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Plant species selection by sheep in semi-natural dry grasslands extensively grazed in the south-western Italian Alps

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Abstract

Sheep can have an important role in the conservation of abandoned and shrub- and tree-encroached, semi-natural dry grasslands because their feeding behaviour is known to affect plant diversity and structure. Nevertheless, little information is available about feeding preferences of sheep at the sward-patch scale and about the effects of stocking density on their selectivity. Consequently, we investigated plant-species selection by sheep managed with a low-intensity grazing, examining the influence of stocking density and plant species abundance by means of vegetation surveys and animal GPS tracking. Sheep grazed a graminoid-dominated, semi-natural dry grassland (Festuco–Brometea) in Piedmont Region, north-west Italy. Plant species, classified into graminoids, suffruticose forbs, and herbaceous forbs, were selected with a different intensity by sheep, which preferred graminoids over suffruticose and herbaceous forbs. Plant species showing a high consumption ratio (CR), i.e. the level of selection of plant species (CR >10%), were mostly graminoids (e.g. *Bromus erectus*, *Koeleria vallesiana* and *Stipa pennata*). Furthermore, *Carex* species were also noticeably selected, in particular *C. humilis*, whereas spiny species and those with a rosette or prostrate forms were rarely grazed. The heterogeneity of stocking density over the pasture allowed testing of the relationships between stocking density and CR. For many species, the higher the stocking density, the higher was the CR, regardless of the abundance of dominant neighbouring species. Results suggest that sheep under low-intensity grazing conditions exert a specific plant-species selection in abandoned dry grasslands. By regulating the stocking density through the management of grazing sheep, it may be possible to condition the consumption of certain plant species, with medium–long-term effects on the botanical composition.

Key words. extensive grazing management, Global Positioning System, grazing spatial patterns, intake value, plant functional group, selective foraging behavior

Nomenclature. Aeschimann et al. (2004)

Abbreviations. SC: Species Cover; SRA: Species Relative Abundance; I: Intake value; CR: Consumption Ratio

Running head: Plant species selection by sheep

Introduction

After World War II, the decline in labour and in the number of stocked animals in human mountain habitats of Italy, such as semi-natural grasslands, favoured shrub and tree encroachment and led to a loss in plant and animal diversity (Falcucci et al. 2007; Lonati et al. 2014; Orlandi et al. 2016) and to a decrease in the yield and nutritive value of forage (Freléhoux et al. 2007).

Nowadays, semi-natural dry Festuco–Brometea grasslands, which are one of the most threatened habitats in Europe because of land abandonment, have a crucial role in sustaining biodiversity. Indeed, they are among the most species-rich plant communities (up to 80 plant species/m², WallisDeVries et al. 2002) and they contain a large number of rare and endangered plant and animal species (Werner and Spranger 2000).

European semi-natural dry grasslands require low-intensity or extensive management to maintain their nature conservation value (Calaciura and Spinelli 2008). Livestock management can play an important role in their conservation given that the combined action of trampling, defoliation, seed transport, and nutrient redistribution through fecal depositions can affect the cover and structure of vegetation (Pittarello et al. 2016a), as well as its botanical composition (Gaujour et al. 2012; Pittarello et al. 2016b). Specifically, small ruminants such as sheep and goats are better suited for grazing on steep slopes and rugged areas than are cattle, because they are lighter and more agile (Crofts and Jefferson 1999). Many authors (Calaciura and Spinelli 2008; Dostálek and Frantík 2008) observed that the reintroduction of grazing sheep within abandoned, rugged dry grasslands was sufficient to control the natural successional processes of vegetation and to support biodiversity conservation. Nevertheless, although sheep are considered very selective herbivores in dry grasslands (Calaciura and Spinelli 2008), little information is available about their feeding behaviour in semi-natural swards at the patch scale (i.e. preference among individual plant species). This aspect is a key factor for dry grassland conservation because defoliation by animals is known to modify botanical composition (Pavlů et al. 2007; Metera et al. 2010). Moreover, although stocking density (*sensu* Allen et al. 2011) can affect animal selectivity (Rosenthal et al. 2012), to our knowledge it has never been taken into account in semi-natural dry grasslands grazed by sheep. The present study aimed to examine sheep feeding preferences in semi-natural dry grasslands by integrating vegetation surveys with stocking density monitoring through modern animal-tracking systems (i.e. global positioning system (GPS) collars). Specific objectives were: (i) to understand which plant species were the most selected and avoided in the sward; (ii) to describe the spatial patterns of grazing of sheep; and (iii) to examine the influence of stocking density and plant species abundance on plant species selection.

