Maintenance of daily intake through bite mass diversity adjustment in sheep grazing on heterogeneous and variable vegetation

Cyril Agreil[a,*], Hervé Fritz[b], Michel Meuret[a]

[a]INRA, Unité d'Ecodéveloppement, Site Agroparc,
Domaine saint Paul, 84 914 Avignon Cedex 9, France
[b]CNRS, Centre d'Etudes Biologiques de Chizé, UPR 1934 du CNRS,
79360 Beauvoir-sur-Niort, France

Abstract

Concerns about biodiversity preservation through grazing have revived interest in feeding choices made by herbivores. In this article, we study the dynamics of behavioural intake response in heterogeneous vegetation, where the size and quality of edible plants is highly diverse and varies from day to day as a result of grazing. We conducted two experiments with ewes grazing in paddocks located in shrubby rangelands. A direct in situ observation method was used, with continuous observation of ingestive bites taken by a continuously monitored individual. A bite coding-grid enabled us to distinguish the extreme diversity between bites masses and structure, including the ones resulting from plant depletion. Flock activities were also scan-sampled. Observations were made throughout complete paddocking sequences, which lasted for about two weeks. Grazing seriously depleted the paddocks since 75–95% of the herbaceous species was consumed. No trend was detected either in daily activity patterns or in intake time-budgets. These two variables were well synchronised between the continuously monitored individuals and their respective flocks. No inter-day trend was observed for dry matter daily intakes, which was twice higher than predictions from existing models on sheep intake. Our data enabled us to explore the relationship between the diversity of instantaneous feeding choices and the quantitative daily intake. On the instantaneous scale (20 s), we confirmed the functional relationship between bite mass and bite frequency. Little variation was observed in daily averages of ingestive behaviour components. But these averages hide the extremely large range of instantaneous values (from 0.04 to 1.2 g DM for bite mass). When

* Corresponding author. Tel.: +33 432 722 584; fax: +33 432 722 562.
  E-mail address: agreil@avignon.inra.fr (C. Agreil).

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 day, as a result of the behavioural quantity–quality trade-off. This article provides knowledge about which type of diversity in plant parts size, structure and composition offers a small ruminant satisfying behavioural leeway in composing its meals and reaching physical satiety. We tend to discard pastoral management practices focused on biomass evaluation, and encourage further studies that will help qualify the nature and structure of vegetation that offers adjustment possibilities at both the individual and flock levels.

1. Introduction

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 (e.g. Wilmshurst et al., 1999 on Thomson's gazelle), both as tests of theory and as ways to adapt models and concepts to produce management guidelines in grazing ecosystems. This is, for instance, the case where grazing practices are developed as management tools to preserve land biodiversity by controlling the dynamics of plant communities. To achieve this objective, the scientists need to understand and quantify the choices made by the herbivores when selecting food from very heterogeneous vegetation. The responses of herbivores vary with the characteristics of vegetation, not only in the amount of biomass removed but also in the nature of the species and the plant organs consumed (Wilmshurst et al., 1999; Forbes, 1995; Provenza, 1995).

Three plant characteristics are generally used to describe, explain, and predict the foraging behaviour of ruminants (Laca and Demment, 1996): plant structure, digestible matter content, and toxin content.

Plant structure determines the accessibility and size of plant organs, hence influencing the two central components of instantaneous intake rate (IIR, g min^{-1}): bite mass (BM, g bite^{-1}) and bite frequency (BF, bite min^{-1}) (Spalinger and Hobbs, 1992). Consequently, plant structure may have a major impact on the daily intake as it is the product of intake rate (IR) by daily feeding time. When ruminants are restricted to one grazing area (e.g. a paddock) long enough, they have to satisfy their requirements by consuming a resource that dwindles in time as a result of grazing. In this case, they adjust their behaviour to maintain their intake rate (Illius and Gordon, 1987; Demment and Greenwood, 1988; Hewitt and Kirkpatrick, 1996). One of the first behavioural adjustments is to compensate for the decrease in bite mass by an increase in bite frequency (Allden and McD-Whittaker, 1970; Spalinger and Hobbs, 1992). When ruminants are faced with different levels of edible biomass, their adjustment is called the 'functional response'. Studies have shown that there is an inverse relationship between BM and BF because of the competition between chewing and cropping processes (Spalinger and Hobbs, 1992). The adjustment between BM and BF

is ultimately constrained by the physical capabilities of the animal to increase bite frequency or chewing rate (Ungar, 1996). Under these conditions of limited IR, ruminants can only maintain their intake level if feeding time is increased.

The digestible matter content of plant organs also plays a role in diet choices. It determines the turnover rate in the gut and can become a constraining factor when fibre content is too high, hence digestibility too low (Westoby, 1974; Belovsky, 1986; Illius and Gordon, 1991). Herbivores thus face a trade-off between food items that ensure adequate intake quantity and those that ensure adequate intake quality. The theoretical framework developed around this trade-off situation is commonly known as the 'forage maturation hypothesis' (Fryxell, 1991). It was developed on the basis of studies on swards that showed a negative correlation between availability, biomass or sward height, and quality, digestibility or nutrient content (McNaughton, 1979; Fryxell, 1991). Under these conditions, availability is the main constraint when animals graze on short swards while quality is the major constraint on higher swards, i.e. when forage is mature. As a consequence, herbivores are expected to select swards of intermediate height as a trade-off between constraints (Fryxell, 1991; Wilmshurst et al., 1999). In heterogeneous vegetation, such as shrubby rangelands, comprising not only grasses but also edible forbs, shrub and tree foliages, the relation between the size of the ingested items and their quality has not been confirmed (Van Soest, 1982; Meuret, 1997). In this situation, the 'forage maturation hypothesis' is probably less readily applicable.

The toxin content in plant parts can also strongly influence the diet choices. When choices are limited, consumption of plant parts containing toxins may quickly lead to post-ingestive malaise (Provenza, 1995). In heterogeneous vegetation, the presence of toxins in the diet also leads to plant aversion. The very wide spectrum of plant species and plant parts observed in the ruminant's diet has also been interpreted as an adaptive response that can dilute the effects of plant toxins (Launchbaugh, 1996; Hägele and Rowell-Rahier, 1999).

The ewes in our experiments were raised on farms that had a contractual agreement to restore biodiversity. The aim of this article is to characterise the dynamics of the behavioural response of these ewes that were faced with a food offer combining heterogeneity and variability. They were grazed on shrubby rangelands, containing a wide variety of grass, forb and shrub species, which meant a wide heterogeneity in both size and nutrient content of edible plants. They were grazed as home flocks for short periods of time in relatively small paddocks, and consequently had to cope with a daily change in both the size and structure of the edible plant parts.

2. Materials and methods

2.1. Study site and on-farm trials

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. In our definition, vegetation is heterogeneous if it contains a great daily diversity of edible items for sheep, which are widely dispersed within the paddocking area. This implies that it is

dominated by multi-stratified vegetation and contains edible plant organs that differ in nature (leaves, twigs, fruits, flowers and blades), phenological stage (vegetative, reproductive and senescent), size and/or density, and resulting nutritional value.

The first experiment was carried out in the month of August in the south of the Drôme region (France) within a flock composed of 214 recently dried, crossbred Prealpes/Merinos ewes. The flock grazed for 16 days on a 4.5 ha paddock, at an elevation of 1100 m. The vegetation was composed of calcareous sward (dominated by *Bromus erectus* Hudson) encroached with shrubs (*Genista cinerea* (DC.), *Juniperus communis* (L.), and *Buxus sempervirens* (L.)) and trees (*Pinus sylvestris* (L.), and *Pinus nigra Arn*. var. *austriaca Loud.*). The second experiment was carried out in April/May in the centre of the Ardèche region within a flock composed of 25 dry Ile-de-France ewes that grazed for 14 days in a 1.1 ha paddock, at an elevation of 980 m. The vegetation was composed of silicaceous mountain grasses (dominated by *Festuca* sp.) on volcanic substrata encroached with shrubs (*Cytisus purgans* (L.) Benth.). In both experiments, the flock had already been grazed in this environment for several years. Before and during the experiments, the flocks were taken to a series of very similar paddocks. They were only allowed to graze in the paddock, and only during daytime. They received a supplement of salt licks and minerals at night in the night paddock.

