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Foraging behaviour of domestic herbivore species grazing on heathlands associated with improved pasture areas

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Foraging behaviour (grazing time, diet selection) and overlap in vegetation use between five beef cows, five mares, 32 ewes and 32 does, suckling their offspring born in late winter–early spring, was compared across the grazing season (May–December). Animals were managed in mixed grazing on heather–gorse vegetation communities with an adjacent area (24%) of ryegrass–clover improved pasture. Equines spent more daily time grazing than the other species in all seasons, averaging 610 min/day compared to 530, 481 and 496 min/day spent by cattle, sheep and goats, respectively. Seasonal changes in both grazing behaviour and diet selection were observed. Generally, cows, mares and ewes spent most of their grazing time on the improved pasture (0.77, 0.73 and 0.59, respectively), whereas goats spent more time grazing on shrublands (0.70). All species concentrated their diurnal grazing activity in the morning and late afternoon, whilst resting occurred mainly in the middle of the day. Herbaceous species were the main component in the diets of cattle, equines and sheep across the whole grazing season, whereas for goats this predominance was only observed during the spring. Cattle, sheep and equines turned to browse only when pasture availability decreased. Cattle and sheep tended to select heather in moderate amounts whereas they avoided gorse across the grazing season. By contrast, horses seemed to be able to deal with the gorse spiny shoots and consumed it in the autumn (averaging 0.29). The goats' diet at the end of the grazing season was mainly composed of heather species, reaching 0.81 in November. Degree of grazing overlap between livestock species was influenced by the animal species and also varied across the grazing season. The greatest similarity indexes (KSI) based on grazing time and diet composition data were found between cattle and equines (0.86) and between cattle and sheep (0.94), whereas the combination of goats with the other animal species resulted in lower KSI values. Dietary overlap decreased as the improved pasture availability decreased during the grazing season. Results suggest that the success of management strategies (type and composition of the flock, mixed or sequential, continuous or seasonal) in these heterogeneous vegetation conditions will depend on plant species characteristics and its proportions. Grazing management options should be based on production (animal performance) or environmental goals (biodiversity, control of shrub encroachment, reduction of fire risk, etc.) previously defined. Goats proved to be

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the best complement to the other animal species for an efficient use of natural vegetation. Nevertheless, studies should be carried out to assess the interactions between grazing behaviour and animal performance in these particular vegetation conditions.

1. Introduction

Heathlands cover large areas in the Northwest of the Iberian Peninsula, mostly marginal and poor lands of acidic soils, constituting a poor resource for animal production due to its low nutritive value (Celaya et al., 2007, 2011; Osoro et al., 1999, 2007). Although in central/north of Europe the conservation of this ecosystem is seriously endangered (Habitats Directive 92/43/EEC, OJ, 1992) as a result of inadequate livestock farming systems and eutrophication (Diemont et al., 1996; Webb, 1998), it is currently widespread in the north of Spain and Portugal as a consequence of the abandonment of agricultural and livestock managements since the 1950s and by frequent wildfires (Rosa García et al., 2013). This type of vegetation is the main fuel of fires observed in these areas, causing serious environmental problems as well as direct economic losses associated with the cost of prevention and extinction of fires. The establishment and development of animal production systems on these less favoured areas could provide an environmental and economic benefit, contributing to the improvement of life conditions of rural populations. However, previous studies (Ferreira et al., 2011; Osoro et al., 2011) indicated that adjacent areas of improved pasture are necessary to meet the animals' nutritional requirements and, consequently, to achieve the sustainability of the systems.

Due to different eco-physiological adaptations (mouth and dental anatomy, digestive strategy), domestic herbivores species exploit the available plant resources differently (Hofmann, 1989; Illius and Gordon, 1993). Consequently, depending on the available quantity and nutritive value of vegetation across the grazing season, it is expected that animals will adapt their foraging behaviour (Vallentine, 2001). Previous studies conducted in the Cantabrian heathland areas (Celaya et al., 2007, 2008) showed clear differences in the foraging behaviour among domestic ruminant species managed in these areas. Cattle and sheep seem to be highly competitive for the more palatable herbaceous species of higher nutritional quality, whilst goats seem to be the best complement for them, combining high quality pastures with woody vegetation such as heathlands, allowing a more efficient and diverse use of the available feed resources (Celaya et al., 2007).

In recent years, the number of equines in these areas has increased mainly due to their ease of management and low risk of predation. However, the foraging behaviour of equines in these particular vegetation conditions is not known. In this way, information on diet selection is essential to set the best management options to promote a more efficient utilization of the existing vegetation leading to an increase in the profitability of the production system. The aim of this work was to compare the grazing behaviour, diet selection and diet overlap of equines with domestic ruminant species (cattle, sheep and goats) and to assess how these variables vary across the grazing season.

2. Material and methods

2.1. Experimental site

The trial was carried out in 2004 on a single plot of 22.3 ha, located at 900–1000 m a.s.l. at the Carbayal Research Station, Sierra de San Isidro, Illano, western Asturias, NW Spain (43° 19′ N, 6° 53′ W). According to meteorological data recorded in the experimental site from 2002 to 2011, mean temperatures range between 4.4 °C in January and 16.0 °C in August, with an annual mean temperature of 9.8 °C. Annual rainfalls average 1500 mm occurring mainly from October to March. Daily mean temperature and rainfalls during the experimental grazing season are shown in Fig. 1. June was somewhat hotter and drier than usual, while August and October were especially wet. The soils are shallow, acidic (pH around 4) and deficient in most nutrients, particularly phosphorus, calcium and magnesium.