Materials and methods

Study area and grazing system

The study was conducted in the Site of Community Interest ‘Oasi xerothermiche della Valle di Susa—Orrido di Chianocco e Foresto’ (SCI IT1110030; hereafter SCI), in the Piedmont Region, north-western Italy (45°08’N, 7°06’E). This site is representative of the changes that have occurred on mountain grasslands over the last 60

years because of agro-pastoral abandonment, and it is now subject to encroachment by shrubs (e.g. *Prunus spinosa* L.) and trees (e.g. *Quercus pubescens* Willd.) (LIFE12 NAT/IT/0008 18 Xero-grazing 2015).

The SCI is characterised by a xerothermic and sub-Mediterranean climate, with an average annual air temperature of 11°C and average annual precipitation of 670 mm (Biancotti et al. 1998). The combination of calcareous substrates and an arid and windy climate provides suitable conditions for sub-continental dry grassland vegetation communities, which are an extraordinary rarity in the Western Alps (Sindaco et al. 2008). These dry grasslands are represented by the alliances *Xerobromion erecti* (Br.-Bl. & Moor 1938) and *Stipo-Poion carniolicae* (Br.-Bl. 1949), dominated by *Stipa pennata* L., *Bromus erectus* Hudson, and *Festuca ovina* s.l.

The study area was a pasture of 120 ha at altitude 510–1260 m a.m.s.l. Slopes ranged from 0° to 80° (average 30.6°), and the mean aspect was 211°N. In 2015, almost 60 years after abandonment, the pasture was grazed by 250 Bergamasca sheep for 32 days (15 April–16 May 2015) at an average stocking rate of 0.36 sheep ha⁻¹ year⁻¹. This stocking rate was lower than those recommended (Calaciura and Spinelli 2008), but it was in equilibrium with the measured vegetation carrying capacity as defined by Cavallero et al. (2007). Moreover, it was suitable both for limiting excessive erosion of this fragile habitat by trampling and for encouraging selective grazing of sheep at the patch scale (*sensu* Bailey et al. 1996). Sheep were confined by a shepherd within herbaceous camp areas at night ('night pen', average area 818 ± 52 m²), to prevent attacks from wolves. Throughout the grazing period, night pens were moved over the pasture every two or three nights and their position was recorded with a hand-held GPS (Stonex S2; Stonex Europe, Monza, Italy). We also recorded the position of the water troughs to which the shepherd headed the flock daily.

Vegetation and plant species selection surveys

To perform vegetation surveys, 44 permanent sampling points spaced at 100-m intervals were selected on a grid basis over the pasture. At each point, the botanical composition was assessed before sheep grazing, and the selection of each plant species was evaluated after grazing.

Botanical composition was assessed by using the vertical point-quadrat method (Daget and Poissonet 1971; Lonati et al. 2009) along 12.5-m linear transects centred on the permanent sampling points. The ends of each linear transect were marked with red permanent pegs to ensure precise re-location of each vegetation survey. Along each transect, at 25-cm intervals, plant species touching a steel needle (i.e. all living plant parts) were identified and recorded. Because rare species are often missed by this method, a complete list was compiled of all other plant species within an area 2 m by 12.5 m (vegetation plot) centred on the transect line (Kohler et al. 2004). In addition, the phenological stage of all herbaceous species recorded along the transect or within the vegetation plot was noted by using the Lambertin schedule (Gorlier et al. 2012; Ravetto Enri et al. 2016). The nomenclature of vascular plants was taken from Aeschimann et al. (2004).

The percentage of species cover (SC) was calculated from the number of occurrences of each plant species recorded in each vegetation transect (i.e. number of occurrences per 50 points of vegetation measurements). An

SC value of 0.5% was attributed to all occasional species (those not recorded along the transect but within the vegetation plot) (Iussig et al. 2015b).