2.2. Observation of flock activities

Observations were made during full daytime periods, starting on the day the flock entered the paddock and every second day thereafter. A flock observer recorded, by scan sampling (Altman, 1974), the time devoted by the flocks to ingestion, movement and rest. Every 10 min as well as for every major and collective interruption in activities, we recorded the proportion of individuals allocated to each of the three activities. Movement only refers to fast, group movement, but does not include the many frequent shorter and slower movements connected to the search for food at the individual level. The resting activity is defined as standing immobile or laying down. It also includes social interactions. The method has been described in detail by Agreil and Meuret (2004).

2.3. Observation of individual behaviour

Direct and continuous observation of bites taken by one individual was used to record the instantaneous ingestive behaviour. This method is a recent improvement (Agreil and Meuret, 2004) of the earlier methods developed by Meuret et al. (1985), Parker et al. (1993) and Dumont et al. (1995) to record foraging choices and intake in a heterogeneous environment. Intake estimated by this method has been validated through a comparison with (a) values obtained with an external marker (Meuret et al., 1985), (b) bite masses estimated using different techniques (Parker et al., 1993), and (c) estimated intake of esophageally fistulated animals (Wallis de Vries, 1995). The main recent improvements are (1) continuous recording instead of 1 min grouped observations (Meuret et al., 1994) and (2) refinement of bite categories to be able to record bites in highly heterogeneous and variable environment. A comprehensive description of the method is given below, but details are also available in Agreil and Meuret (2004).

We used a familiarisation procedure to accustom the animals to having an observer very close to them. It was the same observer who carried out both the familiarisation procedure and the observations. First, the observer spent several entire days in the paddock in order to accustom the whole flock to his presence. The success of the exercise is measured in terms of the distance the animals keep from the observer. This first step ended when the observer could move near and within the flock without any visible effect on the animals' movements and attitudes. Second, while alternating movement within the flock and close monitoring, the observer selected one animal within the flock for close and continuous focal observation during full daytime periods. The monitored individual was subsequently tested to ensure that its behaviour was consistent with that of the flock. The familiarisation procedure ended when the observer was able to move around and talk for the whole day while accompanying the monitored individual at a distance of approximately 0.5–1.5 m.

Individual intake kinetics was recorded using a bite-coding grid developed by Agreil and Meuret (2004). The observer stayed for 3 weeks in paddocks similar to the ones to be used for the experiment, in order to identify and classify all possible bite types carried out by the animal. The different bites were subsequently grouped into 40 bite categories (BC) based on the shape and size of the plant organs selected and the way they were cropped. To ensure that our bite categories were as broadly applicable as possible to small ruminants grazed under various conditions (but not too numerous), we were careful to avoid any botanical distinction at this stage. Information on plant species was recorded during the experiments and added as a modifier to BC.

The observer followed the monitored animal in order to continuously observe its mouth and to identify bites categories and plucked plant species. The observer remained alongside the animal so as not to obstruct its spontaneous line of movement. He dictated the chronology of feed choices in real time on a tape-recorder. Back in the lab, The Observer 3.0 software (Noldus Information Technology, 1995) was used to convert the taped BC codes into tables.

2.4. Analysis of plant samples

Plant samples were removed by the observer who manually simulated each BC recorded during the observations. To simulate prehensive bites as accurately as possible, the observer pinched the plant parts between his thumb and the blade of a blunt knife. These samples were used to estimate BC mass and nutritive quality. Each sample was frozen at $-30\,^{\circ}C$ and then dried in a ventilated oven before being weighed and ground. Temperature and drying duration were carefully adjusted so as to avoid overheating, and hence avoid denaturing the plant material (Meuret et al., 1993). The nutritive quality of each BC was estimated using near infrared reflectance spectrometry (Schenk et al., 1979; Dardenne, 1990). Calibration equations were obtained using conventional forage analysis for grasses, trees and shrub foliage (Dardenne et al., 1991; Meuret et al., 1993). This made it possible to predict the main components of simulated bites, namely, crude protein (CP), ash, and neutral detergent fibre (NDF) according to a method described by Van Soest and Robertson (1985), and the in vitro digestibility of organic matter (dOM), according to Aufrère (1982).

2.5. Estimation of plant consumption rates

The day after the flocks left the paddocks, a visual estimate was made of the plant consumption rate (Schmutz, 1983). The paddocks were divided into land units of very different sizes and shapes, but they were all considered as similar with regard to vegetation communities, ease of circulation for the flock, edible plant abundance and consumption rates (Carpenter and West, 1987; Miellet and Meuret, 1993). Two scores were given to each vegetation unit: one for the herbaceous species and the other for the shrubs. One score, expressed as a percentage, was selected from a total of five classes of consumption rates of potentially edible matter (Meuret, 1988): 0–5, 5–30, 30–75, 75–95 and 95–100%.

2.6. Statistical analyses

The daily intake is calculated for each nutritional component (DM, CP, NDF and dOM) by adding up the contents of all BC recorded in the day. The ingestive behaviour was described using three main characteristics: bite mass (BM, g DM bite^{-1}), bite frequency (BF, bites min^{-1}), and resulting intake rate (IR, g DM min^{-1}). This required the grouping of decision-related events (bites) into time intervals selected to characterise 'instantaneous behaviour'. Research devoted to more homogeneous areas often involved observations over a time period of between 0.5 and 5 min (Gross et al., 1993; Shipley et al., 1994; Ungar, 1996). We consider 'instantaneous' to mean the ingestive behaviour observed over a 20 s time period. In our observation conditions, this time interval was sufficiently long to include several bites, even when BF was low, and sufficiently short to avoid grouping bites with very different characteristics.

Variation over time in the daily characteristics of ingestive behaviour (feeding time, cumulated daily intake, BM, BF, IR) was tested using the Pearson correlation test (routine Splus5; Mathsoft, 1998), over the number of days spent in paddock, with 'no trend' as the null hypothesis.

3. Results

3.1. Grazing seriously depleted paddocks

Within each of the paddocks, flock grazing led to a major decrease in available edible vegetation. In the first experiment, the total consumption rate for the herbaceous species was between 75 and 95%. The consumption rate for shrubs was more varied: between 5 and 75%. In the second experiment, the consumption rate for herbaceous species was also between 75 and 95%. For shrubs (Cytisus purgans (L.) Benth.) the rate was under 5%.

3.2. Daily activity patterns and intake time-budgets were stable

Ewes were herded into paddocks for approximately 12 h during the daytime (Table 1). The continuously monitored individuals spent 7–8 h feeding (Table 1). No trend in the feeding time budget was detected either for the flock as a whole or for the continuously

Table 1

Variation, during the stay in the paddock, in the daily duration of presence in the paddocks and the time the individual and the flock devoted to intake (in hours) for each experiment

Number of days in paddock	Experiment 1			Experiment 2		
	Time spent in paddock (h)	Individual feeding time-budget (h)	Flock mean feeding time-budget (h)	Time spent in paddock (h)	Individual feeding time-budget (h)	Flock mean feeding time-budget (h)
1	11.01	7.28	7.85	12.02	9.75	8.05
3	14.07	6.72	6.10	11.94	8.78	7.89
5	12.83	6.65	6.90	12.02	8.97	8.16
7	11.86	7.42	7.38	12	9.73	8.38
9	12.95	6.97	6.24	11.97	8.30	7.26
11	11.78	8.38	6.83	11.98	10.20	8.47
13	12.99	7.57	6.95	12.01	9.95	8.53
15	11.26	5.57	4.69	–	–	–
Mean ± S.D.	12.34 ± 0.97	6.61 ± 0.96	7.08 ± 0.82	11.99 ± 0.03	9.38 ± 0.70	8.10 ± 0.44
Trend detected	NS	NS	NS	NS	NS	NS

The averages and the standard deviations are presented for each of the three variables. Each variable was tested for any correlation over the number of days spent in paddocks. All Pearson correlation tests are not significant (NS), with a probability threshold level of 5%.

monitored individuals, which means that feeding time remained stable while resources grew scarce. Long intake periods were observed, followed by periods of time devoted to the other activities (Fig. 1). These continuous intake periods corresponded to meals. In both experiments, we systematically observed that at least two meals were taken per day, namely, one at the beginning and one towards the end of the period in the paddock. On some days, especially in the second experiment, shorter meals were also taken in the middle of the day. Intake periods of the continuously monitored individuals are closely correlated to whole flock ingestion periods (Fig. 1).

