Applied Animal Behaviour Science 124 (2010) 35–44

Contents lists available at ScienceDirect

Applied Animal Behaviour Science

journal homepage: www.elsevier.com/locate/applanim

Feeding behaviour of sheep on shrubs in response to contrasting herbaceous cover in rangelands dominated by *Cytisus scoparius* L.

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ARTICLE INFO

Article history:
Accepted 8 February 2010

Keywords:
Bite
Broom
Feeding choices
Grazing behaviour
Shrub encroachment
Shrubland

ABSTRACT

The foraging responses of ewes faced with a diversity of feed items and their effects on broom (*Cytisus scoparius* L.) consumption were examined. The experiment was conducted on a farm in the autumn with ewes ($n = 33$) grazing three small paddocks (0.44 ha on average, for at least 10 days each) located in broom shrubland. The effects of three different herbaceous covers on broom consumption were compared: 100% of paddock area previously grazed in summer; 50% of paddock area previously grazed in summer; and paddock area non-grazed during the year. The characteristics of herbaceous cover (availability and quality) and the ewes' diet selection were encoded as bite categories. Flock activities were recorded through scan sampling. We used logistic regression to assess the relationship between feeding behaviour of sheep on herbaceous vegetation and on broom species, and calculated selectivity indices for this shrub. We showed that the presence of high-quality bite categories in the herbaceous cover affected the way ewes integrated broom into their diet. At the start of each paddock use period, ewes favoured high-quality larger and medium bites of the herbaceous cover. They gradually included larger bites of broom and reduced their bite size, but continued to seek out higher quality herbaceous plants, a pattern which suggested a stabilisation of their daily average digestibility and bite mass over time. A negative relation was observed between the percentage of ewes taking large and medium bites on highly digestible plant parts and the percentage of ewes browsing broom. A maximum of 26% of the flock browsing broom was observed on any given day. Hence, ewes have a threshold for this target shrubby species that they do not exceed during any paddock utilisation period. This finding was interpreted as a mechanism to deal with post-ingestive consequences and complementary interactions between nutrients and toxins. When comparing broom selection between paddocks in autumn, we found an earlier and thus longer broom selection in areas with herbaceous cover that had not been grazed during the year (possibly because of a lower palatability). Our results provide new insights into ways to manipulate diet selection in order to stimulate the use of broom by ewes. Bite categories are proposed as functional feed indicators that facilitate prediction of the herbaceous cover state preliminary to initial broom integration in the sheep's diet.

1. Introduction

Shrubby rangelands in Europe are now considered of high interest for their ecological, landscape and agronomic value (Agreil et al., in press). Many aspects (e.g. biodiversity conservation, accessibility for herbivores, productive goals)

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doi:10.1016/j.applanim.2010.02.002

support the value of maintaining open pastures and a certain level of control of dominant shrub cover in these natural areas (Bossard and Rejmánek, 1994; Casasús et al., 2007). Grazing, especially with small ruminants (sheep and goats), has shown to be an economic way to integrate environmental goals into these production systems (Valderrábano and Torrano, 2000; Bellingham and Coomes, 2003; Frost and Launchbaugh, 2003). From a practical perspective, technical specifications need to be proposed in order to increase the potential use of grazing to control shrub population. However, very few studies have focused on how to graze flocks on highly diversified plant communities, such as shrublands (e.g. Agreil et al., 2005). Understanding the feeding behaviour of livestock faced with high plant diversity is a powerful tool available to managers to modify plant–herbivore interactions to achieve targeted shrub grazing levels (Launchbaugh, 2006).

In shrubby rangelands, it has been demonstrated that herbivores' diet selection is not simply geared to a satisfactory quantity–quality trade-off of food items (Kabaya et al., 1998; Agreil et al., 2005; Rogosic et al., 2007), as suggested by the forage maturation hypothesis (sensu Fryxell, 1991). Two important factors undermine this hypothesis in shrubby rangelands: a lack of correlation between bite masses and bite quality in the case of these vegetation types comprising several plant life forms and architecture (Van Soest, 1982; Agreil et al., 2006), and the necessity for herbivores to mix diets in order to meet their nutritional needs and, at the same time, avoid poisoning (Provenza et al., 2003; Villalba and Provenza, 2005; Rogosic et al., 2007). For the poisoning issue, a recent review (Rogosic et al., 2008) has highlighted the positive influence of biological diversity that, thanks to complementary chemical interactions, helps to prevent toxic effects and/or increase the efficiency of detoxification in small ruminants. Based on these findings, research has been done to identify the causes of foraging behaviour in response to variable ranges of edible items, such as in shrubby rangelands. Herbivores often consume plant species, or plant parts, with different nutritive values, without maximizing their intake rates (Kabaya et al., 1998; Papachristou et al., 2005). In shrubby rangelands, Agreil et al. (2005) have observed that a diversity of food sources enables small ruminants, in a reasonable length of time, to reach satiation by diversity of their instantaneous choices and by increasing their range of bite sizes. Unfortunately, the importance of the diversity of feed items in targeted grazing of dominant shrubs remains unclear.

In this situation, with a high variability in the diversity of edible items, there is also growing evidence that the probability of a target plant being grazed is largely conditioned by management factors, rather than by the plant's intrinsic properties (Baraza et al., 2005; Launchbaugh, 2006). Some of these management factors can directly affect the feeding behaviour, e.g. feed additives (Rogosic et al., 2008), stocking density (Provenza et al., 1983; Mellado et al., 2003; Shaw et al., 2006), grazing route (Meuret, 1996) and even the animal's earlier experiences (Provenza, 1995; Provenza et al., 2003; Villalba et al., 2004). Some other management factors affect the feeding behaviour indirectly by having animals cope with changes in resource availability as a result of changes in the grazing season (Valderrábano and Torrano, 2000; Dumont et al., 2005), the spatial distribution of vegetation (Hester and Baillie, 1998; Holst et al., 2004; Oom et al., 2004) or the relative abundance of species, e.g. with ryegrass and clover associations (Parsons et al., 1994; Penning et al., 1997). However, little attention has been given to the effects of management factors on selectivity in target plants (e.g. shrubs) through the manipulation of resource availability, i.e. abundance, size and quality of alternative feed items in the heterogeneous vegetation community.