Natural vegetation covered 76.2% of the plot, and consisted mostly (67.8%) of a short (less than 50 cm high) heather–gorse shrubland community, dominated by heather species (*Erica umbellata*, *Erica cinerea*, *Calluna vulgaris*) and gorse (*Ulex gallii*), a thorny and woody legume. Tall scrublands (up to 2 m high) dominated by *Erica australis* subsp. *aragonensis* and *Erica arborea* were more sparsely present (7.8%), as well as a small pinewood (0.5%) of Scots pine (*Pinus sylvestris*). The rest of the plot area (23.8%) consisted of improved pasture, established in 1999 by soil breaking-up, dressing, and sowing of perennial ryegrass (*Lolium perenne* cv 'Phoenix'), hybrid ryegrass (*L. x hybridum* cv 'Dalita') and white clover (*Trifolium repens* cv 'Huia'), and reseeded again in 2002 with the same mixture.

2.2. Animals and management

Five Asturiana de los Valles beef cows (490 ± 67.8 kg live weight (LW)), five mature native mares (383 ± 69.7 kg LW), 32 Gallega and Lacha crossed ewes (42 ± 8.9 kg LW) and 32 Cashmere does (34 ± 6.4 kg LW) were managed together in a mixed herd under continuous grazing from late April to late November, to have the same opportunities for diet selection, shelter, etc.

Offspring were born in late winter–early spring and reared outdoors with their mothers until the experimental grazing season began (i.e., 2–3 months of age) on improved ryegrass–clover pastures with accessible heathland areas. All animals were drenched with ivermectin (Oramec®, Merial Lyon, France) against gastrointestinal nematodes 2 weeks before turn out.

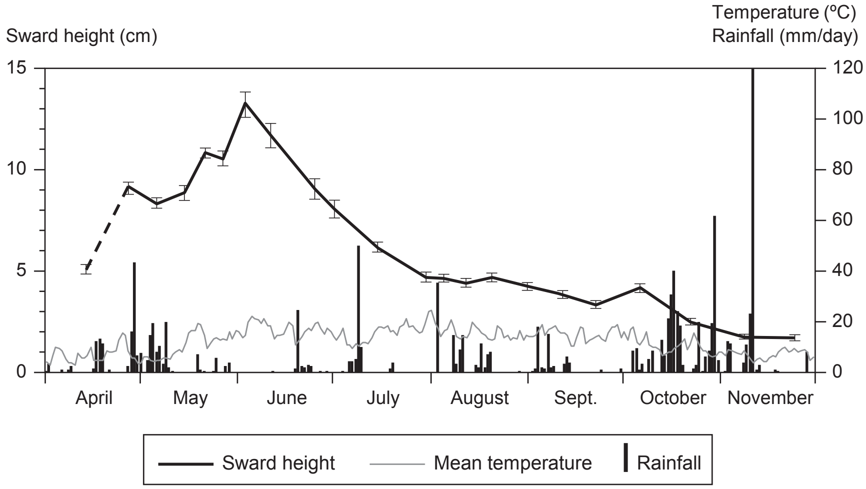

Fig. 1. Sward height in the improved pasture area and daily mean temperatures and rainfalls across the grazing season.

2.3. Vegetation measurements

Chemical composition of the main vegetation components (heather, gorse and herbaceous plants occurring in the heathland area, and improved pasture, i.e. *L. perenne* and *T. repens*), harvested across the grazing season, was analysed following the procedures of the Association of Official Analytical Chemists (AOAC, 2006) for ash and nitrogen (N). Crude protein (CP) was calculated as $N \times 6.25$. Neutral-detergent fibre (NDF), acid-detergent fibre (ADF) and acid-detergent lignin (ADL) were analysed by the methods of Van Soest et al. (1991).

Sward surface height was measured weekly by recording at 200 random points on the improved pasture area using the HFRO swardstick (Barthram, 1986) to assess herbage availability. Botanical composition was assessed in June by recording the plant species, phenological state (green or dead) and height at 300 random hits both in the improved pasture and in the short heathland.

2.4. Grazing behaviour and diet selection

The time spent grazing by each animal species on each vegetation type (short heathland, tall heathland, pinewood, ryegrass–clover pasture) was determined by recording the grazing activity of adult animals every 15 min from dawn to dusk during two consecutive days in 6 occasions across 2004 (May, June, July, August, October, and November). Diet selected by each animal species was estimated using the *n*-alkane markers (Dove and Mayes, 1991). Faecal grab samples were collected across the grazing season (May, June, July, September, October, and November). Since faeces from individual ewes and goats were seldom enough quantity for alkane analysis, samples from all animals were randomly pooled to obtain 6–10 samples for each species. In the case of cattle and equines, samples of each animal were collected individually.

Simultaneously, samples of the main plant components, i.e. leaves and/or green shoots of short heather (including *E. umbellata*, *E. cinerea* and *C. vulgaris*), tall heather (*E. australis* and *E. arborea*), gorse, heath grasses (mostly *Pseudarrhenatherum longifolium* and *Agrostis curtisii*), and improved pasture (including ryegrass and clover) were collected. All samples were stored at −20 °C and then freeze-dried and milled prior to analytical procedures. The alkanes (from C_{21} to C_{36}) were extracted using the method of Mayes et al. (1986) as modified by Oliván and Osoro (1999), and were quantified by gas chromatography using C_{22} and C_{34} as internal standards. Proportions of the plant components in the diet were estimated using a least-squares procedure which minimises the discrepancies between the observed concentrations of each *n*-alkane (C_{25}–C_{33}) in the faeces and the estimated proportions of plant components in the diet (Dove and Moore, 1995). Alkanes C_{21}, C_{23}, C_{24}, C_{35} and C_{36} were not used for diet composition calculations due to their very low concentrations in all plant species. Before diet composition calculations, alkane faecal concentrations of the ruminant species were corrected for their incomplete faecal recovery using data calculated in previous validation studies with cows (Ferreira et al., 2007a), ewes (Ferreira et al., 2007b) and goats (Ferreira et al., 2005). By contrast, alkane faecal concentrations of equines were not adjusted as previous results (Ferreira et al., 2007a) showed that, in this animal species, faecal recovery of these markers is unaffected by carbon-chain length.