3.3. No inter-day trend detected in daily intakes

To account for the differences in the live weight (LW) of monitored individuals, daily intakes were expressed in kilograms of metabolic weight (MW = $LW^{0.75}$). The following numbers in this paragraph apply to experiments 1 and 2, respectively. Daily dry matter intakes (DMI) were similar in both experiments: 77.9 ± 10.2 and 75.1 ± 16.9 g DMI/ kg MW (Table 2). A very high daily intake was observed for 'Day 1' (97.1 and 111.8 g DMI/kg MW), which gave that day a special status. When 'Day 1' was excluded, there was no detectable inter-day variation (Table 2) or any significant difference between the two experiments as the daily DMI were 75.0 ± 7.7 and 69.0 ± 8.5 g/kg MW. Conversely, the crude protein intake (CPI) was lower in experiment 1 than in experiment 2 (7.3 ± 0.9 and 11.2 ± 1.3 g CPI/kg MW). The neutral detergent fibre intake (NDFI) was 45.2 ± 5.6 and 42.2 ± 5.5 g NDFI/kg MW, and the digestible organic matter intake (DOMI) was 32.3 ± 2.8 and 37.1 ± 4.5 g DOMI/kg MW.

3.4. Little variation observed in daily averages of ingestive behaviour components

The daily averages of instantaneous bite mass (BM, Table 3) were systematically higher in experiment 1 than in experiment 2, as the two ranges of value observed did not overlap (multi-day averages were 0.143 and 0.084 g DM). On the other hand, relations between the daily averages of instantaneous bite frequency (BF) were the opposite (multi-day averages were 32.5 versus 42.2 bite min^{-1}). The resulting instantaneous dry matter intake rates (IR) were 4.61 and 3.55 g DM min^{-1}, respectively, for experiments 1 and 2. For the daily averages, the joint representation (Fig. 2) of these three variables (BM, BF, IR) confirms the functional relationships, widely established in literature for periods of less than a day: a higher BM is consumed with a smaller BF and resulted in a higher IR (see in Fig. 2 the position of observed points in relation to theoretical isoclines of DM intake rate, calculated as the product of BM on the x-axis and BF on the y-axis).

The average daily values for BM, BF, IR and organic matter digestibility (OMd) only showed slight inter-day variations. Data for day 1 in each experiment are not outliers in this case and were therefore included in the trend tests. In both experiments, there is a downward trend for BM: a 25 and 43% reduction in BM during the 16 and 14 grazing days in experiments 1 and 2, respectively. In the first experiment, the drop in BM is compensated by the tendency for gradual increases in BF, and hence the absence of a trend for the average daily IR. In experiment 2, the BF was higher than in experiment 1. No trend was observed for BF as the days went by. In this situation, a decrease in BM induced a decrease
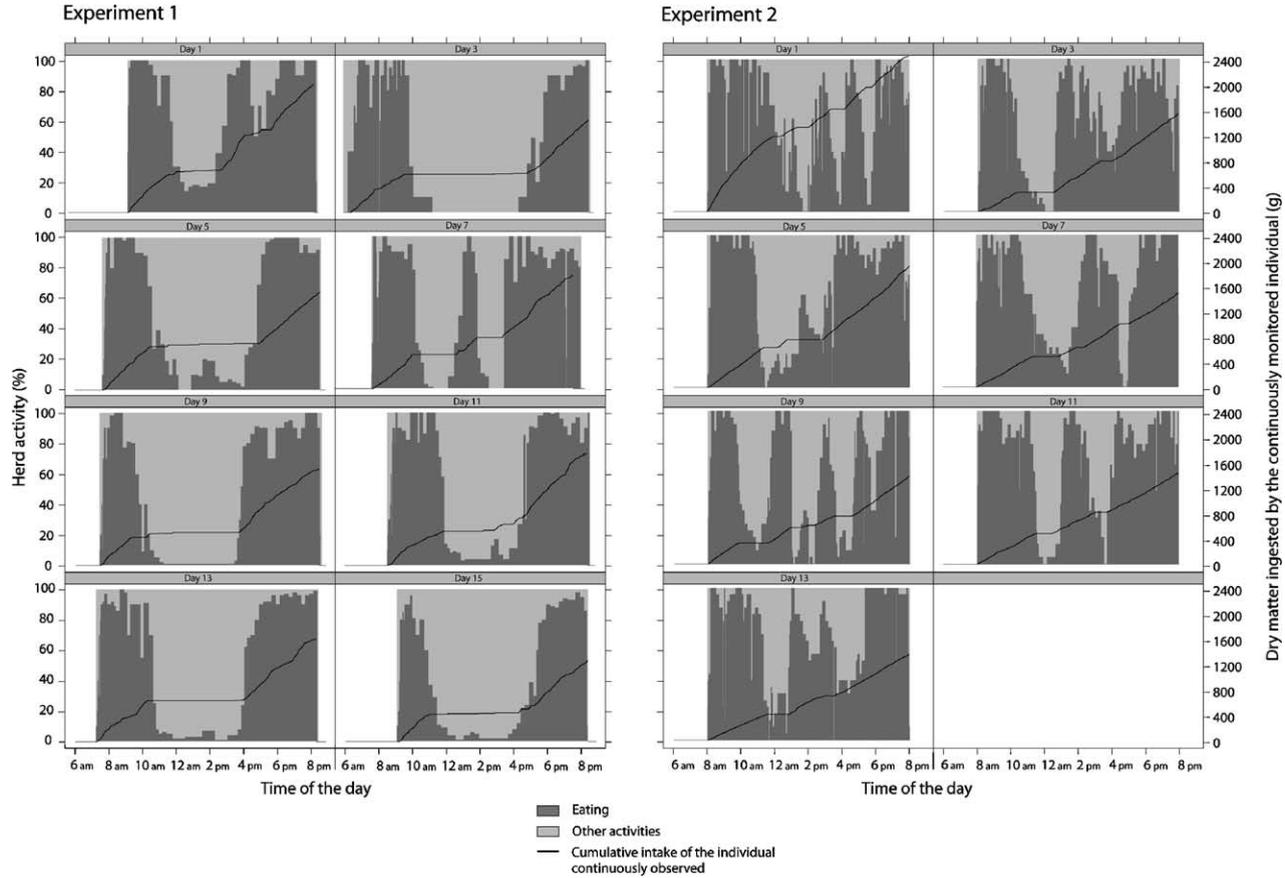
Fig. 1. Daily flock activity patterns and profiles of cumulated intake by continuously monitored individuals in Experiment 1 and Experiment 2. Flock activities (intake is shown in dark grey and rest in light grey) are given as percentages of the total flock. Cumulated intake of the monitored individuals is expressed in grams of dry matter (DM).

Table 2

Variation, during the stay in the paddock, in daily intake expressed in grams per kilo of metabolic weight (MW = $LW^{0.75}$)

Number of days in paddock	Experiment 1				Experiment 2			
	DMI (g/kg MW)	CPI (g/kg MW)	NDFI (g/kg MW)	DOMI (g/kg MW)	DMI (g/kg MW)	CPI (g/kg MW)	NDFI (g/kg MW)	DOMI (g/kg MW)
1	97.1	11.4	54.1	42.7	111.8	23.8	58.2	72.6
3	69.7	7.4	39.8	30.7	70.0	11.7	41.6	38.9
5	73.9	7.4	45.8	30.8	87.0	13.8	53.5	46.2
7	85.6	8.5	52.2	36.5	67.5	10.7	42.3	35.4
9	73.1	6.6	44.0	31.3	62.7	10.0	39.0	33.2
11	84.3	8.1	51.6	35.8	65.3	10.4	40.6	34.5
13	77.8	7.4	47.3	33.1	61.6	10.5	36.0	34.1
15	61.7	5.6	35.5	27.8	–	–	–	–
mean ± S.D.	77.9 ± 10.2	7.8 ± 1.6	46.3 ± 13	33.6 ± 4.4	75.1 ± 16.9	13.0 ± 4.6	44.5 ± 7.7	42.2 ± 13.1
mean ± S.D. (1st day excluded)	75.0 ± 7.7	7.3 ± 0.9	45.2 ± 5.6	32.3 ± 2.8	69.0 ± 8.5	11.2 ± 1.3	42.2 ± 5.5	37.1 ± 4.5
Trend detected (first day excluded)	NS	NS	NS	NS	NS	NS	NS	NS

Four characteristics of the diet are presented in detail: dry matter ingested (DMI), crude protein ingested (CPI), digestible organic matter ingested (DOMI), and neutral detergent fibre ingested (NDFI) consumed each day. The results of Pearson correlation test (over the number of days spent in paddocks) are presented on the last line: NS: not significant with a probability threshold of 5%.