The objective of our study was to identify the role of feed item diversity in targeted grazing of a dominant shrub, namely, broom (*Cytisus scoparius*). We hypothesized that: (i) broom selection by ewes is influenced by the diversity of the feed items available; thus, factors other than the intrinsic properties of the dominant shrub influence the browsing habits; (ii) the diversity of the feed items available, associated with increasing resource heterogeneity in day-to-day grazing, promotes an increase in the range of bite sizes and nutritive qualities selected by the flock over time, thus modifying the browsing effect on the broom. Based on these hypotheses, we predicted that intake of broom would increase with depletion in the size, nutritive quality and structure of plant parts in herbaceous vegetation, rather than the animals selecting larger bites of mature herbaceous cover or increasing bite frequency on such cover.

We carried out a trial on heterogeneous vegetation, a natural broom shrubland located within a farm system. The effect of three contrasting herbaceous covers on broom consumption was compared by investigating and monitoring the adaptive feeding behaviour of the flock over time. Special emphasis was given to the condition of the herbaceous cover at the beginning of broom browsing in order to identify new qualitative indicators, coded as bite categories (Agreil and Meuret, 2004), to influence diet selection for shrub control. We aimed at answering the following questions: (1) How do small ruminants (sheep) select their diets when faced with shrubby rangelands which vary over time and in space? (2) How do abundance, size and quality of alternative herbaceous feed items affect the importance of broom consumption over time?

2. Materials and methods

2.1. Study site and treatments

The experiment was conducted on private property in the southwest of the Ariège-Pyrénées region (France) at a mean altitude of 900 m. The study area (1.3 ha) was composed of multi-stratified vegetation with a wide variety of grasses and forbs encroached with broom (*C. scoparius* L.). In summer, this area was divided by an electric fence into three paddocks of 0.44 ± 0.03 ha each on average. In order to create three future states of herbaceous vegetation for the autumn experiment, we manipulated it by having horses graze in the area from 12 June to 2 July 2008, thus creating differences in paddock characteristics: (1) P1 = 100% of paddock area grazed (3.731 kg LW/ha/day during 8 days); (2) P2 = 50% of paddock area grazed (3.261 kg LW/ha/day during 10 days); and (3) P3 = non-grazed paddock area.

During the experiment, from 30 September to 2 November 2008, 33 dry Tarasconnaise ewes, aged 18 months, grazed in turn each of these three paddocks with highly variable herbaceous covers in terms of the proportions of green and dead material and the phenological stages of herbaceous species. On 30 September, ewes started to use the 100% grazed paddock (P1, 69 ewes/ha for 10 days), followed by the non-grazed paddock area (P3, 73 ewes/ha, for 13 days) and then the 50% grazed paddock area (P2, 85 ewes/ha, for 10 days). The treatments were unreplicated. All the experimental animals were raised on the same farm, and had experience of grazing on shrub vegetation. During the experiment, they had access to mineral blocks and fresh water *ad libitum*.

We decided to carry out this study in the autumn so that mature broom twigs would be browsed, since repeated consumption of mature twigs can cause lasting or even irreversible effects on adult broom phenotypes (Cooper et al., 2003). The characteristics of herbaceous and shrub vegetation at the start of the experiment are given in Table 1.

2.2. Simulation of bites on herbaceous cover and laboratory processing

Every 2 days in each paddock area, simulated bites were made on herbaceous cover by cutting out the selected portions of the plant with a knife (Agreil and Meuret, 2004) into 8 samples of 30 cm × 30 cm, distributed at random. Each bite was recorded and classified according to its mass and nutritive value. The bites were harvested down to the non-edible layer of the herbaceous cover, i.e. around 5 cm above ground level, in order to avoid the base of the sheath and the thicker stems. Four nutritive value categories were established visually on the basis of differences in the proportions of the organs (leaf/stem ratio) and the proportions of dry tissue: A = 100% green leaves; B = 100% green tissue (leaves and stems); C = bites comprising less than 70% dry tissue; and D = more than 70% dry tissue. Furthermore, three categories of bite masses (L, large bites; M, medium bites; S, small bites) were established, visually based on ranges described by Agreil et al. (2005), and based on preliminary observation of the animals. Hence, 12 bite categories were compared (by combining bite mass and bite quality categories). The samples were then oven dried at 60 °C for 48 h and weighed in order to calculate the availability of each category within the paddock.

Herbage quality was analysed using near-infrared reflectance spectroscopy (NIRSystems 5000, which scans the spectral range of 1100–2500 nm) for enzymatic pepsin-cellulase dry matter digestibility (dDM), according to the Aufrere and Demarquilly (1989) method, and crude protein (CP, using Kjeldahl N × 6.25), neutral and acid detergent fibre (NDF and ADF) and lignin (ADL), with the Van Soest and Robertson (1985) method. The samples were ground with a 1 mm screen through a Cyclotec sample mill (Model 1093 FOSS TECATOR Inc., Höganäs, Sweden).