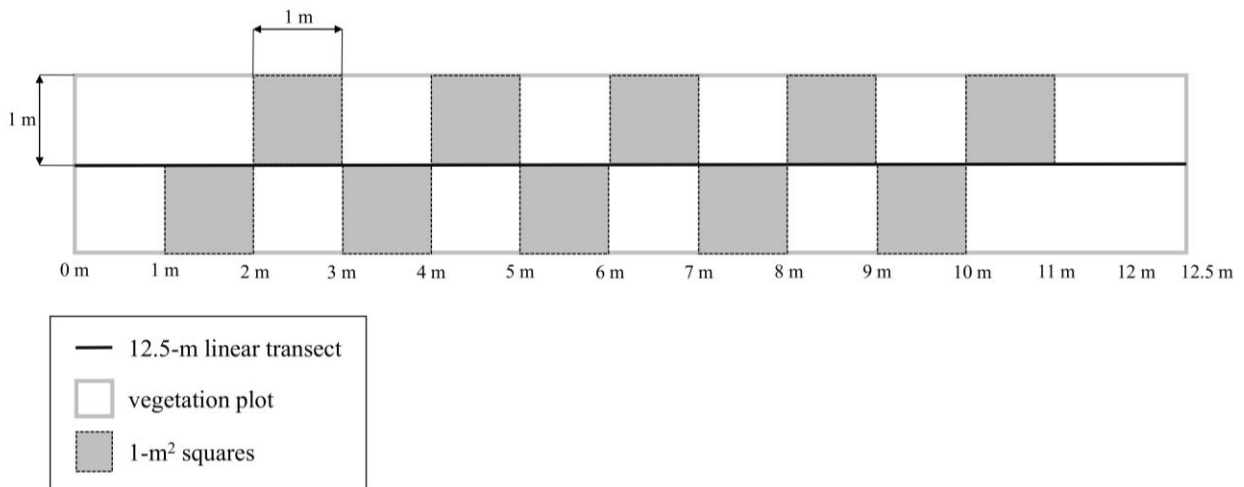
Species relative abundance (SRA) was determined in each transect according to the following equation (Daget and Poissonet 1971; Lonati et al. 2009):

$$SRA_i = \frac{SC_i}{\sum_{i=1}^n SC_i} \times 100(\%) \quad (1)$$

where SC_i is for the species i .

Plant species were classified into the following plant functional groups: graminoids (i.e. grasses and sedges), suffruticose forbs (i.e. chamaephytes, sensu Raunkiaer 1934), and herbaceous forbs. Because non-grass monocotyledons and ligneous forbs (i.e. phanerophytes) represented a minority (SC of 1.0% and 0.6%, respectively), they were not considered in the analyses. Consequently, the SRA of each functional group for each transect was also calculated. We applied the method proposed by Iussig et al. (2015a) to assess plant species selection by sheep at the patch scale. Starting at a distance of 1 m, ten 1-m² squares were alternatively laid out over both sides of each 12.5-m vegetation transect (Fig. 1).

Fig. 1. Schematic representation of vegetation surveys carried out to detect the botanical composition along the 12.5-m linear transect and the other plant species within the vegetation plot, and to assess plant species selection by sheep with ten 1-m² squares.



All species within each square were recorded and an intake value (I), ranging from 0 to 5, was visually estimated for each plant species depending on its consumption percentage: 0, species totally refused; 1, estimated consumption 1–20%; 2, estimated consumption 21–40%; 3, estimated consumption 41–60%; 4, estimated consumption 61–80%; and 5, estimated consumption >80%. Intake values were estimated after grazing by considering variations in height and the missing parts of the aboveground biomass between ungrazed and grazed plants. The consumption ratio (CR) was calculated for each plant species in each vegetation plot using the following equation (Iussig et al. 2015a):

$$CR_i = \frac{\frac{1}{n} \sum_{j=1}^n (I_{ij})}{5} \times 100 (\%) \quad (2)$$

where I_{ij} is for the species i in the square j ; and n is the number of 1-m² squares where the species i was present. The CR represents the level of selection of each plant species within each vegetation plot and it ranges from 0% (ungrazed) to 100% (totally grazed).

Sheep GPS tracking and grazing spatial patterns

Ten randomly selected sheep were fitted with GPS collars and tracked during the grazing period. The collars were GPS Model Corzo (Microsensory SLL, Fernà Nùñez, Spain), which the manufacturer reports having an average accuracy within 5 m in rugged mountain terrains. Collars were fitted one week before the beginning of the grazing period to allow sheep to become accustomed to them. Animal position was recorded at 15-min intervals so that battery life could be conserved for the entire study period.

The number of GPS fixes of the flock within a 30-m buffer area around the 44 sampling points was used to assess the stocking density in the area surrounding vegetation surveys; 30 m was a distance in which vegetation and topographic conditions were relatively homogeneous in our study area.

Data analyses

Vegetation and plant species selection by sheep

Variance normality and homogeneity assumptions for a parametric test were not met, so non-parametric Kruskal–Wallis tests (K-W tests) were used to assess differences: in SRA among plant functional groups (analysis 1); in CR among plant functional groups (analysis 2); and in CR among single plant species (analysis 3). In addition, pairwise comparisons with the Wilcoxon rank-sum test and Bonferroni P-values adjustment were carried out for analyses 1 and 2. Analyses 2 and 3 were performed only considering plant species recorded within at least 30 of the 44 vegetation plots to ensure a robust statistic inference. With R statistical software 3.2.2 (R Core Team 2015), K-W tests were carried out with the ‘kruskal.test’ function (package: stats), and the Wilcoxon rank-sum test and the Bonferroni P-values adjustment with the ‘pairwise.wilcox.test’ function (package: PMCMR).

