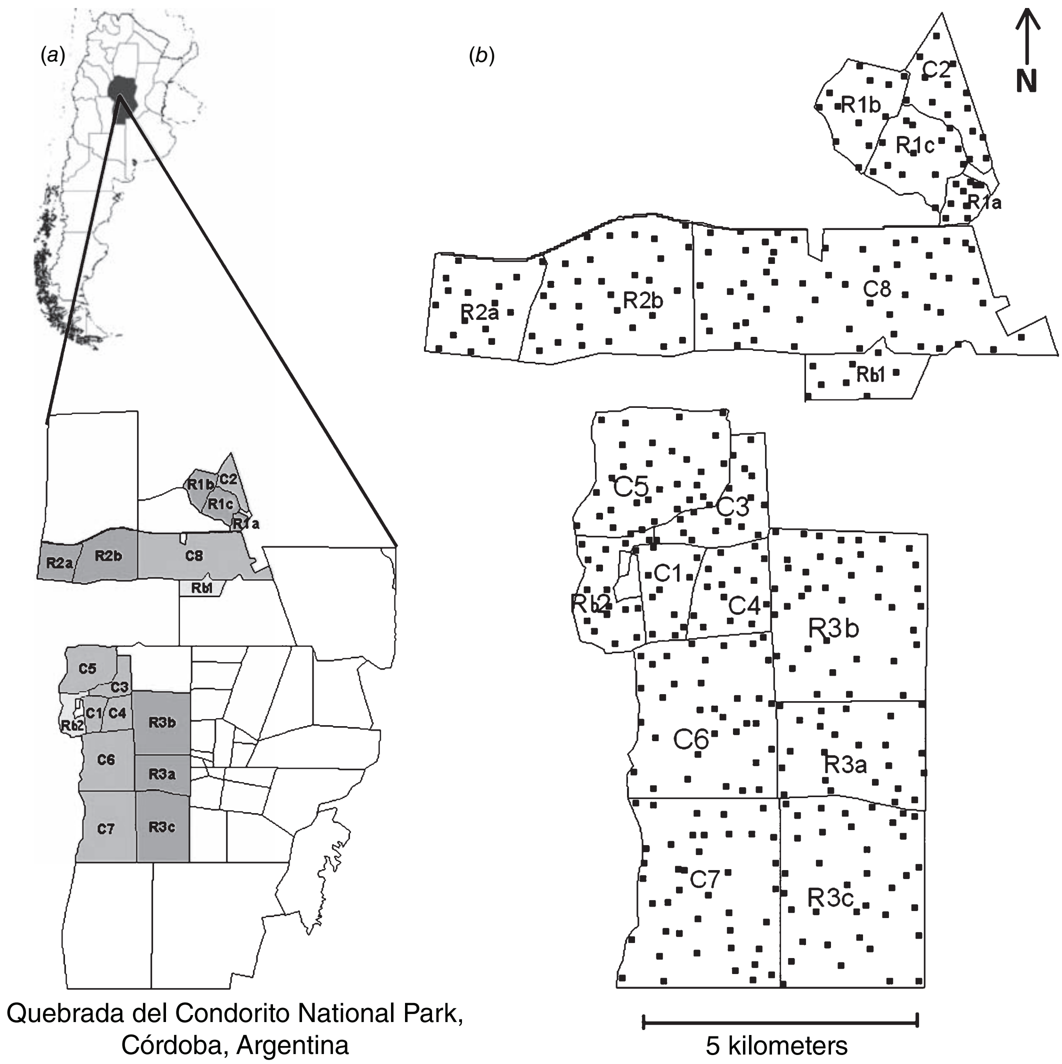

Fig. 1. (*a*) Location of Quebrada del Condorito National Park and Reserve in the Córdoba province (Argentina); and paddocks included in the present study. (*b*) Detail of the study paddocks and 1-ha plots, represented by scale dimensioned squares. Paddocks R2a and R2b belong to the private settlement Santo Tomás, in the National Reserve, and all of the other paddocks belong to the National Park.

continuously grazed paddocks (0.02–0.20 Animal Unit Year (AUY) ha^{-1}; APN 2004, 2007; Table 1).

Within the 18 paddocks, we selected a total of 419 square plots, 1 ha each, covering all the variability in vegetation and physiography. We stratified the study area considering eight landscape units characterised mainly by their dominant vegetation/rock mosaics and topography (Cingolani *et al*. 2004, 2008*b*). Plots were located randomly within each landscape unit with the restriction that the minimum distance between two plots of the same paddock was 150 m to better attain data independence (Fig. 1). Plots were small samples of landscapes, and accurately represented the entire continuous variation in landscape complexity (Cingolani *et al*. 2004). Each paddock represents a unique and non-replicated management factor where the herd grazes, with different sizes, shapes and timing of grazing (continuous or seasonal use at different dates).

Annual cattle use at the plot level

We estimated plot annual cattle use across the whole study area (419 plots distributed within 18 paddocks) based on cattle dung presence. We followed the methodology proposed by von Müller *et al*. (2012). For each plot, we collected dung frequency data during August 2008 and again in March 2009 by registering cattle dung presence/absence in 250 squares of 30 × 30 cm (900 cm^2) widely distributed within the plot. For each date and plot, we converted dung frequency data into a value of plot annual cattle use for the previous year (12 months) using the model fitted and validated by von Müller *et al*. (2012), as follows:

$$\text{Plot annual cattle use (AUY ha}^{-1}\text{)} = 0.017 * \text{dung frequency (\%)} \quad (1)$$

Table 1. Paddocks under study, timing of grazing, size (between brackets the effective size, i.e. discounting rock surface), annual cattle stocking rate and seasonal cattle stocking density of each one (between brackets the values calculated on the basis of effective size)
The number of study plots at each paddock is indicated in the last column