Table 3
Variation, during the stay in the paddock, of the instantaneous bite mass, instantaneous bite frequency and instantaneous intake rate (daily averages ± standard deviation)

Number of days in paddock	Experiment 1				Experiment 2			
	Instantaneous bite mass (g DM)	Instantaneous bite frequency (bite min^{-1})	Instantaneous intake rate (g DM min^{-1})	Instantaneous OMd content (%)	Instantaneous bite mass (g DM)	Instantaneous bite frequency (bite min^{-1})	Instantaneous intake rate (g DM min^{-1})	Instantaneous OMd content (%)
1	0.168 ± 0.122	26.8 ± 13.5	4.51	44.0 ± 11.1	0.100 ± 0.032	46.1 ± 19.9	4.62	64.9 ± 17.7
3	0.157 ± 0.140	25.7 ± 17.2	4.04	44.0 ± 15.1	0.089 ± 0.029	37.4 ± 19.1	3.35	55.6 ± 16.8
5	0.136 ± 0.109	29.5 ± 13.8	4.03	41.7 ± 10.0	0.091 ± 0.044	44.7 ± 19.5	4.07	53.1 ± 13.3
7	0.152 ± 0.157	31.1 ± 16.5	4.75	42.6 ± 12.2	0.087 ± 0.088	37.7 ± 18.8	3.31	52.4 ± 11.7
9	0.127 ± 0.143	34.3 ± 19.7	4.37	42.8 ± 10.8	0.084 ± 0.081	41.5 ± 19.3	3.50	53.0 ± 10.9
11	0.130 ± 0.169	34.1 ± 19.4	4.43	42.5 ± 8.3	0.081 ± 0.090	38.8 ± 18.8	3.15	52.9 ± 12.0
13	0.148 ± 0.200	36.7 ± 21.3	5.41	42.5 ± 8.4	0.057 ± 0.055	49.5 ± 22.5	2.86	55.3 ± 13.5
15	0.126 ± 0.173	42.1 ± 24.1	5.32	45.1 ± 10.3	–	–	–	–
Mean ± S.D.	0.143 ± 0.014	32.5 ± 5.1	4.60 ± 0.49	43.2 ± 1.03	0.084 ± 0.012	42.2 ± 4.3	3.55 ± 0.56	55.3 ± 4.1
Trend detected (first day included)	D ($P = 0.04$)	I ($P = 0.00$)	NS	NS	D. ($P = 0.01$)	NS	D. ($P = 0.01$)	NS

The general mean and inter-day standard deviation is also given for each experiment. The results of Pearson correlation test (over the number of days spent in paddocks) are presented on the last line: D.: Decreasing, I.: Increasing and NS: Not Significant with a probability threshold of 5%.
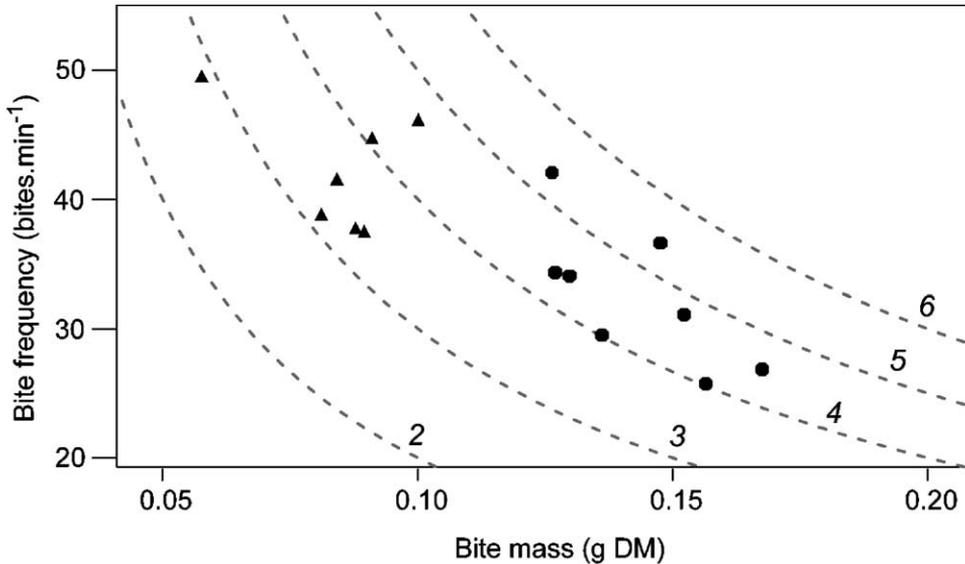
Fig. 2. Daily averages for bite mass (g DM bite^{-1}) and bite frequency (bite min^{-1}) in experiments 1 (round) and 2 (triangular). The dotted curves represent the isoclines of the dry matter intake rate (in g DM min^{-1}).

in the dry matter IR (Table 3). Last, there was no observable trend for the daily average OMd of selected plants (Table 3).

Although the differences between daily average in BM and BF throughout the two experiments were slight, the intra-day standard deviations were high. In both experiments, the downward trends for BM (Table 3) were accompanied by an upward trend in daily standard deviations over the number of days spent in paddocks ($R = 0.82$, $P = 0.007$ and $R = 0.67$, $P = 0.05$, for experiments 1 and 2). This suggests that ewes use an increasingly wider range of bite masses as vegetation size and structure decline.

3.5. The ewe chose large bite masses during the last few days

Compared to variations in daily average values, the range of bite masses was extremely wide (0.04–1 g bite^{-1} and 0.06–1.2 g DM bite^{-1} in experiments 1 and 2, respectively). Although the average bite mass decreased, the day-to-day range of bite masses increased. When log transformed (Fig. 3), a positive trend was detected for the daily range of BM over the number of days spent in paddocks ($R = 0.90$, $P = .001$ and $R = 0.85$, $P = 0.008$). In experiment 2 for instance, bite masses between 0.15 and 1 g DM bite^{-1}, which were practically unused until day 5, were quite regularly observed during the following days (Fig. 3).