The degree of selection–rejection for a determined dietary component (heather, gorse or herbaceous plants) was assessed by calculating the Jacobs' modification of Ivlev's electivity index (Jacobs, 1974) as $S_i=(c_i-a_i)/(c_i+a_i-2c_ia_i)$, where c_i is the proportion of *i* plant component in the diet, and a_i is the proportion of *i* plant component available in the field. The index ranges from −1 (not used) to +1 (exclusively used), with 0 indicating proportional use to its availability.

The overlap in vegetation use (grazing time) and diet composition between animal species was estimated by the Kulczynski similarity index as $KSI=\Sigma 2c_i/\Sigma(a_i+b_i)$, where c_i is the lesser proportion of *i* vegetation type or dietary component in the two animal species, and (a_i+b_i) is the sum of the proportions of each vegetation type/

component in both species. This index ranges from 0 (no overlap) to 1 (total match).

2.5. Statistical analyses

Differences in nutritive quality between plant components (heather, gorse, heath grasses and improved pasture) were analysed by one-way analysis of variance (ANOVA). Tukey HSD test was used to examine pair-wise comparisons between plant components.

Overall diet composition data set across the grazing season could not be normalized nor the variances equalized by transformation due to equal values within groups (variance=0) found at several sampling dates. The same occurred with selectivity data. Thus, they were analysed for each sampling date to examine the differences between cows, mares, ewes and goats' diets, using the non-parametric Kruskal–Wallis test. Comparisons between pairs of livestock species were made applying the Mann–Whitney U test. All analyses were performed using the program JMP version 7.0.

3. Results

3.1. Vegetation availability

Short heathland was dominated by heather species (63.0% cover), mostly *E. umbellata* (53.3%), while other shrubs including gorse accounted for 19.3% cover. Herbaceous cover was 9.7%, with the grasses *P. longifolium* and *A. curtisii* as the most abundant, while the rest was dead matter (8.0%). Mean canopy height in the short heathland was 22.9 cm.

The improved pasture was composed of perennial ryegrass (56.7%), white clover (20.7%) and native plants (16.7%), mostly grasses such as *Agrostis capillaris*. Dead foliage accounted for 6.0%. Mean sward surface height in the improved pasture area across the grazing season was 5.9 cm, although there were strong differences between seasons (Fig. 1). Mean sward height during spring was 10.3 cm, decreasing to 5.2 cm during summer and to 2.7 cm during autumn.

3.2. Chemical and alkane composition of vegetation

Table 1 shows the chemical composition of the main plant species and groups across the grazing season. As expected, herbaceous components (improved pasture and native grasses) were characterized by lower ($P<0.05$) fibre components (NDF, ADF and ADL) than the woody species (gorse and heather), and greater ($P<0.05$) CP content (mean of 153 vs. 98 g/kg DM, respectively). Within the herbaceous species, the improved pasture showed greater CP (203 g/kg DM) content and lower NDF (468 g/kg DM) and ADF (256 g/kg DM) content than native heath grasses (103, 697 and 363 g/kg DM, respectively). The ADL content was particularly great for heather (mean of 360 g/kg DM), whereas the CP content of gorse was on average greater than that of heath grasses (125 vs. 103 g/kg DM, respectively). In general, the nutritive value of all plant species and groups tended to decrease as grazing season advanced, i.e. lower CP content and greater cell wall components.

Results also showed large differences in the alkane profiles between plant species and groups. Improved pasture, heath grasses and gorse showed low alkane concentrations, with C_{31} the alkane with the greatest concentration. By contrast, heather contained the greatest ($P<0.05$) total alkane concentration, with several alkanes exceeding 50 mg/kg DM (Table 1).

3.3. Grazing time

Differences between animal species in daily grazing time and in the proportion of grazing time spent on each vegetation type across the grazing season are illustrated in Fig. 2. Equines spent more daily time grazing than the other species in all seasons, averaging 610 min/day compared to 530, 481 and 496 min/day spent by cattle, sheep and goats, respectively. Equines and goats had the greatest daily grazing time in spring (May–June: 720 and 558 min/day, respectively), whereas in cattle and sheep it was in summer (July–August, 585 min/day) and in autumn (October–November, 553 min/day), respectively. Autumn sampling dates showed shorter grazing periods for cattle and goats (498 and 442 min/day, respectively), whilst for equines and sheep this was observed in the summer.

The proportion of grazing time spent on each vegetation type (short heathland, tall heathland or ryegrass–clover pasture) differed among animal species and grazing seasons. On average, cows, mares and ewes spent most of their grazing time on the improved ryegrass–clover pasture (0.77, 0.73 and 0.59, respectively), especially in the spring sampling dates. By contrast, goats spent more time grazing over shrublands, averaging 0.70 of the grazing time (including short and tall heathland), increasing from an average of 0.47 in the spring to 0.81 in autumn sampling dates. Although equines and sheep also increased their grazing time on shrublands across the grazing season, in the case of equines this behaviour was more evident after the summer season. Regardless of the grazing season, almost 0.80 of the grazing of cattle was spent on improved ryegrass–clover pasture.

Results on animals' diurnal grazing pattern showed large differences between animal species and grazing season (Fig. 3) as a result of variable availability of the improved pasture, weather conditions and daylight hours. In spring and summer seasons, all species concentrated their diurnal grazing activity at the beginning and end of the days, whereas the resting times were mainly observed in the middle of the day. Moreover, it seemed that in these periods of the day grazing activity was mainly on shrublands, especially when improved pasture availability was lower (i.e. summer and autumn seasons). Grazing time of ewes on heathlands at the end of the day could be explained by the route they take to their resting area which was located in the highest area of the plot, where heathlands predominate. Results indicated that goats' diurnal behaviour at the end of the grazing season was more variable compared to the other animal species (Fig. 3c).