Paddock[A]	Timing of grazing	Size (ha)	Annual cattle stocking rate (AUY ha^{-1})[B,D]	Seasonal cattle stocking density (AU ha^{-1})[C,D]	No. of plots
C1	Continuous	199 (182)	0.02 (0.02)	0.02 (0.02)	11
C2	Continuous	226 (123)	0.07 (0.13)	0.07 (0.13)	14
C3	Continuous	258 (230)	0.16 (0.18)	0.16 (0.18)	16
C4	Continuous	266 (242)	0.12 (0.13)	0.12 (0.13)	14
C5	Continuous	608 (414)	0.18 (0.27)	0.18 (0.27)	30
C6	Continuous	875 (696)	0.20 (0.26)	0.20 (0.26)	34
C7	Continuous	1074 (865)	0.16 (0.20)	0.16 (0.20)	41
C8	Continuous	1453 (1027)	0.13 (0.18)	0.13 (0.18)	55
R1a	Seasonal (Dec.–Jan.)	70 (61)	0.13 (0.14)	0.80 (0.92)	9
R1b	Seasonal (Jan. –June)	239 (184)	0.18 (0.23)	0.40 (0.51)	12
R1c	Seasonal (July–Dec.)	256 (207)	0.16 (0.20)	0.36 (0.44)	13
R2a	Seasonal (July–Nov.)	391 (317)	0.18 (0.22)	0.30 (0.37)	16
R2b	Seasonal (Nov.–June)	757 (526)	0.14 (0.21)	0.26 (0.39)	30
R3a	Seasonal (June–July)	573 (437)	0.05 (0.07)	0.43 (0.57)	23
R3b	Seasonal (July–Nov.)	1020 (727)	0.12 (0.17)	0.27 (0.37)	39
R3c	Seasonal (Mar.–May)	1035 (783)	0.07 (0.09)	0.28 (0.37)	37
Rb1	Seasonal (June/Aug.–Nov.)	213 (146)	0.04 (0.05)	0.09 (0.13)	8
Rb2	Seasonal (June/Aug.–Nov.)	242 (150)	0.05 (0.08)	0.11 (0.17)	17
Total[a]/Average[b]		9753 (7319)[a]	0.12[b]	0.16[b]	419[a]

[A]C: paddocks with continuous grazing; R: paddocks with seasonal grazing under rotational grazing management units, where the same number indicates the same unit and the letter indicates the paddock; Rb: paddocks used to isolate bulls out of the mating season.
[B]Cattle annual stocking rate was calculated as the average of monthly stocking density from April 2007 to March 2009, including resting months as zero in seasonally grazed paddocks.
[C]Average monthly cattle stocking density across the grazing months (excluding resting months).
[D]In most cases, overall stocking rates and densities are somewhat higher than shown in the table, as a few numbers of other animals besides cattle also graze the paddocks. Terminology follows SRM (1998) and Allen *et al*. (2011). Lower case letters on the last line indicate whether the number is a total or an average.

Considering as an AUY the forage consumed during one year by one Animal Unit (AU) (Allen *et al*. 2011). Accordingly, we considered an AU as one mature cow of ~400 kg, either dry or with calf up to 6 months of age and 160 kg, consuming ~12 kg of forage/day on an oven-dry basis and including the forage consumed by the calf (Cocimano *et al*. 1975; SRM 1998). Later, we averaged the annual cattle use estimations obtained from data taken at both dates to obtain one value of annual cattle use for each plot.

Seasonal cattle density at the plot level

We estimated plot cattle density by directly registering cattle presence within each plot in the field over 46 dates, every 7–10 days, from April 2007 to June 2008. Due to the complexity of sampling, these estimations were done only in 140 plots out of the total, distributed in six paddocks (C2, C8, R1b, R1c, R2a and R2b; Table 1). This sampling procedure was designed to record cattle density changes during the time in which large herbivores move to different habitats at a landscape scale within paddocks (see Senft *et al*. 1987; Bailey *et al*. 1996). We made a distinction among different cattle categories; considering bulls as 1.3 AU; and cows, steers and heifers as 1 AU; calves were not included in the estimation because they were not weaned (Cocimano *et al*. 1975). Heifers were considered as 1 AU because at the observation distance they cannot be distinguished from cows. However, the potential bias caused by this assumption is very low, as heifers were ~10% of animals in the paddocks, and rarely ascended to 30% for short periods. At each date, all the 140 plots were sampled during the same day. At different sampling dates, every daily trail was started from different plots and paddocks to minimise hourly biased sampling. We calculated animal density (AU ha^{-1}) per visit as the number of animal units observed at each visit in the 1-ha plot). Then we calculated mean monthly animal density for each plot as the average, including zeros, of visits in the same month. Finally, from monthly data we calculated the average cattle density for two different seasons: dry-cold season (from May to October) and wet-warm season (from November to April). The wet-warm season included the plant growth season (Pucheta *et al*. 1998; Giorgis *et al*. 2010). Seasonally grazed paddocks were not sampled during the resting period. Therefore, for each plot, the wet-warm or dry-cold season cattle density reflected the averages of months with animals within the season, and not necessarily the 6-month average.

Selectivity indices at the plot level

We calculated annual selectivity indices for all plots, and seasonal selectivity indices for the 140 plots having seasonal cattle density data. These indices were calculated as follows (adapted from Krueger 1972):

$$SI_{iP} = (C_{ip} - MC_{np})/(C_{ip} + MC_{np}) \qquad (2)$$

where SI_{ip} is the selectivity index for the plot i and the period p (annual, dry-cold season or wet-warm season). C_{ip} is the plot annual cattle use or average cattle density of the plot *i* during the period *p*, and MC_{np} is the mean plot cattle use or density for the paddock *n* (where the plot *i* was located) during the period p (i.e. the averages among all plots within the paddock). The selectivity index SI varies between –1 and +1. A negative SI value indicates that the plot is less used by cattle than the paddock average, whereas a positive SI value indicates that the plot is more used than the paddock average. A value of zero or close to zero indicates indifference; the plot is used in similar proportion to the paddock average. The values of selectivity indices represent the response variables analysed in this study at the plot level.