2.3. Simulation of bites on broom shrubs and laboratory processing

Every 2 days in each paddock (alternating with herbaceous sampling days), 30 twigs, between 2 and 10 mm diameter, of broom species were harvested at random in order to measure their biomass. They were harvested especially below 120 cm above ground level, which was considered to be the maximum height for browsing ewes (Clark, 2000). For each twig, we weighed (after drying at 60 °C for 48 h) the edible (green parts) and total biomass (including inedible woody parts). Using the equations already established in this trial between diameter (x) and biomass (Y) ($n = 190$; $r^2 = 0.93$, $Y = 0.864x^{2.86}$ for total biomass; and $r^2 = 0.88$, $Y = 0.076x^{2.55}$ for edible biomass), we estimated the pre-browsing biomass for each of these twigs ($n = 30$). Hence, from the difference between the biomass estimated prior to browsing and the biomass measured every 2 days, we calculated the proportion of biomass browsed each day.

In 15 of the twigs harvested every 2 days, the same three categories of bite masses described above (see Section 2.2) for herbaceous plants were manually recorded in the edible part. The aim was to remove and count all possible bites per twig and per bite category, starting with the largest ones. From these measures, we determined the proportion of each bite mass category in relation to the total edible biomass of twigs and their changes over time.

During the course of the study (more specifically on 16 October 2008, before the ewes entered the last paddock), nutritive value analyses were made of non-browsed broom twigs ($n = 15$). For each twig, the three bite mass categories were manually recorded and stored for further quality analysis. The drying period was carefully adjusted to avoid denaturing the plant material (Meuret et al., 1993). We analysed the enzymatic pepsin-cellulase dry matter

Table 1
Characteristics of vegetation at start of experiment. P1, 100% previously grazed paddock in summer; P2, 50% previously grazed paddock in summer; and P3, not previously grazed paddock.

	P1	P2	P3
Herbaceous vegetation			
Herbage height (cm) ± S.E.M.	8.6 ± 2.33	14.1 ± 3.41	20.2 ± 5.30
Herbage biomass (kg edible DM/ha)[a] ± S.E.M.	1508 ± 363.5	2002 ± 488.0	2249 ± 941.8
Shrub vegetation			
Total shrub volume (m^3/ha)	4323	7147	4947
Total shrub biomass (kg edible DM/ha)[b]	420	642	462
Number of shrubs	1551	1483	1155

[a] Approx. 5 cm above ground level.
[b] Biomass accessible (less than 120 cm above ground level).

digestibility of these samples using the Aufrere and Demarquilly (1989) method.

2.4. Total shrub biomass and its distribution among the bite categories at the paddock level

Before the start of the experiment, each broom shrub in each paddock was counted individually and assigned to a height class (small, medium, large and extra large). Additional unbrowsed plants ($n = 40$), including a wide range of different heights, were used to estimate the total edible (green parts) and accessible (below 120 cm) biomass per individual. The total shrub biomass per ha was inferred from these data and the number of plants per paddock.

We estimated the biomass distribution among broom bite mass categories by date within each paddock. We applied the changes in the proportions of bite categories obtained from the twigs collected every 2 days in each paddock (see Section 2.3) to the initial broom biomass.

2.5. Observations of flock activities

Every 2 days, flock activities were observed for four 1-h periods during daylight hours (2 h in the morning and 2 h in the afternoon) over the main grazing periods, using the scan sampling method (Altman, 1974). Every 10 min, we recorded the proportion of individuals in each of the three flock activities (ingestion, movement and rest, see Agreil and Meuret, 2004 for details). For the ingestion activity we recorded the proportion of ewes in each of the 12 bite categories described above (Section 2.2). For each herbaceous layer, observers recorded the bite masses and quality categories for the maximum number of ewes that could be observed in 10 min. For broom shrubs, we also classified each bite taken by ewes within the three bite mass categories described above.

2.6. Diet selection of broom bite mass categories

We have defined diet selection as the proportion of a vegetation bite category in the diet relative to the proportion of this category in the paddock. Selection was quantified, every 2 days, by calculating selectivity indexes (S_i) for the broom component, using Jacobs' modification (Jacobs, 1974) of Ivlev's selectivity index, as follows: $S_i = (c_i - a_i)/(c_i + a_i - 2c_ia_i)$, where "$c_i$" is the proportion (between 0 and 1) of ewes browsing the component "i", and "a_i" the proportion (between 0 and 1) of component "i" in the paddock (i.e. the proportion of each broom bite category). S_i varies from −1 (never used) to +1 (exclusively used); with negative and positive values indicating avoidance and selection, respectively, and 0 indicating that a bite category is used in proportion to its availability.

2.7. Statistical analyses

The general linear model (GLM), using the LSD method in post-ANOVA multiple mean comparison tests, was used to test the herbaceous quality categories (3 DF) and bite mass categories (2 DF) and their interaction effect for NDF, ADF, ADL, CP and dDM in Statgraphics Plus (Manugistics, USA). Prior to ANOVA, the chemical composition data were transformed by arcsin (Dagnelie, 1986).

Our statistical analyses have also concentrated on changes in the distribution of sheep foraging behaviour over time, in relation to the consumption of broom. A logistic regression analysis was made to describe the changes in the ratio of the number of ewes browsing each bite mass category of broom species and the number of ewes grazing each herbaceous bite category. Logistic regressions were performed using the GLM procedure (quasi-binomial family) in R (Ihaka and Gentleman, 1996) with R-Commander. Means were used for each paddock, each date and each period of flock activity observation ($n = 64$).

3. Results

3.1. Bite mass categories

We used three bite mass categories in our experiment for herbaceous and broom species. Each herbaceous bite category weighed, on average: 0.37 ± 0.105 g DM for large bites; 0.16 ± 0.051 g DM for medium bites; and 0.05 ± 0.026 g DM for small bites. Each broom bite category weighed, on average: 0.61 ± 0.289 g DM for large bites; 0.17 ± 0.061 g DM for medium bites; and 0.05 ± 0.034 g DM for small bites.

