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Feeding behaviour adjustments by ewes foraging in highly heterogeneous and temporally variable environments

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SUMMARY – The European agri-environmental policy is encouraging livestock farmers to adopt grazing practices that contribute to biodiversity conservation. But there is a serious lack of knowledge, and a better understanding of feeding behaviour adjustments in response to diversity is needed. In order to address this question, we conducted two on-farm experiments with flocks of dry ewes foraging broom shrublands. A direct *in situ* observation method was used, with continuous observation of ingestive bites taken by a continuously monitored individual per experiment. A bite coding-grid enabled us to distinguish the extreme diversity of bites masses and structure. Flock activities were also scan-sampled, in order to check the consistency of individuals' behaviour with those of their flocks. Daily dry matter intakes (DMI) were high in both experiments: 77.9±10.2 and 75.1±16.9 g DMI/kg $LW^{0.75}$, which is twice higher than predictions from existing models on sheep intake. Our data enabled us to explore the relationship between the quantitative daily intakes and the diversity of instantaneous feeding behaviour. Daily averages of ingestive behaviour hide the extremely large range of instantaneous values (from 0.04 to 1.2 g DM for bite mass). When vegetation size and structure declined as a result of grazing, the ewes progressively took larger bite masses with equivalent nutritive quality, thus adopting a pattern of consumption that is not consistent with the general assumption that such bites are chosen during the first days, as a result of the quantity-quality trade-off. This research provides knowledge about which type of diversity in plant parts offers a small ruminant satisfying behavioural leeway in composing its meals and reaching satiety.

Keywords: Foraging behaviour, bite, intake rate, sheep, feeding choices, rangelands.

RESUME *– "Ajustements comportementaux alimentaires des brebis en pâture en milieu fortement hétérogène et variable dans le temps". Les politiques environnementales européennes encouragent aujourd'hui des pratiques de conduite de troupeaux afin de contribuer à la conservation de la biodiversité. Mais les connaissances disponibles font défaut pour la rédaction des recommandations. Afin de mieux comprendre les ajustements comportementaux réalisés par les petits ruminants d'élevages, nous avons conduit deux expériences en ferme, dont les lots de brebis taries sont conduits sur des landes à genêt. La méthode utilisée est celle de l'observation directe* in situ *et en continu des prises alimentaires réalisées par un individu durant la journée, complétée par des observations par scan-sampling des activités du lot. Aucune variation inter-quotidienne des quantités ingérées en matière sèche n'est détectée. Ces quantités (77.9±10.2 et 75.1±16.9 g MSI/kg* $PV^{0.75}$*) sont plus importantes que ce qui est prévu par la littérature concernant des régimes à base de fourrages verts de qualité équivalente. Les jeux de données très précis ont rendu possible une confrontation de ces bilans journaliers avec la grande diversité des principales variables décrivant le comportement d'ingestion. Les moyennes quotidiennes cachent en réalité des valeurs instantanées couvrant une gamme considérable (de 0,04 à 1,2 g MS pour les masses des prises alimentaires). Nous observons des ajustements comportementaux contredisant l'hypothèse assez générale d'une sélection prioritaire des prises alimentaires de masse élevée et de bonne valeur nutritive. Celles-ci ne sont incluses dans les régimes qu'au cours des derniers jours passés dans un parc clôturé. Ces résultats contribuent à pouvoir qualifier mieux qu'auparavant le type de diversité à offrir à des petits ruminants pour leur permettre une bonne organisation de leur ingestion.*

Mots-clés : *Comportement d'ingestion, prise alimentaire, flux d'ingestion, mouton, choix alimentaires, parcours.*

Introduction

European natural grasslands and rangelands are attracting new attention for their environmental values as habitats for threatened fauna and flora species. This explains why the European agri-environmental policy (Buller *et al.*, 2000), is now encouraging livestock farmers to adopt grazing practices that contribute to biodiversity conservation. However, there is a serious lack of knowledge on how to graze flocks on highly diversified plant communities, in particular when plant communities are subject to shrubby dynamics (Hubert *et al.*, 1995). As a consequence, technical specifications in most agri-environmental contracts favour mechanised land clearance (Agreil, 2003), thus undermining the expected impact by the flocks. Knowledge should hence be produced about the foraging value of natural vegetation.