Ecological variables at the plot level

We considered five biotic variables, based on the cover of different forage items (Table 2). These variables were evaluated for each plot in three steps. First, during January and February 2007 we mapped through field survey and satellite images (Google Earth 5.0.1© 2016) the proportion of the different vegetation types within the plot. The types considered were: woodlands, thick tussock grasslands, thin tussock grasslands, lawns, and finally, rocky outcrops and erosion pavements (Flores *et al*. 2012). Second, we visually estimated in the field the cover of different forage items within each vegetation type in 10 subplots 1 m^2 each, proportionally distributed among vegetation types. Initially, forage items were: thick tussock grasses (almost exclusively *Poa stuckertii*), thin tussock grasses (*Deyeuxia hieronymi*, *Festuca* spp. and others), other perennial and annual grasses (e.g. *Chascolytrum subaristatum*, *Bromus* spp. and *Muhlenbergia peruviana*), graminoids (*Carex* spp. and other sedges and rushes) and forbs (*Lachemilla pinnata*, *Eryngium*

Table 2. Variables considered to explain cattle selectivity at the plot level, and cattle selectivity strength and distribution at the paddock level
Their mean, minimum and maximum values are indicated

Variables	Mean	Min.	Max.
Ecologic: biotic (plot level)			
Short plant cover (%)	22.13	0.50	71.40
Woody plant cover (%)	4.97	0.00	120.00
Thin tussock grass cover (%)	28.14	0.00	85.32
Thick tussock grass cover (%)	21.27	0.00	95.00
Rock cover (%)[A]	21.22	0.00	71.25
Ecologic: abiotic (plot level)			
Elevation (m a.s.l.)	2152	2014	2247
Terrain slope (%)	9.36	0.00	50.00
Distance to water sources (m)	410	0.00	1537
Distance to salt sources (m)	1400	85	4178
Insolation index	0.85	0.72	0.92
Roughness index	0.03	0.01	0.07
Topographic position (%)	52.3	0.0	100.0
Management: paddock shape and size (paddock level)			
Total size (ha)	542	70	1453
Effective size (ha)	407	61	1027
Compacity index	0.52	0.30	0.66
Circularity index	0.52	0.29	0.66
Management: grazing intensity and timing (paddock level)			
Estimated annual cattle stocking rate (AUY ha^{-1})[B]	0.13	0.03	0.21
Annual cattle stocking rate (AUY ha^{-1})[C,F]	0.12 (0.16)	0.02 (0.02)	0.20 (0.27)
Annual total stocking rate (AUY ha^{-1})[E,F]	0.15 (0.19)	0.04 (0.05)	0.24 (0.31)
Seasonal cattle stocking density (AU ha^{-1})[D,F]	0.23 (0.28)	0.02 (0.02)	0.55 (0.66)
Seasonal total stocking density (AU ha^{-1})[E,F]	0.26 (0.33)	0.07 (0.13)	0.80 (0.82)
Grazing seasonality index	0.149	–0.741	0.942
Management: vegetation types (paddock level)			
Lawns (%)	18.05	6.88	31.91
Woodlands (%)	3.15	0.00	65.00
Thin tussock grasslands (%)	26.52	9.78	41.05
Thick tussock grasslands (%)	26.26	7.54	46.86
Rocky lands (%)[G]	26.33	15.63	40.32

[A]Rock cover was considered as a biotic factor, as it represents the absence of forage items.
[B]Indirectly estimated from dung frequency (based on von Müller *et al*. 2012).
[C]Average of cattle monthly stocking density including as zero the resting months.
[D]Average of cattle monthly stocking density during the grazing months only.
[E]Average of total (including other animals) monthly stocking density either annual or during the grazing months.
[F]In brackets, values considering effective area (discounting rock).
[G]Rocky lands include rocky outcrops and erosion pavements.

spp. and others), trees (mainly *Polylepis australis*), shrubs (*Berberis hieronymii* and others), and finally mosses, lichens and ferns (Nomenclature follows Zuloaga *et al.* 1994; Zuloaga and Morrone 1996, 1999). Additionally, within each vegetation type we estimated the rock and bare soil cover (%). To calculate the cover of each forage item, we performed an average across the different vegetation types, weighted by their proportion in the plot. The same procedure was followed for rock cover. Finally, we reduced the forage items to five, by combining as additive variables some of the items with high co-variation and similar vertical structure. The five biotic variables ultimately considered in this study were: short plant cover as the sum of short annual and perennial grasses, graminoids and forbs; woody plant cover as the sum of trees and shrubs; thin tussock grass cover; thick tussock grass cover; and finally rock cover, as the absence of forage (Table 2). Due to the low surface covered by bare soil, mosses, lichens and ferns, we decided not to include them as explanatory variables.

We considered eight abiotic variables for each plot (Table 2). We measured average terrain slope with a clinometer, elevation (m a.s.l.) at the centre of the plot with a GPS, and the minimum distance from the plot border to permanent water sources (streams) and salt sources. No watering points existed due to numerous permanent streams dissecting all paddocks. If a permanent stream crossed the plot we considered distance to water as zero. Additionally, from GIS layers we obtained three topographic indices for the central pixel (30×30 m) of each plot: insolation index, roughness index and topographic position (Table 2). The insolation index is dimensionless and varies on a scale from 0 (no direct insolation) to 1 (the sun's rays at 90° in the equinox, which reflect fairly well the annual insolation, without considering projected shadows, values close to 1 are attained in north slopes, whereas lower values are attained in southern slopes). The roughness index is also dimensionless and varies from zero (flat) to increasingly higher values as topographic variations at short distances increased. Topographic position (%) varies between 0 (lowest topographic position in relation to the surrounding landscape) and 100 (highest position). More details on these indices can be found in Cingolani *et al.* (2008*b*).

Selectivity and distribution at the paddock level

For each paddock, we calculated two indicators related to cattle selectivity and grazing distribution. The first, 'selectivity strength' indicated how strong the selectivity was in a given paddock for the most attractive habitat characteristic (i.e. short plants, see Results). More details of these calculations are given in the statistical analyses section. The second, 'grazing distribution index' indicated the heterogeneity in cattle distribution within the paddock. It was calculated as the coefficient of variation of the annual cattle use of plots within the paddock. High values of this index indicate a very uneven distribution, whereas low values, a very uniform distribution (Wang *et al.* 2006). These two indicators represent the response variables analysed in this study at the paddock level.

Management variables at the paddock level

We considered four variables related to paddock size and shape (Table 2). For each paddock, we used the total size and effective size (discarding rock cover, Table 1). We also calculated two dimensionless indices of paddock shape related with its isotropy (adapted from Fortin and Dale 2005; and modified by Montero and Bribiesca 2009), the paddock compacity index and circularity index. Those indices are based on the paddock size (m^2), paddock perimeter (m) and maximal paddock bisectrix (m), as follows:

$$\text{Compacity index} = [\text{paddock size}/\text{paddock perimeter}^2] \times 10 \quad (3)$$

$$\text{Circularity index} = [4 \times \text{paddock size}/(\pi \times \text{maximal paddock bisectrix}^2)] \quad (4)$$

In both cases, high values indicate more isotropic paddock and lower values a more anisotropic paddock (Table 2).