3.2. Nutritive value and availability of bite categories

The main components of simulated bites, namely crude protein (CP), neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL) and *in vitro* digestibility of dry matter (dDM), were significantly different ($P < 0.001$) between our four quality categories (Table 2). There were no significant differences between bite mass categories. A significant interaction between bite

Table 2
Content (g kg^{-1} DM ± S.E.) and statistical significance of neutral detergent fibre (NDF), acid detergent fibre (ADF), acid detergent lignin (ADL), crude protein (CP) and *in vitro* digestibility of dry matter (dDM) in each herbaceous quality category (A, 100% green leaves; B, 100% green tissue (leafs and stem); C, bites comprising less than 70% dry tissue; and D, bites comprising more than 70% dry tissue). Different letters in the same line indicate significant differences between categories in a multiple range test using the LSD method.

	A	B	C	D	*P*
NDF	488.4 ± 26.34a	499.4 ± 46.70a	573.3 ± 40.56b	625.4 ± 38.52c	***
ADF	287.3 ± 14.18a	303.8 ± 22.37b	337.7 ± 20.83c	365.6 ± 20.94d	***
ADL	39.3 ± 4.26a	44.3 ± 5.45b	49.9 ± 4.73c	56.8 ± 4.93d	***
CP	134.8 ± 14.52a	109.7 ± 20.03b	74.2 ± 18.58c	50.9 ± 12.22d	***
dDM	702.0 ± 27.66a	635.7 ± 46.19b	497.6 ± 59.73c	385.3 ± 50.67d	***

*** $P < 0.001$.

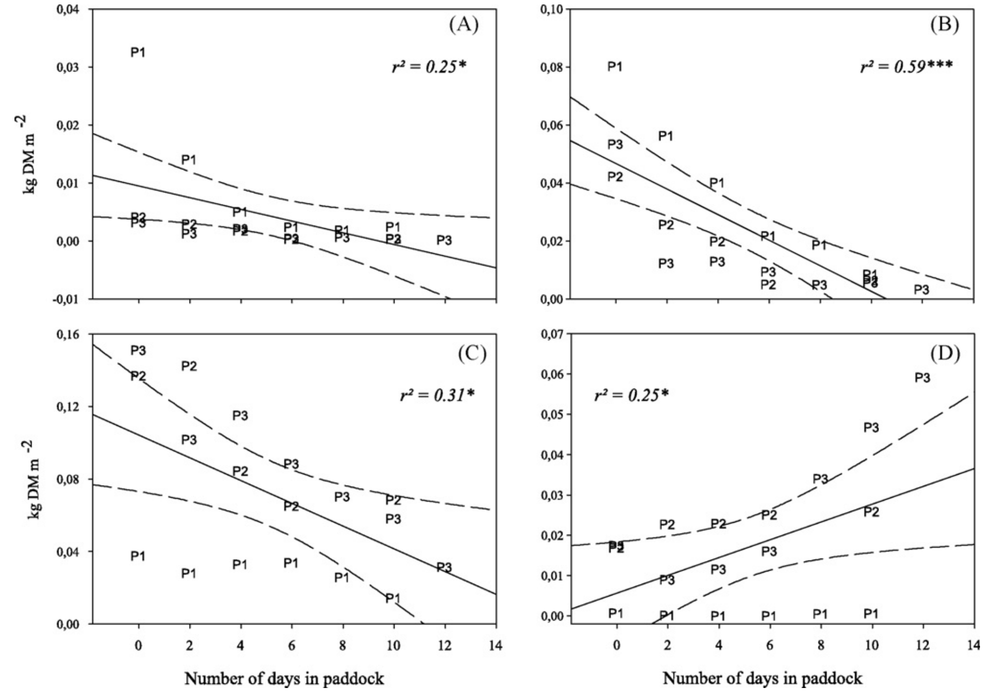

Fig. 1. Edible biomass availability within each bite quality category of herbaceous vegetation. A, 100% green leaves; B, 100% green tissue (leafs and stem); C, bites comprising less than 70% dry tissue; and D, bites comprising more than 70% dry tissue. Solid and dashed lines show the linear regressions and their confidence intervals at 95%, respectively. Abbreviations inside the figure refer to paddock number (see Table 1). $^{*}P < 0.05$, $^{***}P < 0.001$.

mass and quality categories was observed for CP and ADL ($P < 0.01$). However, the total variance explained by these interactions was less than 1%.

Edible biomass availability in each herbaceous category and for each paddock is shown in Fig. 1. Significant reductions of "A" (i.e. 100% green leaves, Fig. 1A), "B" (i.e. 100% green tissue, including stems, Fig. 1B) and "C" (i.e. less than 70% dry tissue, Fig. 1C) resources and an increase in "D" (i.e. more than 70% dry tissue, Fig. 1D) were observed over time. Paddock 1 (P1, 100% of its area previously grazed in summer) showed higher availability for "A" and "B" resources and lower availability for "C" and "D" resources than paddocks 2 (P2, 50% of its area previously grazed in summer) and 3 (P3, none previously grazed, Fig. 1).

Edible biomass availability in each bite mass category and for each paddock is shown in Fig. 2. Significant reductions of large (Fig. 2L) and medium (Fig. 2M) bites were observed over time in herbaceous species. Paddock 1 showed a lower availability for larger bites over time than paddocks 2 and 3 (Fig. 2L and M). No significant variations were observed for small bite availability (Fig. 2S).

The average enzymatic pepsin-cellulase dry matter digestibility for broom species was 481 ± 37.3 g kg^{-1}. There were no differences between bite mass categories. In general, edible broom biomass above 420 kg ha^{-1} (Table 1) was not a limiting factor during any of the trials, regardless of paddock.