The combined representation of the averages of instantaneous BF according to BM is given in Fig. 3. During day 1, bite frequencies are rather homogeneous for the limited range of BM consumed. Thereafter, as the range of BM grew wider, the difference between the frequency of small and large bite masses became more pronounced (Fig. 3). Thus, towards
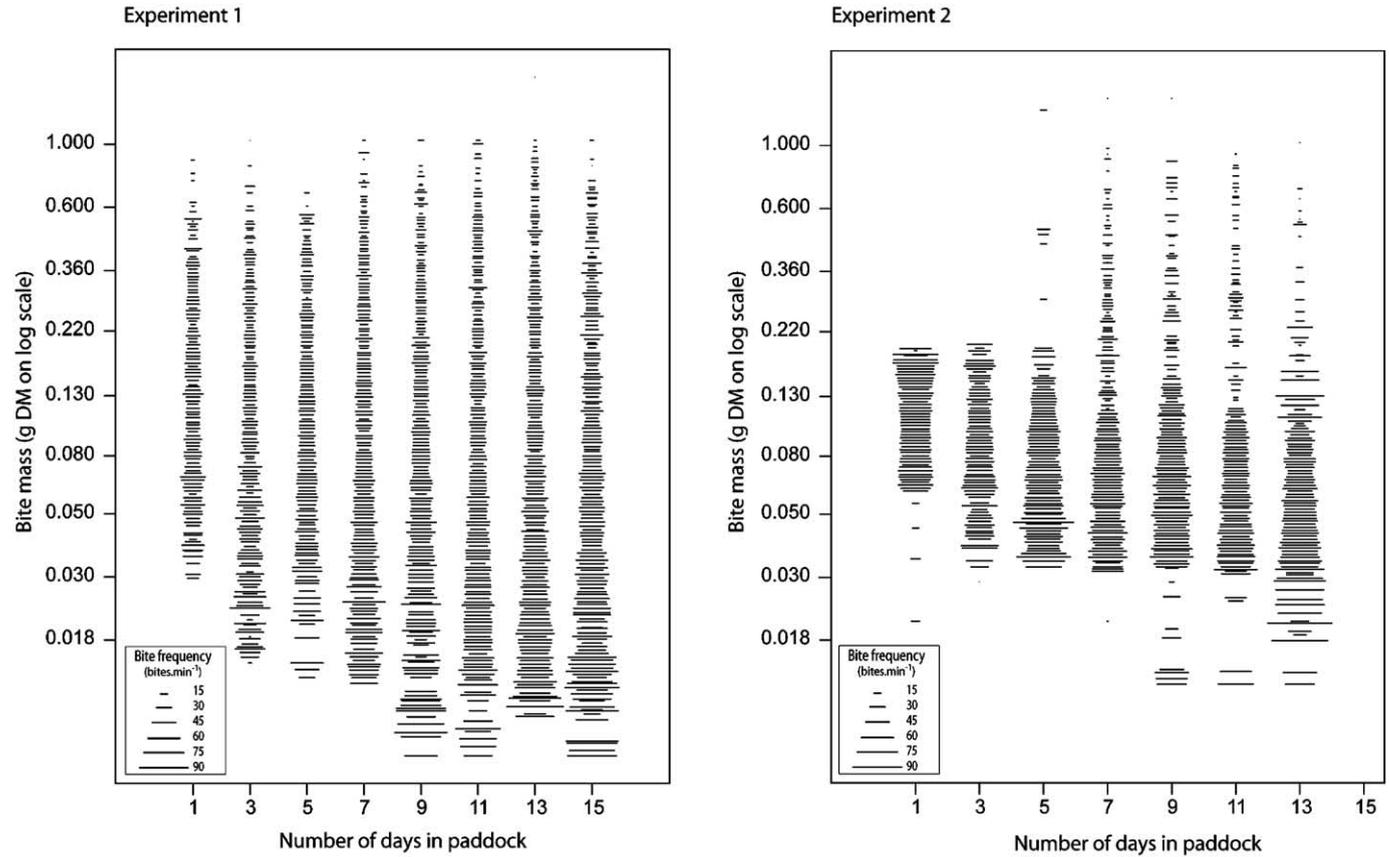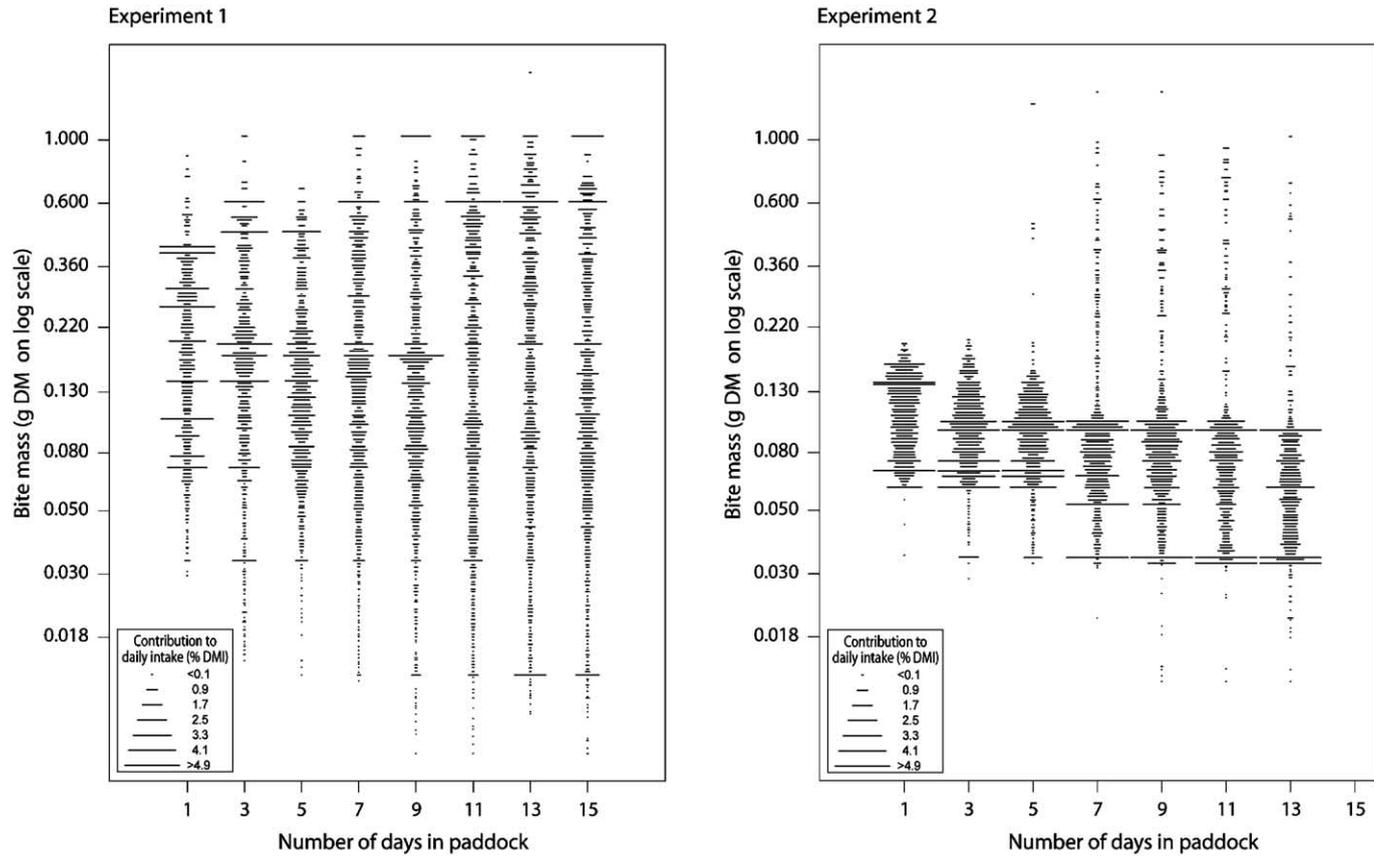
Experiment 1

Experiment 2

Fig. 3. Inter-day variation of the distribution of instantaneous bite masses during the paddocking sequence. The length of the black dashes is proportionate to the average bite frequency for each category of bite mass (in bite min^{-1}).

Fig. 4. Inter-day variation of the distribution of instantaneous bite masses during the paddocking sequence. The length of the black dashes is proportionate to the average contribution of each bite mass category to the total daily intake of dry matter (in %).

the end of the paddocking period, there was a large range of bites within any given day: for BM, between <0.018 and >0.6 g DM bite^{-1} and for BF, between >60 and <15 bites min^{-1}. We did not clearly observe any saturation in bite frequency for small instantaneous bite masses.

The contribution of each observed BM to daily intake (Fig. 4) indicates that the variation in BM range had a major effect on intake. During the first few days in the paddock, the intermediary BM contributed most to dry matter intake (0.04–0.10 g DM bite^{-1} and 0.06–0.15 g DM bite^{-1} for experiments 1 and 2, respectively). As vegetation size and structure changed, the importance of the contribution of intermediary BM to daily intake slackened, and the major contributions to daily intake came from both the smaller and larger bite masses.