We considered six variables related with grazing intensity and timing (Table 2). For each paddock, we calculated annual cattle stocking rate in two different ways. First, as the average of estimations of annual cattle use obtained from dung deposition for all plots within the paddock. Second, as the average of detailed monthly cattle stocking density data provided by National Park administration and land owners from April 2007 to March 2009. To calculate this average we included resting months as zeros (Table 1). From the latter data source, we also calculated total annual stocking rate (including herbivorous grazing animals other than cattle). Additionally, for each paddock we calculated seasonal cattle and total stocking density. For this, we averaged only the stocking density of the months with animals. For all stocking rate and density variables except that estimated from dung, we repeated the calculations considering effective paddock size instead of total size, and reported values in brackets (Tables 1, 2). Finally, we calculated a grazing seasonality index. For this, a previous step was to calculate winter stocking density as the average, including zeros, of June to September, and summer stocking density as the average from December to March. From data on winter and summer stocking densities we calculated the seasonality index (modified from Cingolani *et al.* 2013) as:

$$\text{PSI} = (\text{WSD} - \text{SWD})/(\text{WSD} + \text{SSD} + 0.01) \quad (5)$$

where PSI is the paddock seasonality index, WSD is winter stocking density, and SSD is summer stocking density. In this way, paddocks which were used only in the winter months, had a positive value close to 1, paddocks under a continuous grazing management had a value close to 0, and paddocks used only in summer, had a negative value close to –1.

Finally, we considered five variables describing whole paddock vegetation as the proportion (%) of thin tussocks grasslands, thick tussock grasslands, lawns, woodlands and finally rocky lands as the sum of rocky outcrops and erosion pavements (Table 2), which were obtained from a land-cover map (Cingolani *et al.* 2004). These last variables are management factors as they relate to paddock features and by some extent are the result of transformations produced by long-term grazing (Cingolani *et al.* 2008*a*), and can affect within-paddock selectivity of cattle.

Statistical analyses

Annual selectivity at the plot level

The effect of ecological factors (explanatory variables) on annual selectivity (response variable) was analysed by using general linear models across the 419 plots of the study area. All biotic and abiotic variables were first included in the model (see Table 2 for the list of variables), and the paddock was included as a random factor with 18 levels. We performed a manual backward stepwise procedure discarding all non-significant quantitative variables. When two independent variables were strongly correlated between them (absolute $R > 0.5$), we selected the one which performed best. In this way we retained only significant quantitative variables ($P \leq 0.05$) and the paddock factor. In a second step we tested the interactions between the paddock factor and the selected quantitative variables, to evaluate if the slope of the relationship between independent variables and the selectivity index differed between paddocks. To select the relevant interactions, we proceeded in a similar way as before, discarding in a backward procedure all non-significant interactions.

Selectivity and distribution at the paddock level

The selectivity strength indicator was calculated from the results of the plot-level analysis. We found that the annual selectivity index was affected by a strong interaction between paddock and short plant cover (see Results). From the linear model we calculated, for each paddock, the slope of the relationship between short plant cover and the selectivity index, by summing up the coefficients for the main effect and the coefficient for the interaction term in each case. We considered those slopes as the selectivity strength indicator for each paddock. We correlated this indicator, along with the grazing distribution index, with all management variables at the paddock level (Table 2*c*, *d* and *e*) using Pearson.

Seasonal selectivity at the plot level

We analysed the effects of ecological factors on seasonal selectivity in the same way as previously reported for annual selectivity, but we considered seasonal selectivity indices (warm-wet and cold-dry) instead of the annual index, and only the six paddocks which had that information. We discarded in a backward procedure only the variables which were not significant in any of the models (i.e. we retained in both models variables which were significant in at least one of them). In this way both final models included the same variables, allowing a better comparison among the influence of each variable, by means of the confidence intervals of coefficients.

Results

Annual selectivity at the plot level

Our model explained 51.5% of the variability in plot annual selectivity (Table 3) and indicated that the selectivity index was mainly explained by the biotic variable 'short plant cover' (19.7% of the variability). The interaction between short plant cover and paddock explained an additional 8.9% of the variability. Another biotic variable that influenced selectivity was 'thin tussock grass cover', which explained 4.8% of the variability, whereas the abiotic variables 'roughness index' and 'terrain slope' explained a further 4.6% and 2.0%, respectively. On an annual basis, cattle selected plots with high cover of short plants and thin tussocks, situated in flat and smooth reliefs, while avoiding steep slopes with rugged relief (Table 3). The interaction revealed that the strength of the cattle selectivity for short plants was different among paddocks (Fig. 2).

Table 3. General lineal model for annual cattle selectivity as a function of ecological (biotic and abiotic) variables and paddock as a categorical factor with 18 levels

Source of variation	Beta	d.f.	*F*	Significance	Eta^2
Model[A]		38	10.632	<0.001	0.515
Intercept	–0.335	1	19.335	<0.001	0.048
Short plant cover	0.015	1	93.065	<0.001	0.197
Thin tussock grass cover	0.004	1	19.140	<0.001	0.048
Terrain slope	–0.008	1	16.873	<0.001	0.043
Roughness index	–4.445	1	21.596	<0.001	0.054
Paddock		17	2.620	<0.001	0.105
Paddock × Short plant cover	–	17	2.182	0.004	0.089

[A]$R^2 = 0.515$; $R^{2\ adj} = 0.467$; $n = 419$. Eta^2 indicates the variance explained by each variable.

Selectivity and distribution at the paddock level

The selectivity strength indicator and the grazing distribution index were positively correlated ($r = 0.60$, $P < 0.01$; $n = 18$ paddocks). Both indicators were negatively correlated with annual stocking rate, either calculated from data indirectly estimated by dung frequency or from data provided by National Park administration and land owners (Table 4). The grazing distribution index was negatively correlated with seasonal cattle stocking density, but the correlation was weaker than when considering annual total stocking rate. We did not find significant correlations with paddock size, but found a significant negative correlation between the grazing distribution index and both indicators of isotropy (paddock circularity index and compacity index, Table 4). Additionally, selectivity strength and the grazing distribution index were negatively correlated with the proportion of lawns in the paddock (Fig. 3). In summary, the results showed that selectivity was stronger and/or distribution more uneven when stocking rates were lower, paddocks were less isotropic and had low proportion of lawns dominated by short plants.