3.3. Feeding behaviour of ewes in broom shrubland

Day-to-day variation in the distribution of bite masses (BM, average calculated every 10 min, drawn on a log scale) during the paddock sequence is given in Fig. 3. A limited range of BM was observed at the start of the paddock utilisation. For example, on day 1, most of the ewes were observed taking medium (paddocks 1 and 2) or large (paddock 3) bites of the herbaceous species (Fig. 3). The range was increased over time by including larger bites of broom in the ewes' diet (black dashes in Fig. 3), and by decreasing BM in herbaceous species (grey dashes in Fig. 3). In paddock 2, ewes seemed to maintain a more constant BM in herbaceous species over time compared to paddocks 1 and 3.

At the start of each paddock utilisation period, a higher proportion of ewes was observed taking larger bites (L and M) in "A" or "B" categories (Fig. 4). From day 3, bites in "C" category were observed in paddocks 2 and 3. At the end of the paddock utilisation period, a higher proportion of ewes was observed taking medium bites in "C" category in paddocks 2 and 3, and smaller bites in "C" category in paddock 1. The percentage of total ewes browsing broom species ranged from 2% (day 1) to 26% (day 9) in paddock 1, from 0.3% (day 1) to 23% (day 7) in paddock 2 and from 3% (day 1) to 23% (days 7, 9 and 11) in paddock 3. For all the dates, the average percentage of ewes observed in broom species was: 8.8% in paddock 1, 9.2% in paddock 2 and 15% in paddock 3.

3.4. Relationship between feeding behaviour on herbaceous components and feeding behaviour on broom species

The logistic regression model (Table 3) showed that the total number of ewes browsing broom over an observation period was significantly ($P < 0.05$) and negatively corre-

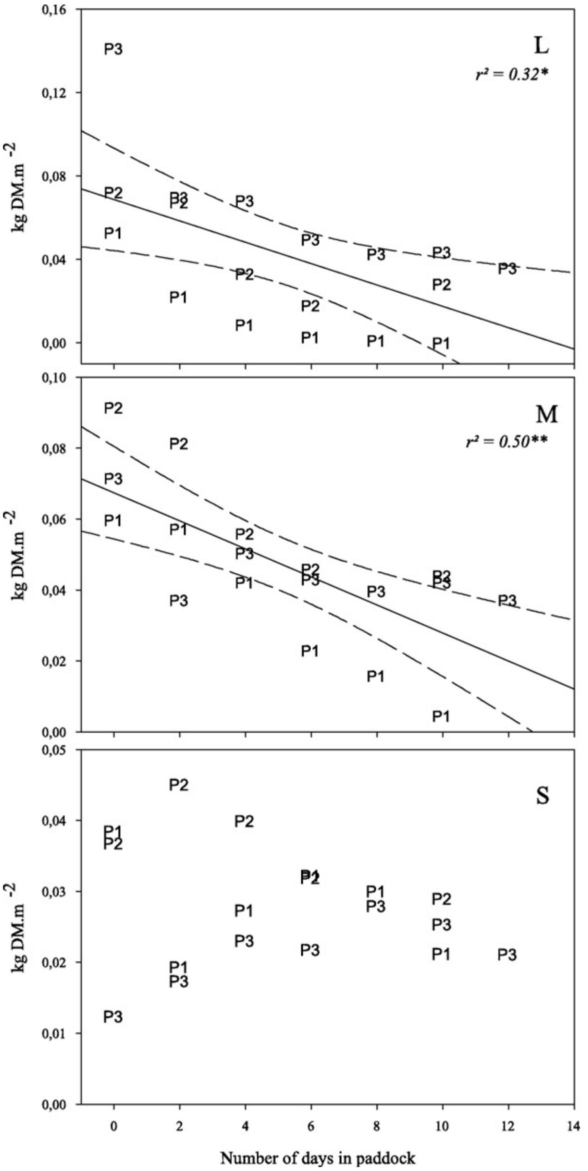

Fig. 2. Edible biomass availability within each bite mass category of herbaceous vegetation (L, large bites; M, medium bites; S, small bites). Solid and dashed lines show the linear regressions and their confidence intervals at 95%, respectively. Abbreviations inside the figure refer to paddock number (see Table 1). $*P < 0.05$, $**P < 0.01$.

lated to the number of ewes taking large and medium bites in "A" and "B" (i.e. A_L, A_M, B_L and B_M). Conversely, significant ($P < 0.05$) and positive slopes were found with "D" categories (Table 3). Using the logistic regression results, we analysed the relationship between the availability of herbaceous biomass for each significant bite category described above (left axis, Fig. 5) and the Jacob's indexes (S_i) for each bite category of broom species (right axis, Fig. 5). Bite categories that show $S_i > 0$ are assumed to be positively selected (preferred). Those for which S_i was <0 are regarded as "not selected" (rejected). We have observed that positive broom selectivity occurred when the availability of large high-quality bites (A_L, A_M, B_L and

Table 3
Logistic regression statistics ($n = 64$) for the relationship between the cohort of sheep browsing *Cytisus scoparius* species and the cohort of sheep grazing each herbaceous bite categories. For abbreviations, see Table 2: L, large bites; M, medium bites; S, small bites.

Bite category	Slope (S.E.)	*P*
A_L	−0.093 (0.0404)	*
A_M	−0.116 (0.0397)	**
A_S	−0.090 (0.0667)	ns
B_L	−0.100 (0.0287)	***
B_M	−0.038 (0.0099)	***
B_S	0.007 (0.0144)	ns
C_L	−0.034 (0.0186)	#
C_M	0.005 (0.0065)	ns
C_S	0.010 (0.0070)	ns
D_L	0.402 (0.1381)	**
D_M	0.102 (0.0283)	***
D_S	0.172 (0.0738)	*

ns, not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
# $P < 0.10$.