Table 1
Chemical composition (g/kg DM) and alkane content (mg/kg DM) of the main vegetation components found in partially improved heathlands across the grazing season.

Species	Season	CP	NDF	ADF	ADL	C_{25}	C_{26}	C_{27}	C_{28}	C_{29}	C_{30}	C_{31}	C_{32}	C_{33}
Improved pasture	May	205	389	219	17	12	4	30	12	127	16	220	10	95
	June	159	453	253	26	16	4	36	11	141	13	199	7	59
	July	178	485	274	33	13	3	30	9	147	14	221	6	31
	September	196	625	322	77	9	2	18	5	93	10	199	6	65
	October	264	358	216	46	11	7	32	15	108	20	191	15	147
	November	215	497	253	65	11	5	30	11	69	13	176	9	100
Native grasses	May	158	489	254	26	12	5	32	13	119	17	205	11	90
	June	132	671	318	38	17	4	25	9	59	11	129	8	60
	July	124	696	334	45	17	4	25	9	62	11	132	8	60
	September	50	793	455	45	15	6	29	15	131	20	278	10	74
	October	75	779	414	39	9	9	28	15	73	14	298	7	76
	November	80	751	403	35	9	5	20	9	57	12	167	7	55
Gorse	May	183	551	420	158	5	4	36	15	84	15	213	6	10
	June	183	660	513	193	3	2	19	8	67	17	309	10	10
	July	104	667	526	205	2	2	7	4	36	10	183	4	5
	September	76	695	540	209	5	2	13	6	43	9	143	5	8
	October	104	644	496	220	3	3	12	13	52	12	146	5	7
	November	101	649	503	236	2	4	14	18	47	11	116	4	6
Heather	May	96	543	405	326	26	10	84	20	359	52	1011	75	487
	June	79	539	456	330	37	11	116	25	701	71	1223	80	518
	July	67	580	444	318	10	5	42	10	245	34	803	58	427
	September	57	686	506	352	9	5	32	14	165	32	784	67	517
	October	63	615	519	367	7	4	27	8	138	27	599	53	377
	November	64	640	537	467	7	7	24	11	144	29	627	51	354

CP: crude protein; NDF: neutral detergent fibre; ADF: acid detergent fibre; ADL: acid detergent lignin.

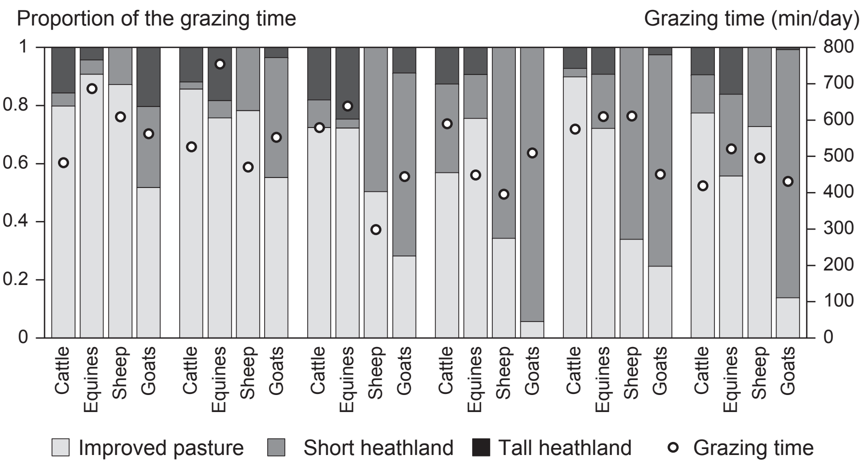

Fig. 2. Proportion of the grazing time spent on each vegetation type by domestic herbivore species grazing on a gorse-heathland with 24% of improved pasture.

3.4. Diet composition

Diets selected by each animal species during the grazing season are shown in Table 2. Herbaceous species were the main dietary component of cattle, equines and sheep across the whole grazing season, whereas for goats this predominance was only observed during the spring sampling dates, averaging 0.75. The greatest proportion of herbaceous species was observed in the diet of cattle and equines in spring (1.00) and the lowest in goats in November (0.19). Whilst in cattle, equines and goats, the proportion of this vegetation component decreased ($P<0.001$) across the grazing season, for sheep the lowest selection of herbaceous species was observed in summer, which was followed by an increase ($P=0.001$) in autumn.

Consumption of gorse was mainly observed in goats during spring–summer (averaging 0.22) and in equines in summer–autumn (averaging 0.25) season. By contrast, cattle and sheep tended to avoid this vegetation component across all grazing season, averaging 0.01. In the diet of cattle and sheep heather species proportion increased ($P<0.001$) across the grazing season. Goats' diet at the