Seasonal selectivity at the plot level

Our model explained 44.1% of the variability in the wet-warm season selectivity (Table 5). As with the annual model, the main driver of cattle selectivity was linked to the biotic factor short plant cover, explaining 25.9% of the variability (Table 5). Other variables significantly influenced selectivity in the wet-warm season, being in order of importance the paddock with 13.4% of the variability, and the abiotic variables terrain slope and the roughness index, explaining 4.2% and 4.1% of the variability, respectively (Table 5). These results showed that in the wet-warm season cattle were attracted by short plants, and tended to avoid steep slopes and rough landscapes. The interaction between paddock and short plant cover was not significant, nor was distance to permanent water sources (Table 5).

For the dry-cold season, our selectivity model explained 39.4% of the variability (Table 6). This model indicated that in the

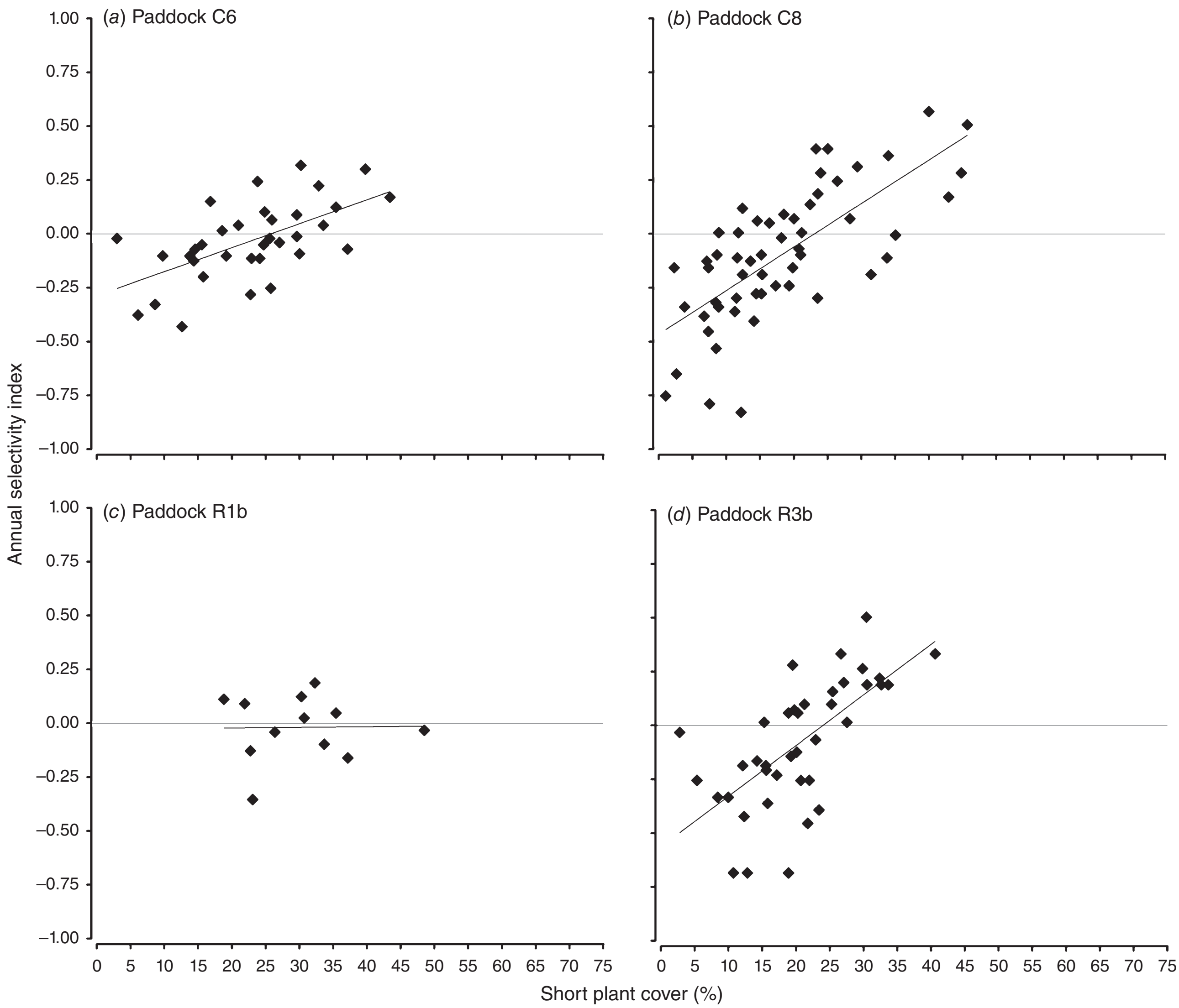

Fig. 2. Annual selectivity index against short plant cover for two paddocks under continuous and two under seasonal grazing as examples. Each point represents a plot. (*a*) The continuously grazed paddock with the lowest slope; (*b*) the continuously grazed paddock with the highest slope; (*c*) the seasonally grazed paddock with the lowest slope; and (*d*) the seasonally grazed paddock with the highest slope. To draw the line, the slope was calculated from the model by adding the coefficient of the term short plant cover plus the coefficient of the interaction term short plant cover × paddock. The intercept was calculated adding all the remaining terms, by considering the other significant variables as constant values equal to the average for all plots (see Table 2).

dry-cold season, animals tended to select areas covered by short plants. This variable explained 31.0% of the variability (Table 6). Additionally, cattle selectivity in the dry-cold season was affected by the paddock and the abiotic variable distance to water sources, explaining 8.9% and 8.6% of the variability, respectively (Table 6). Our results showed that, during the dry-cold season, cattle were attracted to short plants, but avoided landscapes far from permanent water sources. The interaction between paddock and short plant cover was not significant, nor was the influence of roughness and terrain slope (Table 6).

The results indicated that, on a seasonal basis the main determinant of cattle selectivity was short plant cover. Although this factor had a higher slope in the dry-cold season than in the wet-warm season, the overlapped confidence intervals revealed that these differences were not significant (Tables 5 and 6). Different abiotic variables significantly influenced seasonal selectivity patterns, with terrain slope and landscape roughness being important in the wet-warm season (Table 5) and distance to permanent water sources in dry-cold season (Table 6).