Grazing spatial patterns and variables affecting selection of plant species by sheep

The spatial distribution of grazing sheep was assessed through univariate point-pattern analysis with grid cells of 10-m spatial resolution covering the whole study area. A raster map derived from the GPS positions of grazing sheep was used rather than raw GPS positions in order to minimise spatial autocorrelation and any precision issue with GPS accuracy (Probo et al. 2014). The grid map was transformed into a matrix with the categories of pixels of sheep presence or absence, and a mask was applied to take into account the irregular shape of the study area (space restriction effect). Through the univariate pair-correlation function $g(r)$, the grazing spatial pattern of sheep was classified as clustered, random, or regular if the $g(r)$ values were, respectively, greater than, equal to, or lower than the confidence envelopes (Wiegand and Moloney 2004). A completely random spatial pattern was chosen as the null model. The 99% confidence envelopes were computed by running 99 Monte

Carlo simulations at intervals of 1 m from 1 to 50 m, adopting a 1-m lag distance, using Programita software (Wiegand and Moloney 2004).

Counts of GPS fixes recorded within each 10-m grid cell (grazing frequency) were modelled with the slope, distance to night pens, and distance to water troughs of each grid cell to assess whether such factors explained the sheep occurrence (i.e. presence or absence of an animal within a cell grid) and the intensity of use (i.e. number of animal locations within used cell grids). Too many true zeroes were present in the data, so a two-part, mixed-effect hurdle model was used (Zuur et al. 2009). The first part comprised a logistic model between grid cells containing zero values and counts larger than zero, whereas the second part comprised a negative binomial model of counts larger than zero (Zuur et al. 2009). A binomial distribution was used for the logistic part, whereas a negative binomial was specified for the second part because count data were over-dispersed (over-dispersion was tested with the *qcc* R package, according to Scrucca 2004). Predictors were standardised (Z-scores) and generalised linear mixed models (GLMMs, Zuur et al. 2009) were performed by using the *glmmADMB* R package (Fournier et al. 2012).

The selection of each plant species by sheep was evaluated by fitting generalised linear models (GLMs). The CR of each plant species recorded within at least 30 of the 44 vegetation plots was modelled with the animal stocking density (i.e. number of GPS fixes within 30-m buffer), the SC of the subject species, and the SC of the other most abundant species associated with the subject species, i.e. plant species whose cumulative average SRA was >70%. In more detail, the average SRA of plant species related to each subject species was calculated considering only the vegetation plots in which each subject species was found. Therefore, within each model, the most abundant plant species associated with the subject species could be partially different (see Supplementary materials table 1, available at the journal's website). The SC values of the most abundant plant species were used instead of their SRA because they represented an independent measure of plant abundance within the same plot. Moreover, the use of SC as a predictor in the models allowed for the influence of plant species abundance and the abundance of dominant neighbouring species on the sheep feeding behaviour (Iussig et al. 2015a). The dependent variable was proportional data ranging from 0% to 100%, so a binomial distribution was specified. Predictors were standardised (Z-scores) to analyze the size of each effect by comparing model parameter estimates (β coefficients). A stepwise procedure based on the Akaike information criterion (AIC) was implemented by using the 'step-AIC' function (R package: MASS) (Venables and Ripley 2002). All geographical analyses were conducted with Quantum GIS version 2.10 (2015, <http://www.qgis.org/en/site/>) and SAGA (Conrad et al. 2015).

Results

Vegetation and plant species selection by sheep

Within the study area, 191 plant species were recorded (Supplementary materials, table 2). Graminoid species were significantly dominant compared with suffruticose and herbaceous forbs (Table 1). In particular, the most

abundant graminoids were *S. pennata* (average SRA 13.6%), *B. erectus* (13.2%), *F. ovina* s.l. (13.0%), and *Carex humilis* Leyser (7.1%).

Table 1. Results of the Kruskal–Wallis test ($\chi^2 = 92.8$, d.f. = 2, $P < 0.001$) of the differences in average specific relative abundance (SRA) among plant functional groups. Different letters denote differences between values, found by multiple comparisons with Wilcoxon rank-sum test and Bonferroni P-values adjustment

Plant functional groups	SRA \pm SE
Graminoids	67.0 \pm 1.4 ^c
Herbaceous forbs	13.0 \pm 0.7 ^a
Suffruticose forbs	18.5 \pm 1.2 ^b

Eighteen plant species were found within at least 30 of 44 vegetation plots: nine were graminoids, five were herbaceous forbs, and four were suffruticose forbs (Supplementary materials). On average, graminoids were the most selected species by sheep. No differences in consumption were detected between suffruticose and herbaceous forbs (Table 2).