Among the bites selected during the first day, the ones with smaller mass had the highest OMd (Fig. 5). For days 3 and 5 in experiment 1, for instance, (Fig. 5), the bite masses with under 0.030 g DM were richer in OMd than the larger ones. However, during the last few days in both experiments, this negative correlation between BM and OMd was reversed, i.e. bites with higher mass had the highest OMd content. In experiment 1, for instance, a positively correlated quality gradient can be clearly discerned for days 11, 13 and 15.

4. Discussion

4.1. Intake much higher than predicted by existing models

Our patterns of flock activity concur with findings reported in literature. We observed feeding times that were around the median of published values, since time budgets can vary considerably depending on the intake rate (4.5–14.5 h) (Arnold, 1981; Belovsky, 1986). During the 12 h in the paddocks, the flocks devoted regular periods of time to feeding. They organised their intake into meals, and used the time in-between for rumination and rest. They often took their two meals between sunrise and sunset (Arnold and Dudzinski, 1978), but the length, position, and number of meals depended on external factors. Experiment 1 was carried out in the summer; feeding and movement were clearly interrupted in the middle of the day when temperatures were high. Even though the time of entry into the paddock was rather irregular, the morning meal always ended more or less at the same time. In experiment 2, which was carried out in the spring, temperature was not a source of discomfort, and additional meals were observed in the middle of the day. The activity patterns also seemed to be strongly affected by the time at which the farmer comes to withdraw the flock from the paddock at the end of each day. In both experiments, for instance, we observed great regularity in the starting time of the last daily meal. The animals were very accustomed to leaving the paddocks at a given time (around 8 p.m.) and seemed to prepare for it by starting to graze 3.5–4 h before that time.

Our estimates of daily intake are consistent with data from literature. However, they corresponded to an intake of green fodder given indoors, with OMd being between 75 and 80% (Dulphy et al., 1999). In our case the OMd was 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
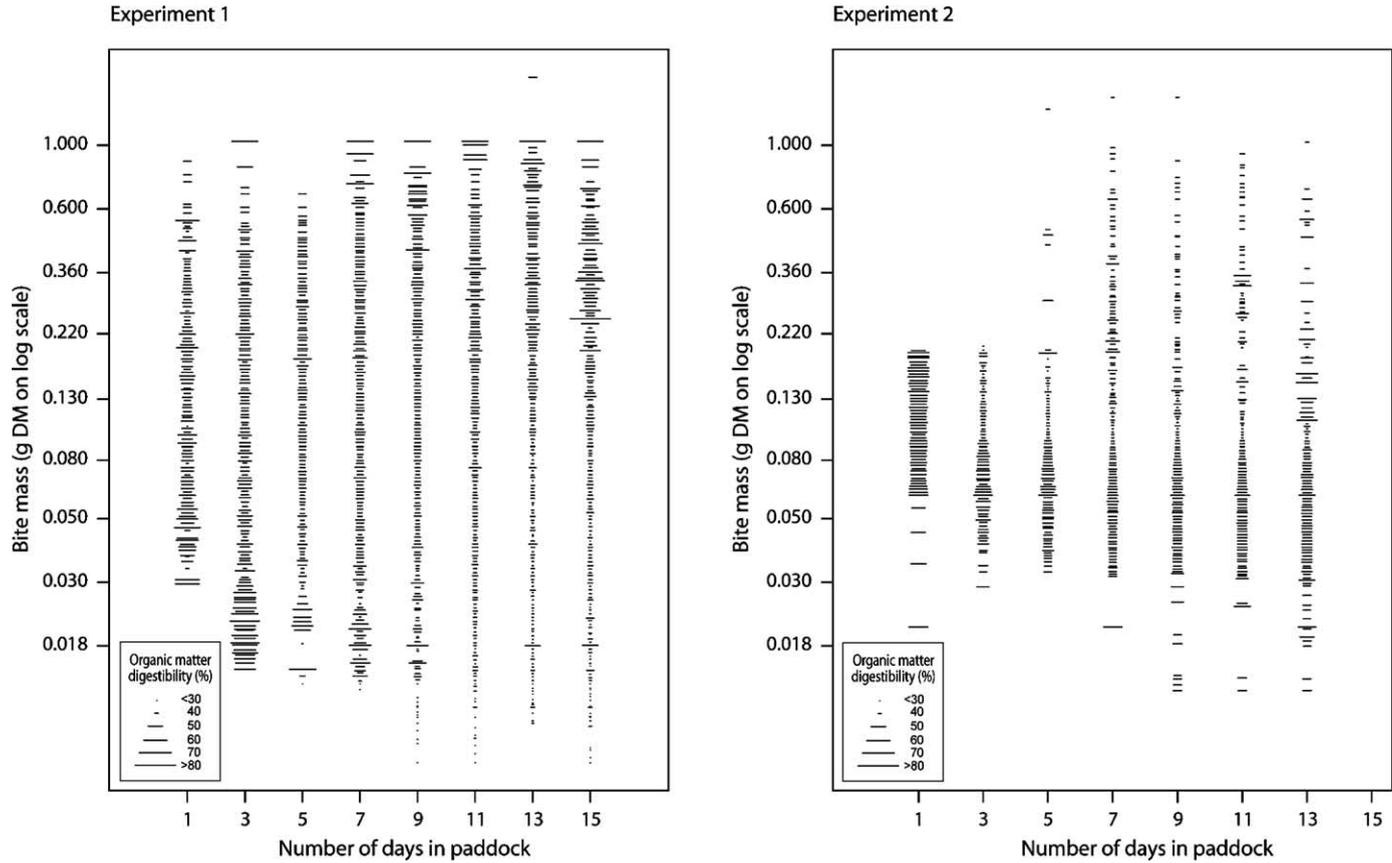
Fig. 5. Inter-day variation of the distribution of instantaneous bite masses during the paddocking sequence. The length of the black dashes is proportionate to the average organic matter digestibility for each category of bite mass (in %).

about twice as high as the ones predicted in the models published by Morley (1981) and Van Soest (1994).

4.2. Relevant time scales for describing feeding adjustments

Our results matched the literature on relative variations in daily averages for bite mass (BM), bite frequency (BF), and intake rate (IR). When the gradual decrease in the average bite mass was accompanied by an increase in average BF, the ewes were able to keep the average intake rate stable. This result confirmed the negative relationship between BM and BF, an ingestive behavioural adjustment described in literature on the basis of data obtained for short time intervals (3 min for Allden and McD-Whittaker, 1970; 1.5 min for Gross et al., 1993). Our multi-day average values for the instantaneous dry matter IR also confirmed the predominance of BM in determining the intake rate (IR) (Allden and McD-Whittaker, 1970; Demment and Greenwood, 1988; Spalinger and Hobbs, 1992).

Since we did not observe bite frequency saturation for the smallest bite masses, we cannot assert the existence of an asymptotic increase in BF, which is said to occur because handling time for low bite masses cannot be reduced (Gross et al., 1993; Ungar, 1996). The maximum instantaneous BF averages that we observed (approximately 50 bites min^{-1}) were relatively low, considering the small values of associated bite masses (<0.06 g DM $bite^{-1}$). This should be analysed in terms of our observation method: our instantaneous values were derived from a full day of continuous observation. The values actually reflected a series of behavioural responses associated to the sequence of different nutritional and motivational states of the ewe. In certain earlier works, the formalisation of relationships between BM, BF, and IR were obtained only with reference to ruminants that were under starvation in order to restrict the analysis to periods during which ruminants grazed at a frequency that was close to maximum BF (Gross et al., 1993; Shipley et al., 1994).

In heterogeneous vegetation, because of the wide range of instantaneous BM and BF, analyses should not be restricted to daily averages. As argued by Senft et al. (1987) and Schmitz (2000), studying a dynamic process in ecology involves preliminary identification of relevant organisational levels to be observed. Concerning ingestive behaviour in a ruminant, Bergman et al. (2001) stressed the fact that the analysis of food choices in response to changes in resources availability requires more than data on average daily behaviour. When we conducted the analysis on daily averages, we observed a tendency for the BM to decline. When we linked these daily averages with the dynamics of instantaneous ingestive behaviour, we were able to show that the decreases in the average daily BM were small in comparison to the range of bite masses. This stressed the fact that the calculation of the daily average bite mass gave proportionally more weight to the most frequent bite masses; as for a given IR, the number of bites is greater when the bite mass is small (Spalinger and Hobbs, 1992; Ginnett and Demment, 1995). When our results were expressed as percentages of the contribution of bites to daily intake, we saw that large bite masses contributed most.