Discussion

Livestock landscape selectivity at the plot level was mainly driven by one biotic factor, the cover of short plants, all year-round, whereas abiotic factors were far less important. However, selectivity strength for short plants and the associated grazing distribution patterns were different in different paddocks, depending on their management and characteristics.

Table 4. Pearson correlations for selectivity strength and the grazing distribution index against management variables at the paddock level (n = 18 paddocks)
* $P < 0.05$; ** $P < 0.001$

Management variables	Selectivity strength[A]	Grazing distribution index[B]
Total area (ha)	–0.05	0.01
Effective area (ha)	–0.05	–0.04
Compacity index	–0.11	–0.54*
Circularity index	–0.19	–0.48*
Estimated annual cattle stocking rate (AUY ha^{-1})	–0.70**	–0.78**
Annual cattle stocking rate (AUY ha^{-1})[C]	–0.60** (–0.65**)	–0.71** (–0.65**)
Annual total stocking rate (AUY ha^{-1})[C]	–0.44 (–0.55*)	–0.66** (–0.62**)
Seasonal cattle stocking density (AU ha^{-1})[C]	–0.33 (–0.36)	–0.47* (–0.45)
Seasonal total stocking density (AU ha^{-1})[C]	–0.21 (–0.25)	–0.39 (–0.37)
Grazing seasonality index	0.28	0.42
Thin tussock grasslands (%)	0.27	0.41
Thick tussock grasslands (%)	0.38	–0.19
Lawns (%)	–0.53*	–0.57*
Woodlands (%)	–0.26	0.02
Rocky lands (%)	–0.25	0.32

[A]Obtained as the slope of the relationship between short plant cover and the selectivity index for each paddock.
[B]Within-paddock stocking rate coefficient of variation.
[C]In brackets, the correlation coefficients considering effective annual stocking rate or seasonal stocking density.

Selectivity at the plot level

According to studies performed in a wide variety of rangelands and at large spatial scales livestock distribution patterns as a consequence of animal selectivity are primarily determined by abiotic factors, which act as landscape constraints within which biotic factors operate (Gillen *et al*. 1984; Bailey *et al*. 1996; Kohler *et al*. 2006; Hunt *et al*. 2007, 2014; Kaufmann *et al*. 2013). In turn, biotic factors were found as determinants of selectivity at smaller scales such as feeding site (Bailey 1995; Teague and Dowhower 2003; Bailey *et al*. 2015) or at the species level (Cid and Brizuela 1998; Díaz Falú *et al*. 2014). Conversely, our results revealed that cattle landscape selectivity is mainly determined by biotic factors either when considering a year-round or shorter (seasonal) study period. This is in line with Gross *et al*. (1995) who observed that, for large herbivores the relative importance of abiotic factors on habitat selection is likely to decrease in spatially complex environments such as our study area, and tend to be replaced by biotic factors.

Worldwide, the most important biotic factors which drive herbivore selectivity are linked to short plants at a wide range of scales and hierarchical levels, from plants or feeding sites to landscapes and ecosystems (McNaughton 1986; Bailey 1995; Cid and Brizuela 1998; Cingolani *et al*. 2002; Landsberg *et al*. 2003; Kohler *et al*. 2006). The attractiveness for short plants has been attributed to their higher nutritional quality related to their higher levels of crude protein as compared with taller plants (McNaughton 1986; Landsberg *et al*. 2003; Oesterheld and Semmartin 2011). In our study area, short plants also appeared to be the main attracting factor for cattle throughout the whole year, despite the marked differences in nutritional quality among seasons (Pucheta *et al*. 1998). Other studies in the mountains of central Argentina also revealed that cattle and other herbivores such as horses, hares (*Lepus europaeus*) and guanacos (*Lama guanicoe*) mainly select short grasses, graminoids and some forbs (Falczuk 2002; Barri *et al*. 2014). Additionally, we found a slight but positive influence of thin tussocks on cattle selectivity. Thin tussocks have a lower nutritional quality than graminoids and forbs, but it has far higher productivity, biomass and fibre content (Pucheta *et al*. 1998; Falczuk 2002; Vaieretti *et al*. 2010). As large herbivores demand fibre in their diet to keep rumen volume and functionality (Hofmann 1989), thin tussocks complete the nutritional demands, enabling animals to balance their diets (Vallentine 2001).

Considering the temporal dimension of selectivity, Ganskopp and Bohnert (2006) support the idea that cattle initially seek areas of high-quality forage, and sacrifice quality for quantity only after more nutritious stands of herbage have been consumed. In a timeline overview, this means that throughout the growing season, herbivores have high selectivity for feeding areas with the best forage quality; whereas out of the growth season, and due to decrease in forage quality, they are forced to consume any forage which is available, widening their distribution. In our study, differences between seasonal attractiveness of preferred forage items were non-existent, and cattle also select short plants during the dry-cold months, although standing biomass was scarce and of lower quality than during the growing season (Pucheta *et al*. 1998). Cattle probably select for short plants during all the year because of their comparatively higher quality than other forage types, even out of the growing season (Pucheta *et al*. 1998). In turn, selectivity for thin tussocks was not detected when considered separately on wet-warm or dry-cold season, which is probably due to the decrease in statistical power because of a reduced number of plots. However, we could visually distinguish a certain seasonal consumption of thin tussock grasses, which are mainly foraged at the end of the dry-cold season (von Muller, pers. obs., 2009). Similar but not identical results were found for the reintroduced *Lama guanicoe*. These wild herbivores consume thin tussock grasses and graze in thin tussock dominated landscapes, but they do not positively select this forage resource (Flores *et al*. 2012; Barri *et al*. 2014).