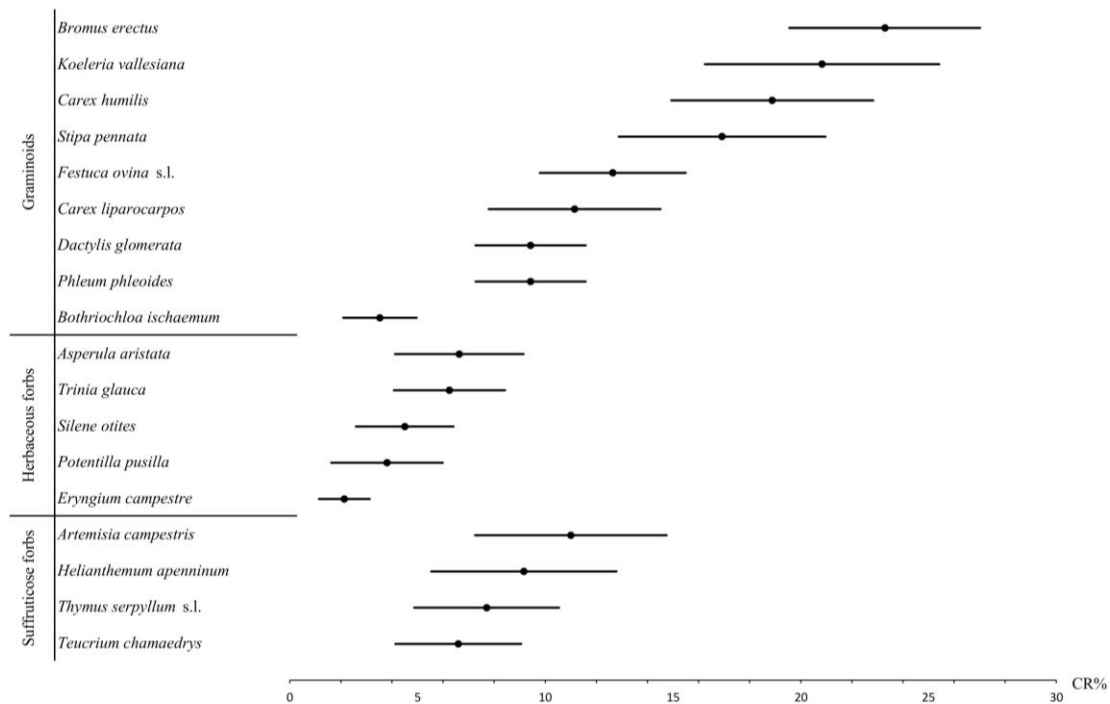
Table 2. Results of the Kruskal–Wallis test ($\chi^2 = 79.18$, d.f. = 2, $P < 0.001$) of the differences in consumption ratio (CR) among the 18 plant species found within at least 30 of 44 vegetation plots and grouped in plant functional groups. Different letters denote differences between values, found by multiple comparisons with Wilcoxon rank-sum test and Bonferroni P-values adjustment.

Plant functional groups	CR \pm SE
Graminoids	13.9 \pm 1.2 ^b
Herbaceous forbs	4.6 \pm 0.9 ^a
Suffruticose forbs	8.4 \pm 1.6 ^a

Plant species were selected with a significantly different intensity by sheep (K-W test, $\chi^2 = 130.14$, d.f. = 17, $P < 0.001$), and variation of the average CR within each plant functional group was noticeable (Fig. 2).

Bromus erectus, *Koeleria vallesiana* (Honckeny) Bertol., *C. humilis*, *S. pennata*, *F. ovina* s.l., *Carex liparocarpos* Gaudin, and *Artemisia campestris* L. were the most preferred species, because they were considerably consumed by sheep (i.e. CR >10%). The remaining plant species were rarely consumed (CR <10%).