In this article, we coupled the analysis of ingestive behaviour at two different time scales: the day, and the 20 s periods that defined our 'instantaneous' scale. Between the two, there are intermediary organisational levels related to the time scales that are relevant

to the ruminants' ingestion study and should be investigated. We will conduct other analyses on these data sets, focusing on the succession of meals and on intra-meal organisation.

4.3. The quantity–quality trade-off revisited under variable grazing conditions

Many experiments conducted on sown swards have shown that ruminants develop a preference in time for plant organs that allow them to clip high bite mass and thus, accelerate ingestion (Chacon and Stobbs, 1976; Black and Kenney, 1984). Unlike situation described above, the ewes we observed did not prioritise large bite masses during the first day in a paddock, even though they were of high OMd. The ewes chose increasingly large bite masses that gradually made up the greatest part of their daily intake during the last day in the paddock, as the size and structure of plant parts decreased. The use of bites with smaller mass than in day 1 choices corresponded to consumption of the remaining parts of previously consumed plant organs. The use of bites with larger mass is indicative of a selection process. The time in the paddock was indeed too short for the plants to grow and, thus, the large bite masses could have been removed during the first day.

Our results do not match the traditional theoretical framework in which ewes facing a diverse offer are assumed to first choose feed items that are most satisfactory in a 'quantity–quality trade-off'. Formalisation of this trade-off has been based mainly on the 'forage maturation hypothesis' (Westoby, 1974; Belovsky, 1986; Fryxell, 1991). According to this theoretical framework, feeding choices are analysed as a response to two main constraints: fodder availability and quality. But the relative importance of these two constraints is still being debated, and depends upon the pastoral conditions and the time scale (Hixon, 1982; Newman et al., 1995; Wilmshurst et al., 1999; Bergman et al., 2001). Rather than prioritising bites that are both heavy and OMd rich, the ewes we observed achieved adjustments of day-to-day feeding behaviour that led to a stabilisation of daily average digestibility and bite mass. This observation makes us suggest that potential high mass and good quality of feed items are not good predictors for estimating the ruminants' choices and temporal variations when faced a variability in the diversity of edible items.

4.4. Reasons for late consumption of high bite masses

We suggest that the late consumption of large bite masses is a functional response that enables the ewe to maintain its daily intake level while the vegetation on offer becomes gradually depleted. But other origins, that we have not yet explored might also be considered.

The forage maturation hypothesis has mainly been used to analyse the behavioural response when a fibre content gradient can be observed from the distal to the proximal parts of the plant. This is the case for grasses (McNaughton, 1979; Bergman et al., 2001) and for the foliage of deciduous trees (Lundberg and Danell, 1990; Shipley et al., 1999). Facing such a gradient, ruminants have to choose either small-size plant parts, which means small mass and highly nutritive bites, or large-size plant parts, which means bites that have greater mass but poorer quality (Shipley et al., 1999; Vivas et al., 1991). In rangelands, the relation between bite mass and bite quality seems much less linear, because of the great

variety in plant architecture. Many species, like the forbs, shrubs and lianas that do not fit into this gradient, (Van Soest, 1982), could explain some apparent contradictions between different studies.

Other characteristics of plant parts have been identified in literature as possible explanations for delaying the selection of feed items by ruminants. On the basis of post-ingestive malaise, ruminants are able to identify and memorise harmful plant organs (Provenza, 1995; Launchbaugh, 1996). In our two experiments, we have not examined the possibility that bite selection patterns could be explained by the toxin content of bites. Under our observation conditions, few species have been identified for containing toxins, such as broom (*Genista* spp.) (Greinwald et al., 1992; Gonzalez–Andres and Ortiz, 1996). More generally, ruminants are sensitive to many plant characteristics that can affect their dietary choices, e.g. odour, colour, accessibility, texture, and taste. Selection criteria probably entail many factors that do not have much to do with satisfying nutritional needs (Provenza et al., 2000). Last, variation in bite choices over time can be related to the successive consumption of various botanical species. There is evidence that the consumption of certain species only begins when the consumption rate for the preferred species has exceeded a certain level (O'Reagain and Grau, 1995). Although we observed that high bite masses were taken off plant species, which were already consumed during the first day (broom species for instance), the delayed consumption of high bite masses should be analysed in relation to the botanical species consumption order.

5. Conclusion

Our results with ewes grazing on heterogeneous vegetation stressed the importance of characterising the dynamics of ingestive behaviour, since behavioural adjustments were made at different time scales. In such an environment, the diversity of resource size, structure and composition provided the small ruminant with more behavioural leeway in composing its meals than it would have grazed a more homogeneous environment. By capitalising on the great diversity of edible items available, the individuals were able to reach physical satiety in a reasonable length of time, despite the conditions imposed by group living and flock management schedules.

With regard to pastoral management, the objective became the maintenance of the functional heterogeneity needed to sustain intake through behavioural adjustment. This required a definition of the nature and structure of vegetation that allowed for adjustment possibilities at the individual level. But, as management is designed for application at the flock level, there is a need for further knowledge in which grazing areas are perceived in terms of spatial structures that enhanced the expression of individual behaviour within a spatio-temporal flock organisation and not in terms of available biomass.

and Odile Villeflayoux. We are also grateful for the outdoor support provided by Marc Vincent, Jean-Paul Chabert, Simon Dufour, Lizzie Napoli and for the indoor support from Richard Agneessens, Claude Bruchou, Joël Chadoeuf, Claudine Clément, Pierre Dardenne, Philippe Lecomte and Pascal Monestiez. Laurence de Bonneval and Tilly Gaillard are to be thanked for the translation into English.

References

Agreil, C., Meuret, M., 2004. An improved method for quantifying intake rate and ingestive behaviour of ruminants in diverse and variable habitats using direct observation. Small Ruminant Res. 54 (1–2), 99–113.

Allden, W.G., McD-Whittaker, I.A., 1970. The determinants of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. Aust. J. Agric. Res. 21, 755–766.

Altman, J., 1974. Observational study of behaviour: sampling methods. Behaviour 9, 227–265.

Arnold, G.W., 1981. Grazing behaviour. In: Morley, F.H.W. (Ed.), Grazing Animals. Elsevier, Oxford, UK, pp. 79–101.

Arnold, G.W., Dudzinski, M.L., 1978. Ethology of Free-ranging Domestic Animals. Elsevier, New York.

Aufrère, J., 1982. Etude de la prévision de la digestibilité des fourrages par une méthode enzymatique. Ann. Zootech. 31, 111–130 (in French, with English abstract).

Belovsky, G.E., 1986. Optimal foraging and community structure: implications for a guild of generalist grassland herbivores. Oecologia 70, 35–52.

Bergman, C.M., Fryxell, J.M., Gates, C.C., Fortin, D., 2001. Ungulate foraging strategies: energy maximizing or time minimizing? J. Anim. Ecol. 70, 289–300.

Black, J.L., Kenney, P.A., 1984. Factors affecting diet selection by sheep: 2. Height and density of pasture. Aust. J. Agric. Res. 35, 551–563.

Carpenter, A., West, N., 1987. Validating the reference-unit method of aboveground phytomass estimation on shrubs and herbs. Vegetatio 72, 75–79.

Chacon, E., Stobbs, T.H., 1976. Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. Aust. J. Agric. Res. 27, 709–727.

Dardenne, P., 1990. Contribution à l'utilisation de la spectrométrie dans le proche infrarouge pour l'étude de critères de qualité des céréales et des fourrages. (in French) Ph.D. Dissertation, University of Gembloux.

Dardenne, P., Sinnaeve, G., Biston, R., Lecomte, P., 1991. Fresh grass analysis by NIR spectroscopy. In: Proceedings of the 4th International NIRS Aberdeen, August 19–23, pp. 277–283.