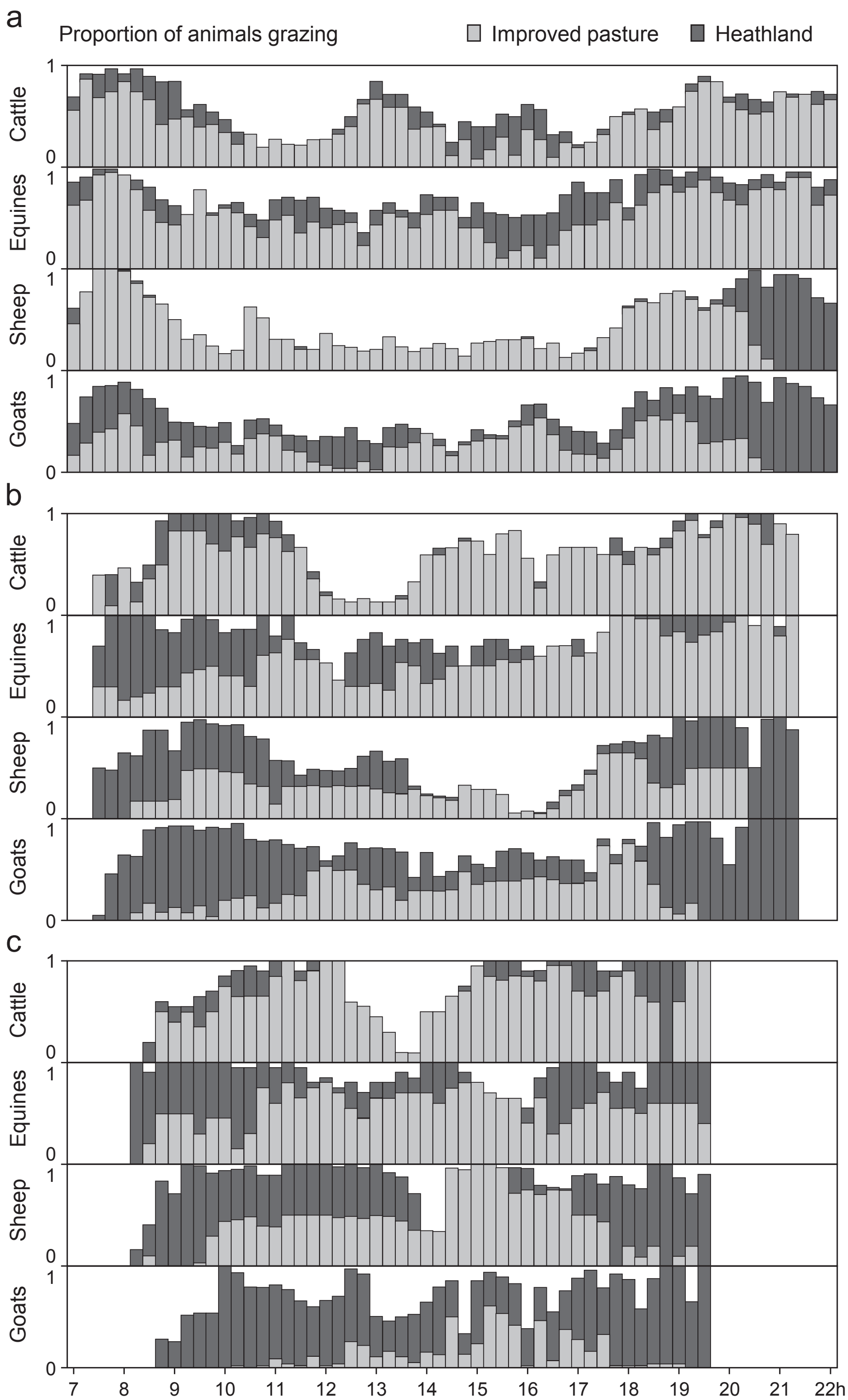

Fig. 3. Diurnal variations in the grazing use by cattle, equines, sheep and goats in a partially (24%) improved heathland plot during spring (a), summer (b) and autumn (c) sampling dates.

end of the grazing season was mainly composed of these woody species, reaching 0.81 in November. A distinct selection pattern was observed in equines, with the greatest consumption of this vegetation component being in September (0.17).

Selectivity indexes showed that cattle, equines and sheep positively selected herbaceous plants during the whole grazing season, while goats reduced their willingness to consume these plants from September onwards (Fig. 4). Gorse was selected in proportion to its availability

Table 2
Diet composition estimates (mean ± SD) of domestic herbivore species grazing on a gorse-heathland with 24% of improved pasture, using the alkane markers.

Month	Plant component	Cattle	Equines	Sheep	Goats	*P*
May	Herbaceous	$1.00^{a} \pm 0.00$	$1.00^{a} \pm 0.00$	$0.97^{b} \pm 0.01$	$0.68^{c} \pm 0.08$	**
	Gorse	$0.00^{c} \pm 0.00$	$0.00^{c} \pm 0.00$	$0.04^{b} \pm 0.01$	$0.18^{a} \pm 0.06$	**
	Heather	$0.00^{b} \pm 0.00$	$0.00^{b} \pm 0.00$	$0.00^{b} \pm 0.00$	$0.15^{a} \pm 0.03$	**
June	Herbaceous	$0.97^{a} \pm 0.02$	$0.99^{a} \pm 0.01$	$0.97^{a} \pm 0.03$	$0.83^{b} \pm 0.06$	***
	Gorse	$0.03^{b} \pm 0.02$	$0.01^{b} \pm 0.01$	$0.03^{b} \pm 0.03$	$0.15^{a} \pm 0.04$	***
	Heather	$0.00^{b} \pm 0.00$	$0.00^{b} \pm 0.00$	$0.00^{b} \pm 0.00$	$0.03^{a} \pm 0.03$	**
July	Herbaceous	$0.92^{b} \pm 0.02$	$0.94^{ab} \pm 0.01$	$0.96^{a} \pm 0.04$	$0.68^{c} \pm 0.09$	***
	Gorse	$0.00^{b} \pm 0.00$	$0.01^{b} \pm 0.01$	$0.00^{b} \pm 0.00$	$0.15^{a} \pm 0.05$	***
	Heather	$0.08^{b} \pm 0.02$	$0.05^{bc} \pm 0.01$	$0.04^{c} \pm 0.04$	$0.18^{a} \pm 0.08$	**
September	Herbaceous	$0.89^{a} \pm 0.03$	$0.66^{c} \pm 0.03$	$0.74^{b} \pm 0.05$	$0.27^{d} \pm 0.21$	***
	Gorse	$0.01^{b} \pm 0.02$	$0.17^{a} \pm 0.03$	$0.01^{b} \pm 0.03$	$0.39^{a} \pm 0.21$	***
	Heather	$0.10^{c} \pm 0.02$	$0.17^{c} \pm 0.01$	$0.25^{b} \pm 0.03$	$0.34^{a} \pm 0.04$	***
October	Herbaceous	$0.85^{a} \pm 0.05$	$0.68^{b} \pm 0.14$	$0.85^{a} \pm 0.08$	$0.27^{c} \pm 0.08$	***
	Gorse	$0.02^{b} \pm 0.05$	$0.30^{a} \pm 0.17$	$0.00^{b} \pm 0.00$	$0.05^{b} \pm 0.12$	**
	Heather	$0.13^{b} \pm 0.02$	$0.02^{c} \pm 0.03$	$0.15^{b} \pm 0.08$	$0.68^{a} \pm 0.09$	***
November	Herbaceous	$0.85^{a} \pm 0.03$	$0.71^{b} \pm 0.11$	$0.76^{b} \pm 0.07$	$0.19^{c} \pm 0.12$	***
	Gorse	$0.03^{b} \pm 0.04$	$0.28^{a} \pm 0.12$	$0.00^{b} \pm 0.00$	$0.00^{b} \pm 0.00$	***
	Heather	$0.12^{c} \pm 0.04$	$0.01^{d} \pm 0.02$	$0.24^{b} \pm 0.07$	$0.81^{a} \pm 0.12$	***