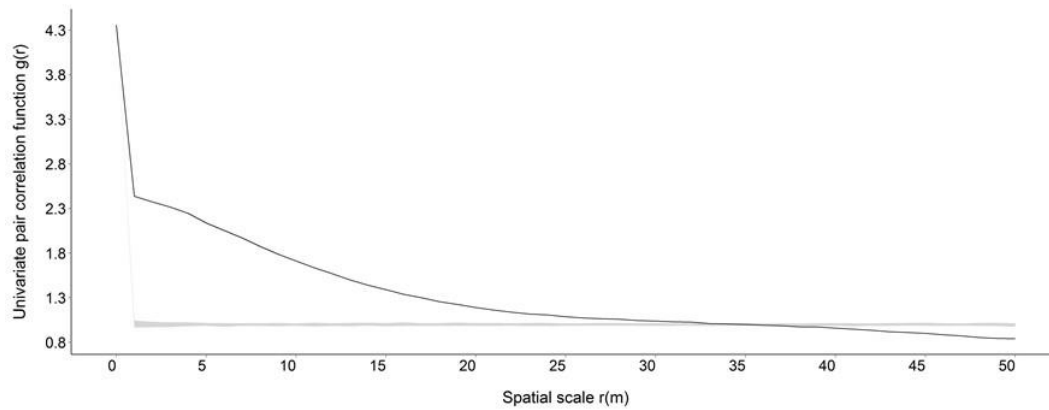
Fig. 2. Average consumption ratio (CR) \pm standard error of the mean of the 18 species found within at least 30 of 44 vegetation plots. Species are grouped into plant functional groups.



Effects of stocking density and vegetation variables on selection of plant species by sheep

In total, 8855 spatial locations were recorded by eight of 10 GPS collars during the grazing period (two collars failed). The number of GPS spatial locations was heterogeneously distributed within the study area, ranging from 0 to 55 GPS fixes within the 10-m grid cells. The spatial distribution of sheep herded by the shepherd was aggregated up to a distance of ~32 m and significantly differed from the random spatial pattern of the null model (Fig. 3). Over that threshold, sheep were more regularly distributed. In other words, sheep grazed with a clustered spatial pattern within areas with a radius of ~32 m, whereas over that distance sheep were less aggregated.

Fig. 3. Univariate analysis of the spatial pattern of grazing sheep within the study area. The black line indicates the pair-correlation function $g(r)$ and grey shaded areas encompass the non-significant (i.e. random) distribution constructed at 99% confidence level (99 Monte Carlo simulations) of the null model.



According to β coefficients of GLMs, both sheep occurrences and intensity of use (stocking density) were affected by the distance to night pens ($P < 0.001$), to gentler terrain ($P < 0.001$), and to water troughs ($P < 0.001$) (Table 3). Distance to night pens influenced sheep-grazing spatial patterns more than slope and distance to water troughs.

Table 3. Hurdle model results showing the effects of distance to night pens, slope, and distance to water troughs on the spatial use by sheep during grazing. Stand. β indicates that each coefficient of the variables (β) has been standardised, that is measured from their means in units of standard deviations. SE, Standard error of standardised coefficients (β)

	Sheep occurrences (Binomial part)			Sheep intensity of use (Negative binomial part)		
	Stand. β^1	SE ²	<i>P</i> -value	Stand. β	SE	<i>P</i> -value
Intercept	-1.94	0.04	<0.001	0.81	0.02	<0.001
Distance to night pens	-1.68	0.04	<0.001	-0.70	0.02	<0.001
Slope	-0.31	0.03	<0.001	-0.23	0.02	<0.001
Distance to water troughs	-0.31	0.03	<0.001	-0.06	0.02	<0.001

¹Stand β indicates that each coefficient of the variables (β) has been standardized, that is

measured from their means in units of standard deviations.

²SE is of standardized coefficients (β).

Stocking density was an important predictor ($P < 0.05$) for explaining the CR for nine plant species (*B. erectus*, *K. vallesiana*, *C. humilis*, *S. pennata*, *F. ovina s.l.*, *C. liparocarpos*, *A. campestris*, *Thymus serpyllum s.l.*, and *Teucrium chamaedrys* L.), showing a positive relation with the CR values (Table 4). Conversely, the SC of

these nine species and the SC of the other most abundant species associated with them were not important predictors (Table 4).

Table 4. Beta coefficients (β) for stocking density and average percentage of plant species cover (SC) affecting the consumption ratio of the 18 plant species found within at least 30 of 44 vegetation plots in the study area in stepwise GLM models. AIC, Akaike information criterion. Plant species are presented by plant functional groups. * $P < 0.05$; ** $P < 0.01$; * $P < 0.001$; n.s., not significant ($P > 0.05$)**