In ruminant herbivores, most studies on the behavioural and mechanistic adjustment of grazing have been carried out in rather simplified conditions, i.e. homogeneous vegetation or artificial swards in which heterogeneity remains controlled (e.g. Black and Kenney, 1984; Spalinger and Hobbs, 1992; Lundberg and Danell, 1990; Ginnett and Demment, 1995). These approaches have great heuristic value but need to be tested under more complex grazing conditions, both as tests of theory and as ways to adapt models and concepts to produce management guidelines in grazing ecosystems. It is often pointed out that coping with plant diversity and variability is one of the major challenges ruminants are faced with (Provenza *et al.*, 2003). But little is known about the functionality of plant diversity when grazing in highly diversified environment.

Materials and methods

The results reported in this paper come from two experiments conducted on sheep farms where flocks were used to graze within paddocks made of heterogeneous vegetation. Sheep were offered a great daily diversity of edible items (nature of plant organs, their phenological stages, size and nutritive value), that were widely dispersed within the paddock. The two experiments were carried out respectively in August and April in the south of France within flocks composed of 214 and 25 recently dried ewes. The flocks grazed respectively for 16 days in a 4.5 ha paddock and 14 days in a 1.1 ha paddock, at an elevation of approx. 1000 m in both cases. The vegetation was composed of swards encroached with shrubs and trees.

Observations were made during full daytime periods. The method used is a recent improvement of earlier direct observation methods and has been described in detail by Agreil and Meuret (2004). We used a familiarisation procedure to accustom the animals to having an observer very close to them. Within each flock, an individual was identified for continuous recording of bites, and was subsequently tested to ensure that its behaviour was consistent with that of the flock (scan sampling). Direct and continuous observation of bites taken by each continuously monitored individual was achieved thanks to a bite-coding grid (Fig. 1). The grid allow to distinguish 40 bite categories (BC) based on the shape and size of the plant organs selected and the way they were cropped. Information on plant species was recorded during the experiments and added as a modifier of each BC. *The Observer 3.0* software was used to convert the taped BC codes into tables. Each BC observed for any plant species was afterward simulated for at least 100 repetitions by the observer. The plant samples (grouping of 20 simulations) were then oven dried, weighted and analysed by the Near Infrared Spectroscopy method. The daily intake was calculated by adding up the contents of all BC recorded in the day. Variation over time in the daily characteristics of ingestive behaviour was tested using the Pearson correlation test, over the number of days spent in paddock, with "no trend" as the null hypothesis.

Results

Daily Dry Matter Intakes (DMI) were 77.9 ± 10.2 and 75.1 ± 16.9 g DMI / kg $LW^{0.75}$, respectively for Experiment 1 and Experiment 2. As daily intake was very high for "Day 1" (97.1 and 111.8 g DMI / kg $LW^{0.75}$), we excluded that day for trend detection. There was then no detectable inter-day trend or any significant difference between the two experiments as the daily DMI were 75.0 ± 7.7 and 69.0 ± 8.5 g / kg $LW^{0.75}$. The Crude Protein Intake (CPI) was 7.3 ± 0.9 and 11.2 ± 1.3 g CPI / kg $LW^{0.75}$, the Neutral Detergent Fibre Intake (NDFI) was 45.2 ± 5.6 and 42.2 ± 5.5 g NDFI / kg $LW^{0.75}$, and the Digestible Organic Matter Intake (DOMI) was 32.3 ± 2.8 and 37.1 ± 4.5 g DOMI / kg $LW^{0.75}$. Our estimates of daily intake are consistent with data from literature. However, DMI we observed correspond to an intake of green fodder given indoors, with organic matter digestibility (OMd) being between 75 and 80% (Dulphy *et al.*, 1999). In our case the OMd was respectively 43 and 55%. The intakes were then considerably higher than those estimated for green fodders with about the same OMd. Intakes we observed, i.e. +50 g DMI and +35 g DMI per kilo of metabolic weight, were about twice as high as the ones predicted in the models published by Morley (1981) and Van Soest (1994).