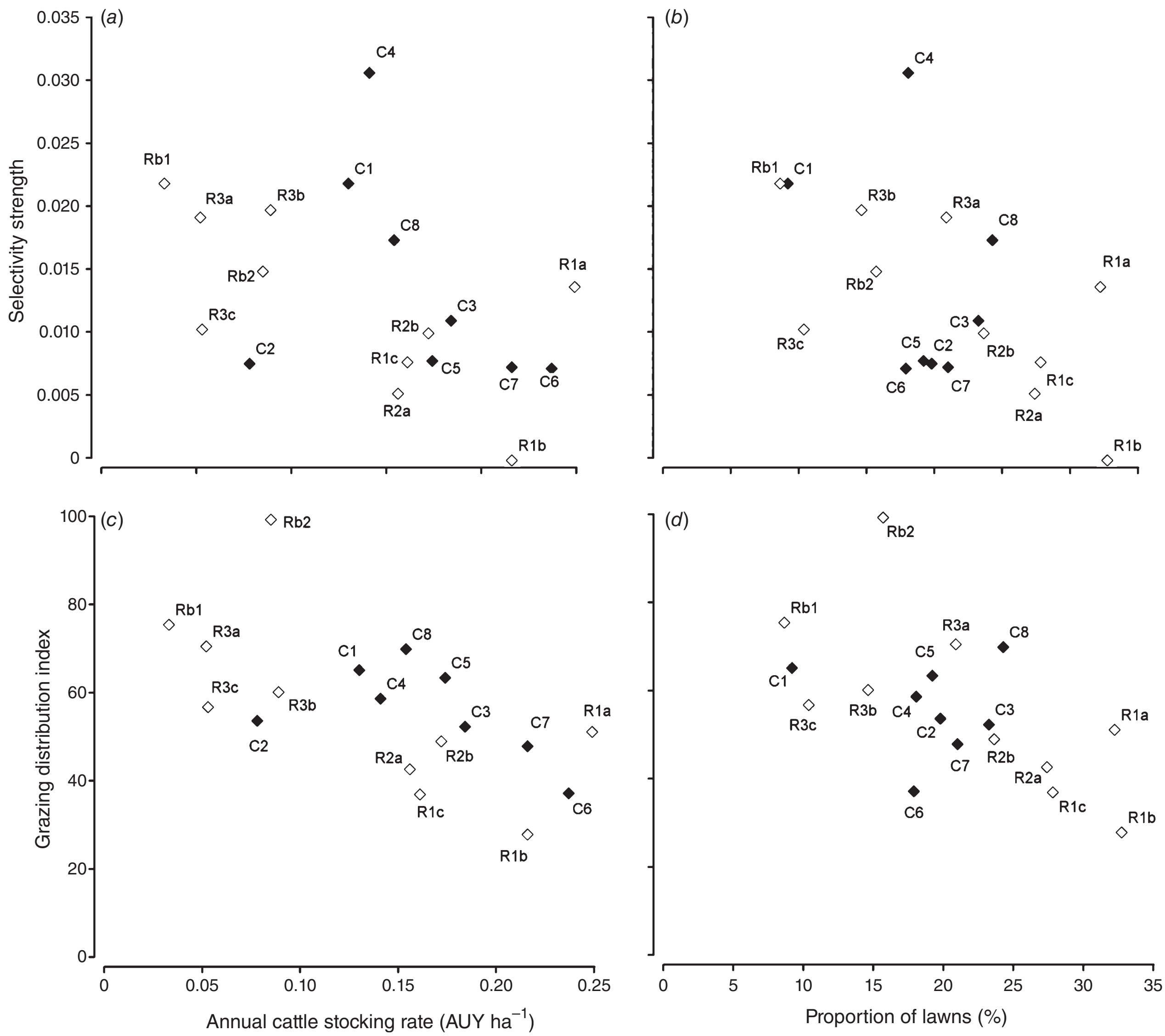

Fig. 3. Relationship of selectivity strength and grazing distribution index with management factors at the paddock level. Symbols represent paddocks under continuous (♦) and seasonal (◇) grazing. (*a*) selectivity strength against annual cattle stocking rate; (*b*) selectivity strength against paddock lawn proportion; (*c*); grazing distribution index against annual cattle stocking rate; and finally (*d*) grazing distribution index against paddock lawn proportion.

Abiotic factors were far less important than biotic factors either when considering year round or seasonal selectivity, which contrasts with other studies that found a large number of abiotic variables regulating selectivity (Brock and Owensby 2000). Our results revealed that in the dry-cold season, the most limiting abiotic factor related to cattle selectivity was distance to water, keeping cattle near permanent streams and water sources as generally reported for arid environments (Adler and Hall 2005). In turn, in the wet-warm season, cattle tended to select flat and smooth landscapes in which animals could reduce energy costs of moving through the environment, without any influence of proximity to water sources. The lack of any influence of water was probably due to the numerous temporary ponds and streams that dissect the study area during the wet-warm season. The high proportion of fibre and low energy composition of grasses demands herbivores to be more efficient in the use of body reserves for movement within the environment they explore (Hofmann 1989), and therefore steep slopes and rough landscapes are rejected by cattle. Thus, similarly to distance to water sources in the dry cold season, in the wet-warm season terrain slope and roughness act as constrains on cattle selectivity and consequently in their distribution (Bailey 2004). Slope and landscape roughness were also significant in the annual analysis, but not in the dry-cold season when distance to water seem to be masking the influence of these factors.

Selectivity and distribution at the paddock level

Selectivity and distribution indicators were correlated suggesting that the main determinant for distribution is cattle selectivity.

Table 5. General linear model for wet-warm season cattle selectivity as a function of ecological (biotic and abiotic) variables and paddock as a categorical factor with six levels

Source of variation	Beta[A]	d.f.	F	Significance	Eta^2
Model[B]		9	11.39	<0.001	0.441
Intercept	–0.475 ± 0.307	1	4.79	0.003	0.035
Short plant cover	+0.020 ± 0.006	1	45.36	<0.001	0.259
Roughness index	–7.293 ± 6.071	1	5.65	0.019	0.042
Terrain slope	–0.013 ± 0.010	1	5.56	0.020	0.041
Distance to water	$-7.9\ E^{-5} \pm 2.1\ E^{-4}$	1	0.51	0.477	0.004
Paddock		5	4.04	0.002	0.134

[A]Coefficients and their 95% confidence intervals.
[B]$R^2 = 0.441$ ($R^{2\ adj} = 0.402$; $n = 140$). Eta^2 indicates the variance explained by each variable.