B_M) approached zero (Fig. 5). Ewes selected large bites from broom shrubs after day 8 in paddock 1, day 6 in paddock 2 and in paddock 3 (Fig. 5). A selection for broom (S_i) seems not to be correlated to "D" availability in paddocks (Fig. 5). Medium and small bites from broom shrubs appear to be negatively selected in paddocks 1 and 2. In paddock 3, ewes selected medium bites in broom species from day 5 and small bites from day 9 (Fig. 5, P3).

4. Discussion

4.1. Feeding behaviour of ewes in broom shrubland

Our flock of dry ewes grazed for approximately 10 days within small paddocks consisting of multi-stratified vegetation dominated by grass species encroached with broom. Because of their higher nutritive value, ewes grazed "A" (100% green leaves) and "B" (100% green tissue, including stems) herbaceous categories more intensively at the start of paddock utilisation. Sheep are highly selective in what they consume (Milne, 1994; Hülber et al., 2005). Hence in order to maximize their net intake rate of digestible nutrients (Wilmshurst et al., 1995) they probably maintained lower ranges of bite masses (e.g. around 0.19 g DM bite^{-1} in paddock 1, see Fig. 3) and bite quality classes (e.g. "A" and "B" in paddock 1, see Fig. 4) in the beginning. This explains why the ewes seem to favour larger and medium sized good-quality bites. These findings are in agreement with the observation by Negi et al. (1993), that animal feeding behaviour is highly selective when food sources are diverse and abundant.

In the paddock, the availability of larger bites of higher nutritive value ("A" and "B" categories) declined and gradually reached depletion, thus persuading the ewes to consume poorer herbaceous nutritive quality, such as "C" category, i.e. bites comprising dry tissue. Thereupon, broom species offering larger bites became particularly attractive. The ewes gradually included larger bites of broom species in their diet, which they had not selected before then, thus increasing their dry matter intake rate

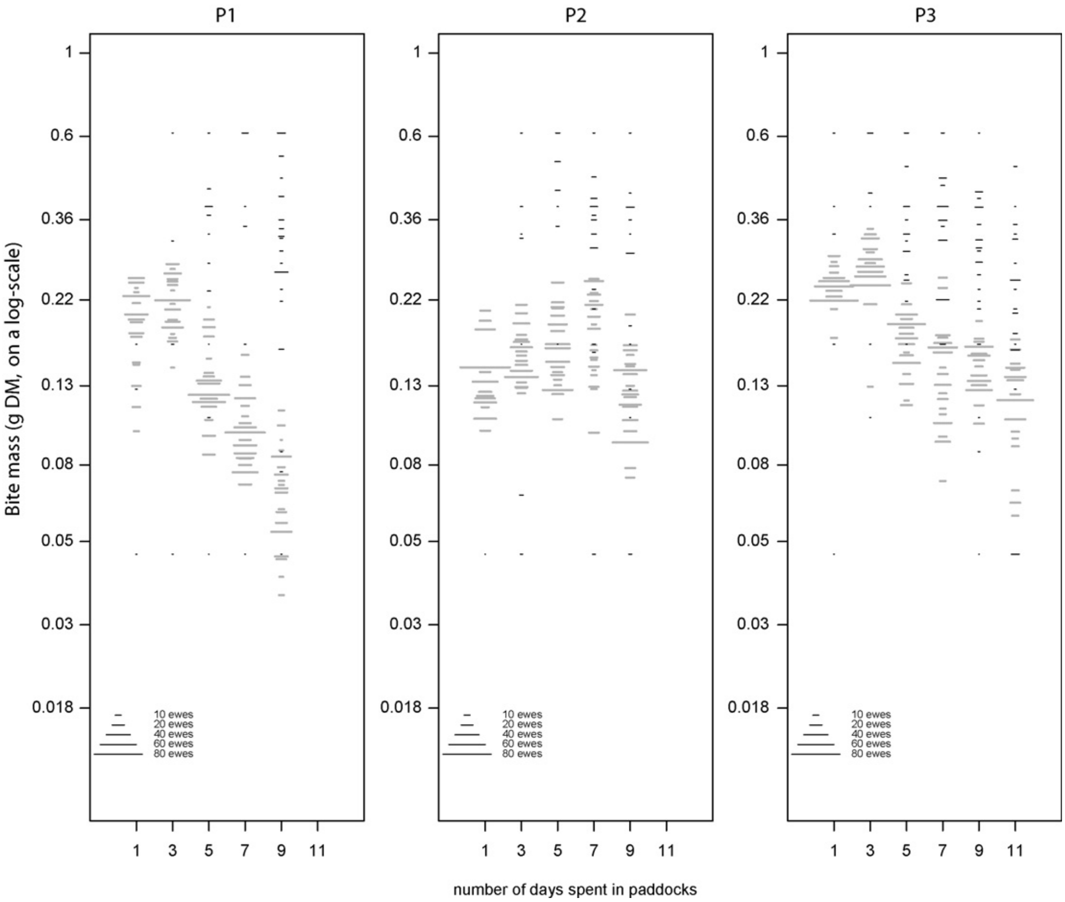

Fig. 3. Inter-day variation of the distribution of bite masses during the paddock sequence (P1, P2 and P3, see Table 1 for paddock abbreviations). The length of the dashes is proportional to the average number of ewes for each bite mass category for *Cytisus scoparius* (black dashes) and herbaceous species (grey dashes).