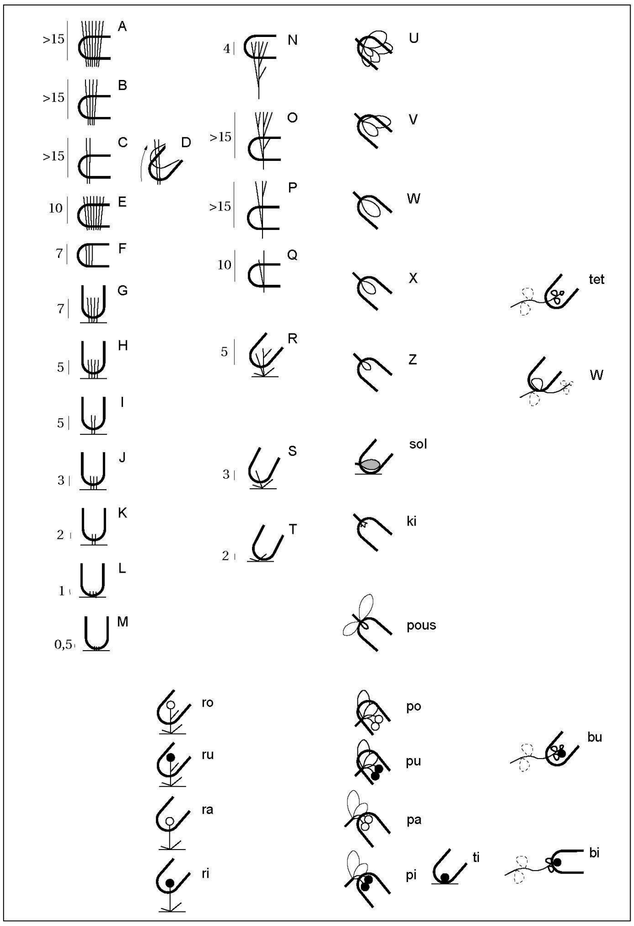

Fig. 1. The bite coding grid used for the continuous observation of bites. Bite categories are based on the nature and structure of plant portions clipped. The "U" shape icon stands for the jaws of the small ruminant. The plant portions are indicated by small icons that symbolise their physiognomy: fine lines (chlorophyllic stems of shrubs or leaf blades and stems of grasses), ovals (tree and shrub leaves), open circles (flowers) and black circles (fruits). See Agreil and Meuret (2004) for details.

Concerning the description of ingestive behaviour, when expressed as daily average values, there is a downward trend for bite mass (BM): a 25 and 43 % reduction during the 16 and 14 grazing days in experiments 1 and 2 (Table 1). In the first experiment, the drop in BM is compensated by the tendency for gradual increases in bite frequency (BF), and hence the absence of a trend for the average daily IR. No trend was observed for BF as the days went by. In this situation, a decrease in BM induced a decrease in the dry matter IR. Last, there was no observable trend for the daily average OMd of selected plant parts.

But these variations in daily average values appeared to be very slight, when they are compared to the range of instantaneous behaviours, which were extremely wide, in particular for bite masses (from 0.04 to 1 g DM/bite and from 0.06 to 1.2 g DM/bite in experiments 1 and 2, respectively). Although the average bite mass decreased, the day to day range of bite masses increased (Table 1). The combined representation of the daily averages and the instantaneous BM during experiment 1 is given in Fig. 2 (on a log scale). The decrease of average bite mass (thick grey line in the left box) is small in comparison to the range of bite masses used each day. As the days went by, the size of the remaining plant parts dwindle and the ewes selected numerous small bite masses at high bite frequencies (left box). These small bites, however, do not contribute significantly to daily intake (central box). From day 7, ewes added to their diet bites of high masses that contributed most to daily intake. This late selection of large bite masses may be attributed to their poor nutritive quality. This was not the case, as large bite masses selected during the last days had an OMd (top right, in the right box) that was at least equivalent to the bites selected during the first days.