Table 6. General lineal model for dry-cold season cattle selectivity as a function of ecological (biotic and abiotic) variables and paddock as a categorical factor with six levels

Source of variation	Beta[A]	d.f.	F	Significance	Eta^2
Model[B]		9	9.38	<0.001	0.394
Intercept	–0.781 ± 0.332	1	12.96	<0.001	0.091
Short plant cover	+0.025 ± 0.006	1	58.54	<0.001	0.310
Terrain slope	–0.001 ± 0.012	1	0.01	0.923	<0.001
Roughness index	–1.210 ± 6.563	1	0.13	0.716	0.001
Distance to water	$-4.2\ E^{-4} \pm 2.4\ E^{-4}$	1	12.28	<0.001	0.086
Paddock		5	2.54	0.031	0.089

[A]Coefficients and their 95% confidence intervals.
[B]$R^2 = 0.394$ ($R^{2\ adj} = 0.352$; $n = 140$). Eta^2 indicates the variance explained by each variable.

We found that cattle selectivity for short plants was stronger, and consequently distribution more uneven, in paddocks with low stocking rate and low proportion of lawns, and weaker in paddocks with high stocking rates and high proportion of lawns. As stocking rate and lawn proportion were correlated across paddocks in our dataset (R varying between 0.55 and 0.73 depending on the stocking rate estimator, $P < 0.05$, $n = 18$ paddocks) it may be argued whether the main driver of selectivity strength and consequent animal distribution is lawn proportion, stocking rate, or the combination of both.

The result that paddocks with higher stocking rate showed less selectivity is in line with literature and management practices, as stocking rate is the main management tool applied by managers to control livestock selectivity and improve distribution (Vallentine 2001; Bailey and Brown 2011; Rinella *et al*. 2011; Hunt *et al.* 2014). Many authors have proposed that when grazing pressure increases, animals begin to forage in non-preferred areas of the paddock (Hart *et al*. 1993; Brock and Owensby 2000; Ganskopp and Bohnert 2006; Hunt *et al*. 2007, 2014; Kaufmann *et al*. 2013). However, selectivity strength was not correlated with seasonal stocking density in our study, but only with annual stocking rate, showing that rotational management does not result in a reduction of selectivity and a better cattle distribution. A similar result was obtained by Bailey and Brown (2011) in arid rangelands. It is possible that the temporary increase in animal density is compensated by the previous resting, which deferred forage. Thus, in rotational management units, grazing pressure may not strongly increase when animal density is increased (Vallentine 2001).

However, the comparison among seasons showed that selectivity for short plants is similar in the cold-dry season with low abundance of forage, as in the warm-wet season with high abundance of forage. This strongly suggests that an increase in grazing pressure does not result in better distribution patterns. Thus, we hypothesise that the proportion of lawns in the paddock is the main determinant of selectivity, and not stocking rate itself. Although, at a larger temporal scale, the proportion of lawns in a landscape is in part the result of high historical stocking rates combined with burning of tussocks (Díaz *et al*. 1994; Cingolani *et al*. 2008*b*). This means that long-term high stocking rates have contributed to maintain a larger proportion of lawns in the landscape, leading to a better distribution of animals.

As shown by our results, the selectivity for short plants is strong even in the dry-cold season, suggesting that animals need this forage item even when overall forage availability and quality is low (Pucheta *et al*. 1998). Accordingly, when this forage item is scarce in a paddock (i.e. low proportion of lawns), cattle still concentrate on the few lawns, where this item is available. Conversely, in paddocks with a high lawn proportion, cattle are spread across the paddock, and thus selectivity is weaker and distribution is more uniform.

Variables related to paddock shape were drivers of cattle distribution patterns, but not of selectivity for short plants. This result revealed that cattle distribution was more uniform in more rounded and isotropic paddocks than in anisotropic paddocks. Our results are in line with studies of Broweleit *et al*. (2000), Sevi *et al*. (2001), Barnes *et al*. (2008). The explanation of this pattern is related to maintenance and walking costs for herbivores, which limits animal explore far from attractors such as lawns and watering points in dry-cold season (Valentine 1947; Holechek 1988); grazing distribution as occurs with watering points in arid environments (Bailey *et al*. 1996). As a result, in more anisotropic paddocks it is possible to find large unused areas, independent of the type of vegetation.

Management implications

In our study area, after the creation of the National Park in the early 90s, livestock were removed to reduce soil erosion, but this triggered an advance of thick tussock grasslands, leading to landscape homogenisation (Cingolani *et al*. 2014). As a consequence, the National Park Administration reintroduced livestock, and later a small population of *Lama guanicoe*, to control the *Poa stuckertii* tussock advance, and to maintain heterogeneous mosaics of vegetation including lawns with their high diversity (Cingolani *et al*. 2005, 2014). In established lawns, grazing herbivores could stop the advance of *Poa stuckertii* isolated plants by associational palatability (Cingolani *et al.* 2014). But neither wild *Lama guanicoe*, nor livestock could alone hold back the advance of *Poa stuckertii* tussock grasslands at least with the conservative stocking rates considered in the present and previous studies (Cingolani *et al*. 2014). The present study suggests that it neither will be useful to reduce paddock size nor change grazing management from continuous to rotational, at least within the range of situations which we evaluated, but it could be possible to improve livestock distribution by subdividing paddocks to modify their shape. As we have discussed, the role of stocking rate remains unclear, but even if the increase in annual stocking rate would lead to an improvement in distribution, this tool should be used with caution due to high erosion risk (Cingolani *et al*. 2013).

Historically, the prevailing livestock management strategy in our study area was to adjust paddock stocking rates according to lawn proportion in the paddock, and to increase lawn covered areas by burning patches of tussocks grasses. The long-term consequences of this practice allowed the generation and maintenance of large areas of grazing lawns, but as a consequence, almost 20% of the area became completely denuded of its soils (Cingolani *et al*. 2013). In summary, fire in combination with herbivory seems to be the only way to increase the proportion of lawns, but high post-fire soil erosion rates indicates that this management practice is risky (Cingolani *et al*. 2013). Studies are needed to determine whether fire could be managed to minimise post fire soil erosion, for example burning small patches or during the wet season (Jaacks 2015).

As a conclusion from our study, we can state that cattle landscape selectivity in our spatially complex mountain grassland and their consequent distribution patterns are mainly driven by biotic factors. The most effective methods of changing cattle landscape selectivity include the manipulation of forage types when fencing or subdividing paddocks, and maybe through the use of fire. Additionally, distribution may be improved by manipulating the paddocks shape. The role of stocking rate should be further investigated.

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