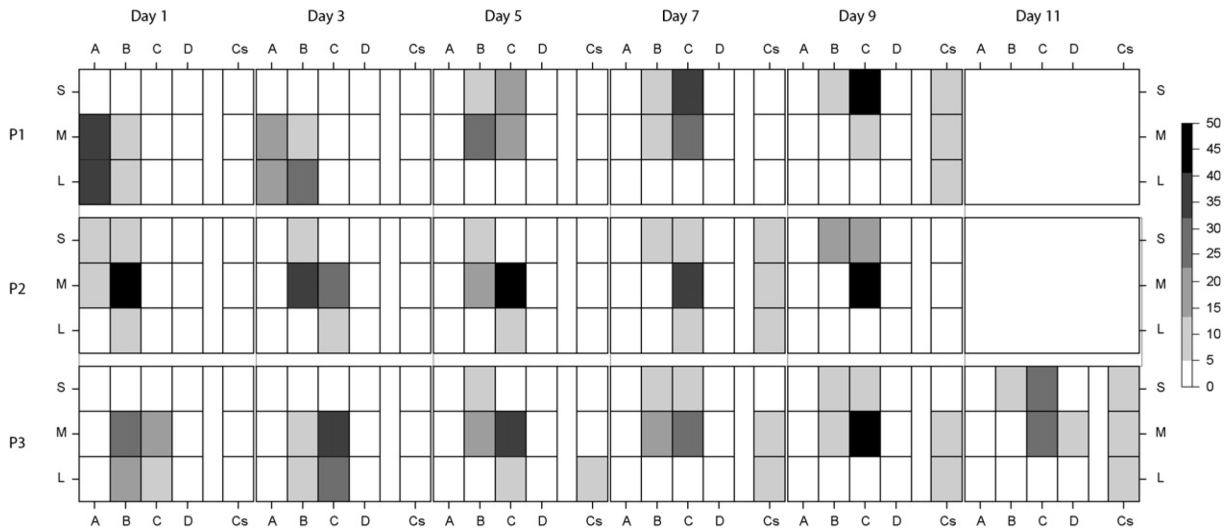

Fig. 4. Percentage of ewes in each vegetation bite category for each sampling day (columns), and each paddock (lines, P1, P2 and P3, respectively). For paddock abbreviations, see Table 1. A, 100% of green leaves; B, 100% of green tissue (leafs and stem); C, for bites comprising less than 70% dry tissue; and D, more than 70% dry tissue. Cs represents the *C. scoparius* species. L, M and S represent the bite mass: L, large bites; M, medium sized bites; and S, small bites.

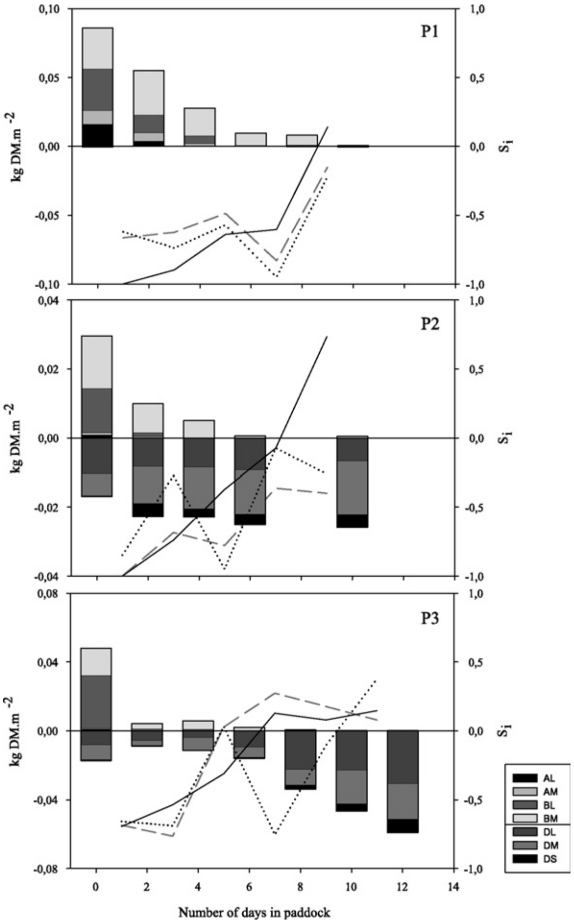

Fig. 5. Edible biomass availability (left axis) for significant bite categories described in Table 3 in each paddock (P1, P2 and P3). Values on the left-hand axis are positive for A_L, A_M, B_L and B_M categories and negative for "D" categories. Average Jacob's indexes (S_i) for the *C. scoparius* species are shown on right-hand axis. Values (S_i) are positive for *selected* feed items, i.e. mean > 0. Values (S_i) are negative for *avoided* items, i.e. mean < 0. Solid line indicates S_i for large bites, dashed line indicates S_i for medium bites and dotted line indicates S_i for small bites. For abbreviations, see Fig. 4.

(Meuret, 1997). The later selection of large bite masses of broom (>0.15 g/bite or 50 mg/kg $LW^{0.75}$, according to Agreil et al., in press) probably contributed to maintaining the stability of the daily intake rate per meal, a beneficial development that lasted until nearly the end of the stay in the fenced pasture (Agreil et al., 2005). Large bites of broom were more intensively consumed than large bites of the "D" category (less than 30% live tissue), which is consistent because of their greater digestibility. Furthermore, ewes took large bites of broom at the same time as they took smaller bites of herbaceous plants (e.g. paddock 1, day 9). This temporal pattern of diversified bite mass consumption has been reported by Agreil et al. (2005), who observed that ewes, when faced with a diverse supply, increased their range of bite sizes as the size and structure of previously grazed plant parts decreased, thus stabilising daily average digestibility and bite mass. Thus ewes may take smaller and more nutritious bites of herbaceous plants and larger bites of broom in order to maximize daily energy intake.