Table 1. Variation, during the stay in the paddock, of the instantaneous behaviours (daily averages ± standard deviation). The results of Pearson correlation test are presented on the last line: D. = Decreasing, I. = Increasing and NS = Not Significant with a probability threshold of 5 %

Number of days in paddock	Experiment 1				Experiment 2			
	Instantaneous bite mass (g DM)	Instantaneous bite rate (bite/min)	Instantaneous intake rate (g DM/min)	Instantaneous OMd content (%)	Instantaneous bite mass (g DM)	Instantaneous bite rate (bite/min)	Instantaneous intake rate (g DM/min)	Instantaneous OMd content (%)
1	0.17 ± 0.12	26.8 ± 13.5	4.51	44.0 ± 11.1	0.10 ± 0.03	46.1 ± 19.9	4.62	64.9 ± 17.7
3	0.16 ± 0.14	25.7 ± 17.2	4.04	44.0 ± 15.1	0.09 ± 0.03	37.4 ± 19.1	3.35	55.6 ± 16.8
5	0.14 ± 0.11	29.5 ± 13.8	4.03	41.7 ± 10.0	0.09 ± 0.04	44.7 ± 19.5	4.07	53.1 ± 13.3
7	0.15 ± 0.16	31.1 ± 16.5	4.75	42.6 ± 12.2	0.09 ± 0.09	37.7 ± 18.8	3.31	52.4 ± 11.7
9	0.13 ± 0.14	34.3 ± 19.7	4.37	42.8 ± 10.8	0.08 ± 0.08	41.5 ± 19.3	3.50	53.0 ± 10.9
11	0.13 ± 0.17	34.1 ± 19.4	4.43	42.5 ± 8.3	0.08 ± 0.09	38.8 ± 18.8	3.15	52.9 ± 12.0
13	0.15 ± 0.20	36.7 ± 21.3	5.41	42.5 ± 8.4	0.06 ± 0.06	49.5 ± 22.5	2.86	55.3 ± 13.5
15	0.13 ± 0.17	42.1 ± 24.1	5.32	45.1 ± 10.3	------	------	------	------
mean ± std	0.14 ± 0.014	32.5 ± 5.1	4.60 ± 0.49	43.2 ± 1.03	0.08 ± 0.01	42.2 ± 4.3	3.55 ± 0.56	55.3 ± 4.1
trend detected	D. (p = 0.04)	I. (p = 0.00)	NS	NS	D. (p = 0.01)	NS	D. (p = 0.01)	NS

These results stress the fact that in heterogeneous vegetation, because of the wide range of instantaneous BM and BF, analyses should not be restricted to daily averages (Schmitz, 2000; Bergman *et al.*, 2001). Unlike in experiments conducted on sown swards (Chacon and Stobbs, 1976; Black and Kenney, 1984), ewes facing spatially varied and temporally variable environments do not systematically prioritise large bite masses during the first days in a paddock, even though they are of high OMd. Ewes observed in this study chose an increasingly broad range of bite masses and the larger ones gradually made up the greatest part of their daily intake during the last days in the paddock, as the size and structure of plant parts decreased. The coupling of the instantaneous-scaled analysis of ingestive behaviour with the large-scaled expression of intake levels and diet quality gave a more realistic overview of behavioural adjustment achieved by small ruminants. One of the major challenges for scientists is probably to model such behavioural adjustments under the hypothesis of an incomplete knowledge by the animals of the available feeds. This leads us to argue for a better consideration of stabilisation functions when modelling feeding strategies. An interesting framework is the "satisficing rule" (Ward, 1992) which postulate that animals only modify their feeding choices when the consequences of previous ones are below a particular threshold.

Conclusions

With regard to flock feeding and pastoral management, we argue for a better attention to the functional heterogeneity needed to sustain intake through behavioural adjustments. Our study of the small ruminants' feeding strategy confirms the assertion that several types of vegetation have been unjustly denigrated in livestock farming. More specifically, we are referring to vegetation that includes time-saver feeds, in other words, feeds that can be consumed in large bites such as large grasses, lianas, shrubs and tree foliages.