Dulphy, J.-P., Baumont, R., L'Hotelier, L., Demarquilly, C., 1999. Improvement of the measurement and prediction of forage ingestibility in sheep by taking into account the variations of their intake capacity using a standard forage. Ann. Zootech. 48, 469–476 (in French with English abstract).

Demment, M.W., Greenwood, G.B., 1988. Forage ingestion: effects of sward characteristics and body size. J. Anim. Sci. 66, 2380–2392.

Dumont, B., Meuret, M., Prud'Hon, M., 1995. Direct observation of biting for studying grazing behaviour of goats and llamas on garrigue rangelands. Small Ruminant Res. 16, 27–35.

Forbes, J.M., 1995. Voluntary Food Intake and Diet Selection in Farm Animals. CAB International, Oxon, UK, p. 532.

Fryxell, J.M., 1991. Forage quality and aggregation by large herbivores. Am. Nat. 138, 478–498.

Ginnett, T.F., Demment, M.W., 1995. The functional response of herbivores: analysis and test of a simple mechanistic model. Funct. Ecol. 9, 376–384.

Gonzalez–Andres, F., Ortiz, J.M., 1996. Potential of *cytisus* and allied genera (Genisteae: Fabaceae) as forage shrubs: 2. Chemical composition of the forage and conclusions. N. Z. J. Agric. Res. 39, 205–213.

Greinwald, R., Bachmann, P., Witte, L., Acebes-Grinoves, J.R., Czygan, F.C., 1992. Taxonomic signifiance of alkaloids in the genus *Adenocarpus* (Fabaceae–Genisteae). Biochem. Sys. Ecol. 20, 69–73.

Gross, J.E., Shipley, L.A., Hobbs, N.T., Spalinger, D.E., Wunder, B.A., 1993. Functional response of herbivores in food-concentrated patches: tests of mechanistic model. Ecology 74, 778–791.

Hägele, B.F., Rowell-Rahier, M., 1999. Dietary mixing in three generalist herbivores: nutrient complementation or toxin dilution? Oecologia 119, 521–533.

Hewitt, D.G., Kirkpatrick, R.L., 1996. Forage intake rates of ruffed grouse and potential effects on grouse density. Can. J. Zool. 74, 2016–2024.

Hixon, M.A., 1982. Energy maximizers and time minimizers: theory and reality. Am. Nat. 119, 596–599.

Illius, A.W., Gordon, I.J., 1987. The allometry of food intake in grazing ruminants. J. Anim. Ecol. 56, 989–999.

Illius, A.W., Gordon, I.J., 1991. Prediction of intake and digestion in ruminants by a model of rumen kinetics integrating animal size and plant characteristics. J. Agric. Sci. 116, 145–157.

Laca, E.A., Demment, M.W., 1996. Foraging strategies of grazing animals. In: Hodgson, J., Illius, A.W. (Eds.), The Ecology and Management of Grazing Systems. CAB International, Oxon, UK, pp. 137–158.

Launchbaugh, K.L., 1996. Biochemical aspects of grazing behaviour. In: Hodgson, J., Illius, A.W. (Eds.), The Ecology and Management of Grazing Systems. CAB International, Oxon, UK, pp. 159–184.

Lundberg, P., Danell, K., 1990. Functional response of browsers: tree exploitation by moose. Oikos 58, 378–384.

Mathsoft, 1998. S-PLUS 5 for UNIX Users Guide, Data Analysis Products Division, MathSoft, Seattle, WA.

McNaughton, S.J., 1979. Grazing as an optimization process: grass-ungulate relationships in the Serengeti. Am. Nat. 113, 691–703.

Meuret, M., 1988. Feasibility of in vivo digestibility trials with lactating goats browsing fresh leafy branches. Small Ruminant Res. 1, 273–290.

Meuret, M., 1997. Préhensibilité des aliments chez les petits ruminants sur parcours en landes et sous-bois. Prod. Anim. 10, 391–401 (in French, with English abstract).

Meuret, M., Bartiaux-Thill, N., Bourbouze, A., 1985. Feed intake of dairy goats on woody rangelands: direct observation of biting method; chromic oxide method. Ann. Zootech. 34, 159–180 (in French with English abstract).

Meuret, M., Dardenne, P., Biston, R., Poty, O., 1993. The use of NIR in predicting nutritive value of mediterranean tree and shrub foliage. J. Near Infrared Spect. 1, 45–54.

Meuret, M., Viaux, C., Chadoeuf, J., 1994. Land heterogeneity stimulates intake during grazing trips. Ann. Zootech. 43, 296.

Miellet, P., Meuret, M., 1993. Savoir faire pâturer en SIG. Mappe. Monde. 2, 12–17 (in French).

Morley, F.H.W., 1981. Grazing animals. In: Neimann-Sorensen, A., Tribe, D.E. (Eds.), World Animal Science B1. Elsevier, p. 411.

Newman, J.A., Parsons, A.J., Thornley, J.H.M., Penning, P.D., Krebs, J.R., 1995. Optimal diet selection by a generalist grazing herbivore. Funct. Ecol. 9, 255–268.

Noldus Information Technology, 1995. The Observer, Base Package for the Macintosh. Reference Manual, Version 3.0, Netherland.

O'Reagain, P.J., Grau, E.A., 1995. Sequence of species selection by cattle and sheep on South African sourveld. J. Range. Manage. 48, 314–321.

Parker, K.L., Gillingham, M.P., Hanley, T.A., 1993. An accurate technique for estimating forage intake of tractable animals. Can. J. Zool. 71, 1462–1465.

Provenza, F.D., 1995. Postingestive feedback as an elementary determinant of food preference and intake in ruminants. J. Range. Manage. 48, 2–17.

Provenza, F.D., Kimball, B.A., Villalba, J.J., 2000. Roles of odor, taste, and toxicity in the food preferences of lambs: implications for mimicry in plants. Oikos 88, 424–432.

Schenk, J.S., Westerhaus, M.O., Hoover, M.R., 1979. Analysis of forage by infrared reflectance. J. Dairy Sci. 62, 807.

Schmitz, O.J., 2000. Combining field experiments and individual-based modeling to identify the dynamically relevant organizational scale in a field system. Oikos 89, 471–484.

Schmutz, E.M., 1983. Browsed-class method of estimating shrub utilization. J. Range. Manage. 36, 632–637.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E., Swift, D.M., 1987. Large herbivore foraging and ecological hierarchies. Bioscience 37, 789–799.

Shipley, L.A., Gross, J.E., Spalinger, D.E., Hobbs, N.T., Wunder, B.A., 1994. The scaling of intake rate in mammalian herbivores. Am. Nat. 143, 1055–1082.

Shipley, L.A., Illius, A.W., Danell, K., Hobbs, N.T., Spalinger, D.E., 1999. Predicting bite size selection of mammalian herbivores: a test of a general model of diet optimization. Oikos 84, 55–68.

Spalinger, D.E., Hobbs, N., 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. Am. Nat. 140, 325–348.

Ungar, E.D., 1996. Ingestive behaviour. In: Hodgson, J., Illius, A.W. (Eds.), The Ecology and Management of Grazing Systems. CAB International, Oxon, UK, pp. 185–218.

Van Soest, P.J., 1982. Nutritional Ecology of the Ruminant. Cornell University Press, London, UK.

Van Soest, P.J., 1994. Nutritional Ecology of the Ruminant, 2nd ed. Cornell University press, New York, USA.

Van Soest, P.J., Robertson, J.B., 1985. Analysis of Forages and Fibrous Foods: a laboratory manual for animal science. Cornell University Press, London, UK.

Vivas, H.J., Saether, B.E., Andersen, R., 1991. Optimal twig-size selection of a generalist herbivore, the moose Alces alces: implications for plant–herbivore interactions. J. Anim. Ecol. 60, 395–408.

Wallis de Vries, M.F., 1995. Estimating forage intake and quality in grazing cattle: a reconsideration of the hand-plucking method. J. Range. Manage. 48, 370–375.

Westoby, M., 1974. An analysis of diet selection by large generalist herbivores. Am. Nat. 108, 290–304.

Wilmshurst, J.F., Fryxell, J.M., Colucci, P.E., 1999. What constrains daily intake in Thomson's gazelles. Ecology 80, 2338–2347.