We have observed a maximum of 26% of the flock browsing broom on any given day, suggesting that ewes have a threshold for this shrubby legume that they do not exceed during a paddock's utilisation period. A diverse range of dietary plant chemicals can be found in leguminous shrubs, e.g. quinolizidine alkaloids in broom, whose total amount rises at the end of the growing period (i.e. in autumn, Gresser et al., 1996). These plant chemicals can have an adverse effect on herbivore feeding behaviour (Rogosic et al., 2007, 2008). Therefore, the daily ingestion of only small amounts of broom may be a mechanism whereby animals can test it for an adverse reaction and/or complementary nutrient/toxin interactions (Shaw et al., 2006; Rogosic et al., 2007), especially when changes in nutritional quality are very rapid (Dumont, 1995). However, adequate understorey availability and quality in rangelands dominated by chemically rich shrubs is necessary in order to provide a balanced mixture of nutrients to allow for a detoxification process and to maintain animal performance (Baraza et al., 2005; Villalba and Provenza, 2005; Shaw et al., 2006).

4.2. Role of availability of feed item diversity in broom consumption

Previous studies have mainly evaluated diet selection by herbivores in grass/clover mixtures (e.g. Parsons et al., 1994) or throughout the year in heterogeneous vegetation (Kabaya et al., 1998; Dumont et al., 2005). In heterogeneous vegetation, shrub species are shown to be selected when they offer more palatable organs (e.g. flowers in broom, Frutos et al., 2002; Ammar et al., 2004) or to fill the "hungry gap" periods of the year (Papachristou et al., 2005). In the present experiment, we explored further aspects of ewes' diet selection. We show that the feed items selected by ewes are determined by environmental circumstances, i.e. the relative availability of bite categories from which the choice is made. Our results show that ewes added broom to their diet differently and more abundantly when the bites offered by herbaceous cover were of medium or low potential palatability. For example, ewes selected broom early in paddock 3, which had lower "A" and "B" availability (i.e. bites of higher nutritive value). Since this paddock had not been grazed during the year, herbage biomass was presumably a result of an increased development of stems and spikes (Smethan, 1990), a lower leaf:stem ratio (Boval et al., 2002) and a high cell wall content (Waite et al., 1964). These responses highlighted our hypothesis that factors other than the intrinsic properties (e.g. the presence of secondary compounds, Gresser et al., 1996; Rogosic et al., 2007) of dominant shrub species influence the browsing behaviour.

To summarise, ewes effectively integrate the shrubs into their diet, even when herbaceous vegetation (i.e. "C" and "D" categories) is readily available in the paddock. Broom can play a significant role in increasing dry matter intake (Meuret, 1997) and in providing protein-rich fodder, as a supplement to more fibrous herbaceous biomass (Tolera et al., 1997). Hence, the ewe's diet is composed of a combination of broom and herbaceous plants. Interestingly enough, observations have shown that diet-mixing behaviour does not adversely affect animal performance (Shaw et al., 2006; Papanastasis et al., 2008).

4.3. Implications for shrub encroachment control

In the literature, several aspects have been identified in order to control shrub spread by grazing, in particular the kind of livestock and their grazing pattern (duration, timing and intensity, Launchbaugh, 2006). Here we have shown that a target shrub population (broom) may be grazed differently depending on the herbaceous ground cover. Our results show that in high-quality herbaceous cover (paddock 1), broom selection by ewes became positive later in the paddock utilisation period. From that time the herbaceous biomass is scarce, with bite masses around 0.06 g DM bite^{-1}, which is probably inadequate to sustain intake rates through bite frequency (Penning, 1986). Hence, the grazing period in this paddock should not be extended, reducing the time for broom twig consumption by ewes. Unlike the situation in the paddock 1, motivation to browse broom species was anticipated when the herbaceous cover was of medium or low potential palatability (particularly in paddock 3). Therefore, the objective became the determination of functional heterogeneity, i.e. abundance, size and quality of plant organs (Agreil et al., 2005), that would motivate browsing of broom target parts during a targeted grazing period, but at the same time maintain satisfactory intake levels for livestock sheep production, such as in paddock 3.

Our study provides new qualitative indicators, encoded as bite categories, on the state of herbaceous cover and whether it can trigger initial shrub consumption. More explicitly, in the absence of A_L, A_M, B_L and B_M bite categories (i.e. large and medium bites with 100% of green tissue), ewes started to browse broom. As far as we know, these results have never been reported before. However, for effective manipulation of population dynamics, further information is required to determine the longer term impact of twig browsing on the demography of the broom population, and to understand the role of the consumption of different organs.

5. Conclusion

Our results illustrate the complex dynamics of the feeding behaviour of ewes grazing on heterogeneous vegetation containing a dominant shrub (broom species). Earlier, and consequently longer lasting, broom browsing in autumn was observed in areas with herbaceous cover that had not been grazed during the year (possibly with lower palatability). Our study thus shows how resource managers can manipulate diet selection to stimulate the consumption of broom by ewes, and probably to modify the demographic behaviour of this shrub. Furthermore, knowledge of the availability and quality of bite categories in a pasture, as proposed in this study, may provide information needed to predict the likely degree of control of broom by sheep.

Acknowledgements

The authors are especially grateful to livestock producers Mathias, Françis and Gila Chevillon. We are also grateful to P.A. Portela, E. Lecloux, C. Moder and M. Perreu for their skilful assistance during the experiment. This study was financially supported by ANR-DIVA and PSDR (Program "Pour et Sur le Développement Régional"). L. da S. Pontes acknowledges the support of INRA for a post-doctoral grant.

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