	Plant species (average consumption ratio)	Stocking density	SC ¹ Stipa pennata	SC Helianthemum apenninum	SC Carex humilis	SC Festuca ovina s.l.	AIC
Graminoids	Bromus erectus (23.3)	0.80 *		-0.48 n.s. ²			33.33
	Koeleria vallesiana (20.8)	0.81 *					21.70
	Carex humilis(18.9)	0.87 *					17.32
	Stipa pennata (16.9)	1.11 **					17.02
	Festuca ovina s.l. (12.6)	1.01 *					12.88
	Carex liparocarpos (11.1)	1.34 *					10.60
	Dactylis glomerata (9.4)						8.53
	Phleum phleoides (9.0)	1.19 n.s.			-1.20 n.s.	-0.89 n.s.	24.19
	Bothriochloa ischaemum (3.5)						4.59
Herbaceous forbs	Asperula aristata (6.6)	0.76 n.s.					10.57
	Trinia glauca (6.3)	0.83 n.s.					11.38
	Silene otites (4.5)						11.24
	Potentilla pusilla (3.8)						30.28
	Eryngium campestre (2.1)						3.60
Suffruticose forbs	Artemisia campestris (11.0)	1.36 *					14.79
	Helianthemum apenninum (9.2)	0.80 n.s.	1.61 n.s.				12.13
	Thymus serpyllum s.l. (7.7)	1.44 *			-1.39 n.s.		17.61
	Teucrium chamaedrys (6.6)	1.14 *					12.40

¹SC percentage of plant species cover

²n.s. indicates not significant ($P > 0.05$)

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

For the remaining nine plant species (*Asperula aristata* L., *Trinia glauca* L. Dumort, *Silene otites* L. Wibel, *Potentilla pusilla* Host, *Eryngium campestre* L., *Dactylis glomerata* L., *Phleum phleoides* L. Karsten, *Bothriochloa ischaemum* L. Keng, and *Helianthemum apenninum* L. Miller), characterised by an average CR <10%, stocking density was not a significant predictor ($P > 0.05$) of the consumption ratio.

Discussion

The noticeable dominance of graminoids, i.e. *F. ovina* s.l., *S. pennata*, and *B. erectus*, within the dry grasslands of the SCI can be considered a consequence of the long-lasting abandonment of this area, as also reported by many authors for dry grasslands. For example, several years after the cessation of agro-pastoral activities, Malatinszky et al. (2008) detected a dominance of *S. pennata* and species related to the genus *Festuca* on the driest and steepest zones of dry grasslands, and many other authors reported a dominance of *B. erectus* (Wells 1971; Hegedüšová and Senko 2011; Maccherini and Santi 2012) after abandonment.

Conversely, as observed by Schwabe et al. (2013) over a 12-year study, the regular exploitation of abandoned and graminoid-dominated grasslands can favour a decrease in graminoids and an increase in non-graminoid species. The combined actions of defoliation and trampling by sheep contribute to reducing the litter layer and supporting the diversity of all plant species and of non-graminoid species, leading to a more botanically balanced vegetation community (Schwabe et al. 2013). In our study area, graminoids (e.g. *B. erectus*, *K. vallesiana*, *C. humilis*, *S. pennata*, and *F. ovina* s.l.) were generally preferred by grazing sheep over herbaceous and suffruticose forbs, and this result may represent the starting-point of a balancing process of botanical composition.

Sheep exerted a marked selection among single plant species, and within each plant functional group (e.g. *Bothriochloa ischaemum* L. Keng was almost completely refused within graminoids). Although sheep are considered grazers (sensu Hofmann 1989) and they are relatively non-discriminatory among plant species at the patch scale (Gordon 2003), our results highlighted that in semi-natural dry grasslands they exert a selective foraging behaviour, as also pointed out by other authors (Calaciura and Spinelli 2008; Catorci et al. 2012). Rook et al. (2004) indicated that sheep can behave as grazers (feeding mainly on graminaceous plants) or intermediate feeders (feeding on a mixture of woody and non-woody dicotyledonous and graminaceous plants) depending on botanical composition. They can be more selective when the species with high quality or with desirable characteristics are rare (i.e. low percentage SC) or difficult to harvest within the pasture. Moreover, in our study area, the low average stocking density encouraged a selective foraging by sheep by maintaining a high forage-to-animal ratio, as also indicated by Provenza et al. (2003).

Within the study area, the spatial distribution of sheep herded by the shepherd was strongly heterogeneous as sheep assumed a clustered pattern, with a more intense use of sites in proximity of night pens, gentler terrains, and water troughs than in less accessible areas. Such spatial pattern is a common feature in extensive grazing systems in mountain areas (Güsewell et al. 2005). Sheep usually concentrate within flat areas because they can maximise the average energy intake rate through optimal foraging (MacArthur and Pianka 1966), but in our study conditions, the arrangement of night pens by the shepherd was the main factor determining the sheep spatial aggregation. If correctly managed, this pastoral practice can provide some important benefits to grassland habitats by exerting a very high grazing pressure both within the night pen and in the surrounding area. Tocco et al. (2013) and Pittarello et al. (2016b) demonstrated that the implementation of temporary night camp areas for cattle positioned in the sub-alpine belt (1800–2200 m a.m.s.l.) was a valuable tool in restoring grassland

vegetation and increasing plant diversity, herbage mass, and forage quality. Therefore, the strategic arrangement of night pens in dry grasslands may represent not only a practice to prevent attacks from wolves, but also a solution to enhance the botanical composition, plant diversity, and sward forage quality.