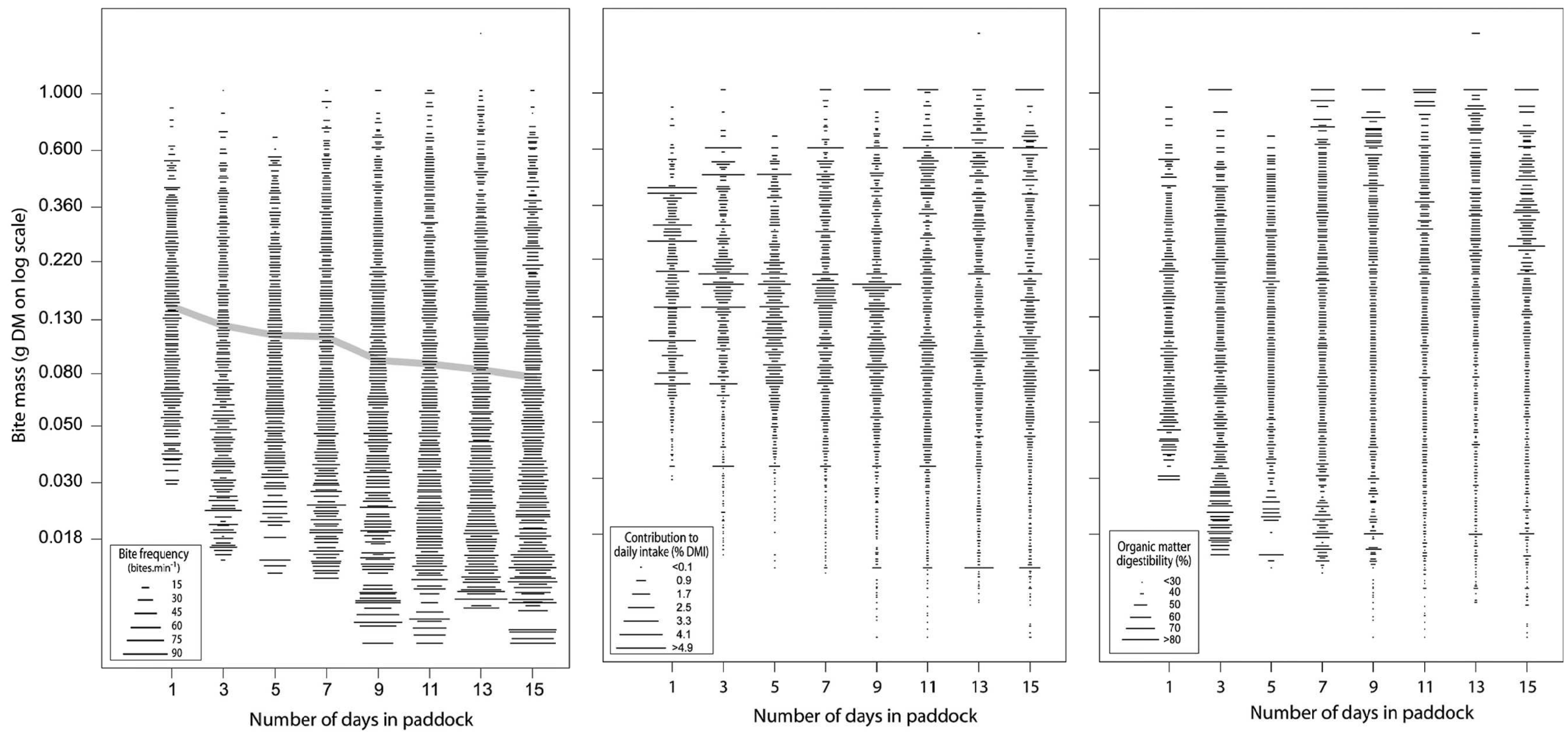

Fig. 2. Inter-day variation of the distribution of instantaneous bite masses during the paddocking sequence in experiment 1. For each category of bite mass, the length of the black dashes is proportionate to: the average bite frequency (left box, in bite/min); the average contribution to the total daily intake of dry matter (central box, in %); the average organic matter digestibility (right box, in %).

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