^{a,b,c,d}Within a row, means without a common superscript differ ($P < 0.05$).

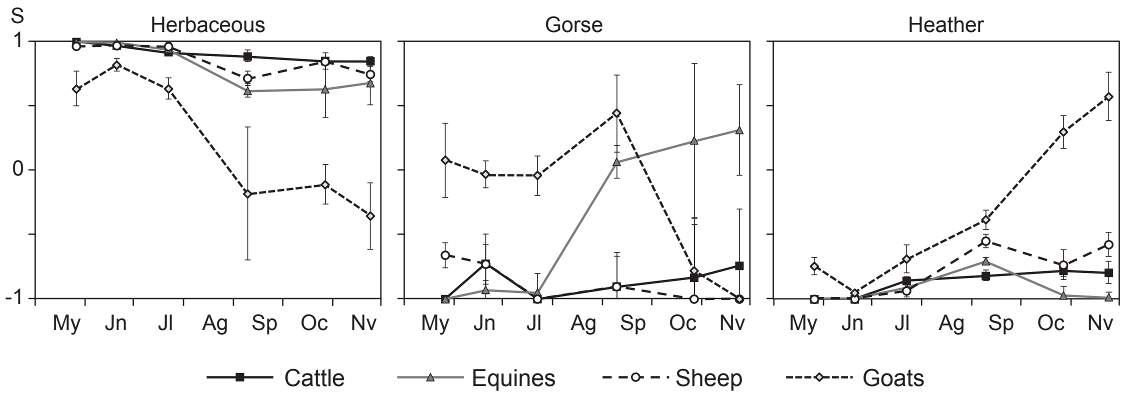

Fig. 4. Selectivity index (S) for herbaceous, gorse and heather plants of domestic herbivore species grazing on a gorse-heathland with 24% of improved pasture. Each point represents the mean ± 95% confidence interval.

Table 3
Overlapping level (Kulczynski similarity index) between domestic herbivore species in vegetation use (grazing time) and diet composition across the grazing season.

	May	June	July	August	September	October	November	Mean
Grazing time								
Cattle–equines	0.858	0.900	0.820	0.964		0.823	0.784	0.858
Cattle–sheep	0.842	0.817	0.859	0.734		0.369	0.831	0.742
Cattle–goats	0.723	0.650	0.573	0.647		0.305	0.273	0.529
Equines–sheep	0.919	0.806	0.888	0.770		0.525	0.695	0.767
Equines–goats	0.584	0.614	0.753	0.678		0.461	0.423	0.586
Sheep–goats	0.588	0.737	0.700	0.903		0.887	0.410	0.704
Mean	0.752	0.754	0.766	0.783		0.562	0.569	
Diet composition								
Cattle–equines	1.000	0.978	0.970		0.777	0.721	0.754	0.867
Cattle–sheep	0.965	0.998	0.956		0.851	0.975	0.881	0.938
Cattle–goats	0.676	0.854	0.759		0.385	0.422	0.309	0.567
Equines–sheep	0.965	0.976	0.981		0.842	0.698	0.722	0.864
Equines–goats	0.676	0.832	0.735		0.608	0.336	0.202	0.565
Sheep–goats	0.711	0.856	0.715		0.534	0.424	0.428	0.611
Mean	0.832	0.916	0.853		0.666	0.596	0.549	

by goats during spring–summer but negatively in autumn, while it was avoided by cattle and sheep across the grazing season. Equines showed an increasing trend to consume gorse as season advanced, with positive values in autumn. Heather was generally rejected by all herbivore species, but especially by equines. Avoidance was lower by goats, and they showed a positive selection of heather in autumn.

3.5. Overlap between livestock species

Results showed that the degree of grazing overlap between livestock species (KSI) was influenced by the animal species. Overall, the greatest KS-indexes based on grazing time and diet composition data (Table 3) were found between cattle and equines (0.86) and between cattle and sheep (0.94), respectively, whereas the lowest ones were observed between cattle and goats (0.53 and 0.57, respectively) and between equines and goats (0.59 and 0.56, respectively). In general, the combination of goats with the other animal species resulted in lower KSI values. The KS-indexes also varied across the grazing season when considering either the grazing time spent on each vegetation type or the diet composition. The greatest KSI values were observed in the sampling dates of the beginning–middle of the grazing season (May–August) whereas the lowest ones were found in the autumn.