The heterogeneity of stocking density over the study area allowed the testing of the relationships between the stocking density and the CR of single plant species. Stocking density affected the consumption of certain plant species, regardless of the abundance of dominant neighbouring species, underlying the importance of grazing management as a tool to condition the foraging behaviour of sheep. In general, plant species with an average CR >10% were selected proportionally to stocking density. In this group of plant species, *B. erectus* and *K. vallesiana*, which are generally considered medium-quality forage species, were the most selected (Molinillo et al. 1997). Species belonging to the genus *Carex* were also noticeably selected by sheep, in particular *C. humilis*. Even though Cyperaceae species are usually considered plants of low palatability owing to the accumulation of silica in vegetation tissues (Heady 1964; Ollendorf 1992), Carnelli (2001) determined that *Carex* species growing in the Alps have a low biogenic silica content, and this may explain their selection by sheep. In addition, *A. campestris* was among the preferred species, even though it is known as a toxin-containing plant (Provenza et al. 2003; Kazemi et al. 2009). In general, given that nutrients facilitate detoxification processes and forage mixture can mitigate toxicity, herbivores graze to accomplish a balanced intake of nutrients by mixing their diet rather than avoiding certain species containing toxins (Provenza et al. 2003). Conversely, the least selected plant species, whose CR did not show any relation with stocking density, were in general avoided even within overused areas. For instance, *E. campestre* was the least consumed plant because it is a spiny species, whereas plants with a rosette or prostrate form (e.g. *S. otites* and *P. pusilla*) were barely grazed owing to the difficulty in harvesting by sheep. Surprisingly, *D. glomerata*, which is considered a good forage plant species (Allen et al. 1995), was poorly selected by sheep; however, such species can have a wide range of digestibility rates depending on the ecotype (Clark and Santhirasegaram 1972). Probably, as pointed out for other grass species (Utrillas and Alegre 1997), dry conditions typical of this area may have led to a thickening of cell walls and, consequently, to decreased palatability.

Conclusions

In this study, we assessed that sheep managed with a low-intensity grazing pressure in abandoned dry grasslands exerted selection of specific plant species. Grass and *Carex* species were generally more selected than forbs. Nevertheless, noticeable differences in selection of plant species were assessed within each plant functional group, with some species scarcely consumed because of their habit.

For many species, consumption at the patch scale was proportional to the stocking density. Therefore, management of grazing sheep may become a tool to promote the consumption of certain plant species and, consequently, affect grassland botanical composition in a medium–long-term period. A long-lasting implementation of grazing with a stocking rate in equilibrium with the vegetation carrying capacity may lead to

a decrease in graminoid abundance in favour of an increase in non-graminoid abundance, determining a more balanced botanical composition with higher plant diversity levels.

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Supplementary material

Supplementary 1. List of independent variables used in the Generalized Linear Model (GLM) for each plant species (i.e. subject species) found at least within 30 out of 44 vegetation plots (Table 4). The dependent variable of each model is the Consumption Ratio (CR) of subject species. Variable codes: **CR** = Consumption Ratio; **SC** = Percentage of Species Cover. Species code (in subscript): **AA** = *Asperula aristata*, **AC** = *Artemisia campestris*, **BE** = *Bromus erectus*, **BI** = *Bothriochloa ischaemum*, **BR** = *Brachypodium rupestre*, **CH** = *Carex humilis*, **CL** = *Carex liparocarpos*, **DG** = *Dactylis glomerata*, **EC** = *Eryngium campestre*, **FO** = *Festuca ovina* s.l., **FP** = *Fumana procumbens/ericoides*, **HA** = *Helianthemum apenninum*, **KP** = *Koeleria pyramidata*, **KV** = *Koeleria vallesiana*, **PO** = *Potentilla pusilla*, **PP** = *Phleum phleoides*, **SO** = *Silene otites*, **SP** = *Stipa pennata*, **TC** = *Teucrium chamaedrys*, **TG** = *Trinia glauca*, **TS** = *Thymus serpyllum* s.l.

Supplementary 2. List of the plant species recorded in botanical surveys, with the corresponding family, plant functional group, average phenology, average Species Relative Abundance (SRA), average Consumption Ratio (CR), and number of species occurrences out of 44 vegetation surveys. Species showing a species occurrence equal to "0" were those found within the vegetation plots but not within the 1-m² squares used to assess plant species selection by sheep. The plant species found at least within 30 out of 44 vegetation plots are highlighted in boldface. Species nomenclature follows Aeschimann et al. (2004).