4. Discussion

The low nutritive value of the natural vegetation found in these marginal heathland areas, as in previous studies (Celaya et al., 2007, 2008; Mandaluniz et al., 2009) suggest that the development of sustainable animal production systems requires the incorporation of more nutritional feed resources (i.e., improved pasture areas) in order to try to cover animal nutritional requirements (Osoro et al., 1999, 2007).

The amount of time spent feeding varied largely between animal species and across the grazing season. Equines had the highest average time spent feeding with more than 10 h/day compared to those presented by the ruminant species (8 h/day). Equines are known to possess very high grazing times (14–17 h/day) as previously observed in different vegetation conditions (Edouard et al., 2009; Fleurance et al., 2001). Although our results were in average lower, these only represent daylight grazing activities, and nocturnal grazing may represent 20–50% of total time spent grazing by equines (Martin-Rosset and Doreau, 1984). Regarding ruminant species, they are known to prefer grazing during daylight hours, maybe due to their difficult to feed in the dark (Linnane et al., 2001) or as a vestigial defence mechanism against predation (Rook and Huckle, 1997), although grazing may occur during the night especially during the hotter days and when day-length is shorter (Linnane et al., 2001). Nevertheless, grazing times observed in this study for the ruminant species are similar to those reported in previous studies (7–12 h/day: Duncan et al., 1990; Linnane et al., 2001; Vallentine, 2001).

As the length of the observation period (i.e. daylight hours) varied across the grazing season it was necessary to express grazing time in terms of percentage of the daylight hours. As a compensatory variable, it is expected that grazing time increases as intake per bite decreases in response to sward characteristics (i.e. low sward height and density) to maintain intake level. Our results are consistent with this suggestion as all animal species presented the greatest percentage of daylight time in autumn coinciding with the lowest pasture availability. Nevertheless, it should be pointed out that the lowest percentage of the daylight hours dedicated to grazing was observed in summer despite pasture availability was higher in spring (Fig. 1). Besides feed availability, weather conditions are also able to modify animals' grazing behaviour. In fact, animals seem to be reluctant to graze during the hot days (Vallentine, 2001) and a reduction of mid-day grazing activities is expected. In the present study it was possible to observe cattle and horses entering the heathland area searching for shade during the hot hours of the day. In addition, this more intensive presence in the heathland area could be the result of a search for herbaceous natural vegetation within scrubland.

Results also showed a clear diurnal eating pattern with animals concentrating their grazing activities in the beginning (sunrise) and especially at the end (sunset) of the day. Similar patterns were previously reported by several authors (Linnane et al., 2001; Smith et al., 1986; Van Soest, 1994; Velez et al., 1991) in very different environments. According to Linnane et al. (2001), diurnal grazing patterns may be related to changes in sward quality. In fact, the highest carbohydrate content of grasses in the evening suggested by Orr et al. (1997) may explain the more intensive grazing activities at the end of the day.

Besides temporal variation in grazing activity within day and across the year, results also suggested large variation in the spatial choice (i.e. plant community where to graze) between animal species throughout the grazing season. The plant community choices of cows, mares and ewes seemed to be related with both nutritive value and availability of feed resources, as animals spent most of their grazing activity on the vegetation cover dominated by palatable herbaceous species of higher nutritional quality (Bailey et al., 1996), shifting their grazing activity towards less preferred vegetation as improved pasture availability decreased. By contrast, goats combine grazing activities spent on both high quality pastures and woody vegetation even when improved pasture availability was high, highlighting different diet preferences. In fact, Vallentine (2001) suggested that animals are attracted to vegetation communities where more preferred plants are found, and for that reason diet preferences are a major factor influencing grazing distribution patterns.

Results on animals' diet composition estimated by the alkane markers are consistent with the observation data discussed previously, with large differences between species and across the grazing season. The diet preferences of cattle, sheep and horses were almost exclusively for improved pasture especially when its availability was high. This intensive use of grasslands when herbage allowance is high is well known in cattle (Celaya et al., 2007, 2008;

Mandaluniz et al., 2011; Putman et al., 1987), equines (Lamoot et al., 2005; Lechner-Doll et al., 1995; Menard et al., 2002; Putman et al., 1987) and sheep (Celaya et al., 2007, 2008; Grant et al., 1984) and, for that reason, they are normally classified as grazers (Hofmann, 1989; Rook et al., 2004). As also suggested from the observation data, the availability of the more palatable herbaceous vegetation had an important effect on animals' diet preferences, i.e. a decrease on its availability resulted in the use of less desirable vegetation (herbaceous natural vegetation and woody species). This effect differed among herbivore species. Cattle and sheep tended to incorporate heather in their diets, although sheep made this switch sooner (September vs. October, respectively) and in larger amounts (0.21 vs. 0.12). Both species tended to avoid gorse across all season, which is consistent with observations made in previous studies conducted in similar conditions (Benavides et al., 2009; Celaya et al., 2007, 2008). Nevertheless, gorse avoidance by sheep seemed to be highly dependent on specific vegetation types, as Osoro et al. (2013) found levels of gorse incorporation in their diets between 0.16 and 0.22 in grass-, gorse- and heather-dominated heathland.

Cattle reluctance to modify diet preferences towards woody vegetation species was only surpassed when improved pasture availability went below 4 cm. This sward height is also indicated by Mandaluniz et al. (2011) as a threshold value for cattle to increase attention for shrub vegetation, aiming to maintain nutrient intake, despite its lower digestibility and higher fibre content of the woody or herbaceous native vegetation (Table 1). This low diet flexibility of cattle may be due to a greater morph-physiological specialization for grass-feeding (Putman et al., 1987). For example, cattle feed prehension form (i.e. mobile tongue) and their large and flat muzzle makes them less efficient in short swards. In the case of sheep, their smaller mouth parts and longer and narrower muzzle allows them to take smaller bites, being more selective and effective on leaves of browse species (Vallentine, 2001). Nevertheless, previous studies showed that cattle are able to include heather species up to 0.20–0.50 (Celaya et al., 2011; Mandaluniz et al., 2011; Putman et al., 1987) when the availability of quality feed items is very limited. It should be noted that cattle left the improved pasture area after sheep and equines, which is quite surprising as these species are more efficient on shorter pastures by using their teeth as feed prehension form.

Equines showed the same diet flexibility as sheep incorporating woody vegetation species in their diets as high quality grasslands availability decreased. Although a moderate percentage of heather was observed in equines diets in September (0.17), they showed a preference for gorse (average of 0.25) at the end of the grazing season. Similar preferences were observed by Putman et al. (1987) in ponies grazing in the New Forest (UK) as dietary percentages of *Ulex* spp. were higher than those of *Calluna vulgaris* when herbage quality and quantity was lower. This preference of horses for *Ulex* spp. was also suggested by Rigueiro-Rodríguez et al. (2012), and used as a biological tool to reduce gorse encroachment in the understorey of Galician *Pinus radiata* stands.

Results showed that goats had the most distinct diet selection by combining high quality pastures with large quantities of browse species even when improved pasture availability was higher. This greater browser behaviour of goats compared to other domestic herbivore species was also observed in very distinct ecosystems (Bartolomé et al., 1998; Celaya et al., 2007, 2008; Narvaez et al., 2012; Vallentine, 2001) although breed (Fedele et al., 1993; Osoro et al., 2007) and physiological state (Mellado et al., 2005) can influence this selectivity. According to Vallentine (2001), goats have small mouth parts and are known to possess mobile upper lips and prehensile tongues that allow them to select leaves of browse species even from thorny species. Moreover, goats are more agile compared to other species, grazing with their heads up, and in higher vegetation strata allowing them to select more attractive but less accessible feed items (i.e. green shoots) within the woody vegetation (Bartolomé et al., 1998). Nevertheless, in the present study seasonal changes were observed within woody species selection by goats. Gorse was selected in the first part of the grazing season, may be due to its high nutritive value (for example, CP content above 180 g/kg DM in May) and the absence of developed thorns in this season, allowing also sheep to select it when herbaceous vegetation availability is low (Osoro et al., 2013). However, as gorse thorns harden and protein content is reduced, goats shift their preferences towards heather, reaching very high levels of selection (0.81). This intensive selection of heather can be the result of a self-medication instinct by consuming plant secondary compounds, as indicated by the lower parasitic burdens found in goats consuming heather with moderate tannin content (Moreno-Gonzalo et al., 2012).

As a result of different diet preferences and large variation in the spatial choice between animal species throughout the grazing season, dietary overlap varied between them. As stated previously, the greatest KSI values were observed in the sampling dates of the beginning–middle of the grazing season (May–August), when pasture availability was higher, values decreasing as sward height decreased. A similar relationship between dietary overlap and pasture availability was previously reported by Walker (1994). Vallentine (2001) suggested that competition between animal species for the same feed resources is expected to increase with increasing grazing pressures, as a result of higher stocking rates or low pasture production, and fewer options for selectivity. However, in the present study the lower dietary overlap was observed at the end of the grazing season when pasture availability was lower, reflecting the distinct preferences for the woody vegetation showed by the animals.

In general, an intensive competition for the same high quality grasslands between cattle, equines and sheep was observed across all grazing season. However, combination of goats with the other animal species resulted in lower dietary overlap. These results were predictable as cattle and horses belong to the same feeding type category (i.e. grazers) and sheep are mixed feeders with a preference for grass, whereas goats are usually considered as mixed feeders with a preference for browse. Although diet overlapping between animal species is dependent on the vegetation community and can vary greatly with the grazing season (Vallentine, 2001), our results are consistent with those observed in a thornbush savannah pasture (Lechner-Doll et al., 1995), in Pyrenees mountain conditions (Aldezabal, 2001), and in the Wyoming Red Dessert (Krysl et al., 1984).

One of the most important grazing management goals is to achieve a more efficient and uniform use of the vegetation resources, which is dependent on the dietary overlap between animal species. Our results showed that the combination of goats with any of the other species will most certainly result in a more efficient use of the heterogeneous vegetation resources of heathland areas. Additionally, goats' distinct foraging behaviour may result in different plant dynamics by (1) controlling more efficiently shrub encroachment, material with high flammability, and thus fire occurrence; (2) enhancing biodiversity by promoting greater vegetation structural complexity that could benefit a wider variety of herbaceous and arthropod species (Rosa García et al., 2013); (3) enhancing re-growth of more nutritious herbaceous plants (Jáuregui et al., 2009), with possible effects on animals' diet selection and improvement of animal performance. Benefits of managing two or more animal species within a landscape were thoroughly reviewed recently by Anderson et al. (2012) and also include reduction of parasitism, animal performance improvement, reduction in predation losses and greater economical flexibility to farm enterprises.

5. Conclusions

Results obtained in this study showed that all animal species tend to concentrate their grazing activities in two main moments of the day (i.e. beginning and end), increasing these activities with the decrease on the availability of more palatable and nutritive feed resources. A high level of competition by the same feed resources is expected between cattle, equines and sheep as they intensively select herbaceous plants, turning to browse only when high quality grasslands availability decreased. Goats proved to be the best species to complement to the other animal species for an efficient use of natural vegetation, selecting a large amount of woody species in their diets even when herbaceous availability was high. Results suggest that the type and composition of the flock in these vegetation conditions should depend on its characteristics (main plant species and its proportions), and on the goals (productions and/or environmental) previously defined.

Conflict of interest statement

None.

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