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Does sward height affect feeding patch choice and voluntary intake in horses?

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ABSTRACT

The numbers of horses grazing at pasture are increasing in developed countries, so a proper understanding of their feeding selectivity and of the tactics they use for extracting nutrients from swards is essential for the management of horses and grasslands. Resource acquisition in herbivores can be optimised through the modulation of their intake and patch selection, both being strongly dependent on the characteristics of swards. However, the principles by which horses adjust their grazing behaviour in response to variations in sward features are not completely understood. The aim of this study was to determine whether the behaviour of horses conforms to optimal foraging models. We hypothesized that, faced with binary choices between vegetative swards of a good and similar quality at three different heights, horses would select the taller sward, *i.e.* that allowing a higher reward in terms of dry matter intake rate. Three groups of three 2-year-old saddle horses were grazed on a semi-natural pasture that was managed to produce three contrasting sward heights at 6, 11 and 17 cm, in a Latin-square design. The instantaneous intake rate was determined from bite rate measured at pasture on the three sward heights, and bite mass estimated from measurements using swards offered indoors in experimental trays. Daily dry matter intake was estimated individually by total faecal collection and an estimation of digestibility from faecal nitrogen. Short-term (first 30 min) and daily preferences were assessed from the time spent grazing each sward offered in pair-wise tests at pasture. The results show that daily voluntary intake (an average of 21 g DM kg LW^{-1} day^{-1}) and total grazing time (an average of 14 h day^{-1}) were independent of sward height and of the choice of patches offered. In choice situations, the animals spent more time grazing on the taller sward, both during the first 30 min and at the daily scale. These results show that horses choose between vegetative patches of a good and similar quality according to the predictions from optimal foraging models, and select the one that they can ingest faster. Further research will now have to explore how the horses will adapt their feeding behaviour when they face a trade-off between sward height and quality.

1. Introduction

Horses play an increasing role in the management of grasslands in Europe so a proper understanding of the tactics they use for extracting energy and nutrients from swards is essential for the management of animals and pastures. Resource acquisition in herbivores is determined

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by their voluntary intake and the quality of the diet. Patch selection, a key element of the animals' foraging tactics (Roguet et al., 1998), is strongly influenced by grass characteristics. The principles underlying patch selection by large ruminant herbivores are becoming better understood and are now being used as a basis for management: among the key concepts, the Optimal Foraging Theory (Stephens and Krebs, 1986) assumes that animals should maximise their net benefits. However, it is not known if this principle can be applied to equids, since horses at pasture, with their two sets of incisors, show a marked selection for short patches, where they may not maximise their energy intake rate, and avoid feeding on mature tall grass, at least during the grass growing season (Edwards and Hollis, 1982). This has for a long time been interpreted as an anti-parasite strategy, with horses avoiding feeding on the tall swards where their faeces are concentrated (Taylor, 1954); however a recent study has suggested that the maintenance of patches of short swards of high nutritional value could enable the horses to maximise their digestible nutrient intake (Fleurance et al., 2005). Further, this behaviour could perhaps result from differences in species composition of the short and tall swards, and it is difficult to distinguish causes from effects by observation alone (Putman et al., 1991).

The question of the applicability of the principles of optimal foraging to horses demands an experimental test of the extent to which these models allow patch selection in horses to be predicted successfully. If animals forage in ways to optimise the long-term acquisition rate of energy (which is often taken to be a surrogate for fitness; Stephens and Krebs, 1986) they should select food items that maximise the rate of energy intake at the instantaneous level too (Van Wieren, 1996). Studies of patch selection by horses have shown that they can discriminate among vegetative patches (perennial rye-grass, *Lolium perenne*) of 5, 8 and 15 cm, and prefer the taller ones (Naujeck et al., 2005) on which their intake rates are assumed to be higher. However as the quality of the patches was not measured, it is possible that the animals were tracking quality and not their intake rate.

From previous studies, intake rates in herbivores are determined by factors which depend both on the animals (morphological/behavioural constraints) and on the plants involved (spatial structure and mechanical properties of the swards) (Laca et al., 1992a, for a review). In horses, the functional response, *i.e.* the quantity of food consumed per unit of time as a function of food availability, has been described to be asymptotic as in most mammalian herbivore species (Gross et al., 1993; Fleurance et al., 2009). This could result from competition between harvesting and chewing activities (Spalinger and Hobbs, 1992). This implies that, on vegetative swards, intake rates should increase with sward height until they reach an upper limit on high biomass swards.

Changes in sward height are generally confounded with changes in the nutritional value of grasses, since plant growth results in more structural fibre, which in turn decreases quality (Van-Soest, 1982). Previous work on patch choice by horses, in permanent pastures (Fleurance et al., 2001, 2007; Ménard et al., 2002; Lamoot et al., 2005) or more controlled conditions (Naujeck et al., 2005), has not so far measured the effect of sward height independently of sward quality. In the present study, the response of horses to a decrease in grass height (between 17 and 6 cm), while the quality was kept similar, was investigated. Our aim was to determine whether horses, offered pair-wise choices between vegetative patches of different heights, would express choices on the basis of maximising their nutrient intake rates, as predicted by optimal foraging models (Stephens and Krebs, 1986). By doing this, the animals should select the taller swards, where their dry matter instantaneous intake rate is higher. The horses were maintained over a week in these choice situations so that their intake was fully regulated by constraints that may apply on a daily, rather than an instantaneous, basis. The preferences of the animals were recorded at the start of the day (during the first 30 min of tests), and over the whole day to allow us to detect any adjustments. The consequences of variations in height for daily dry matter intake and grazing time were investigated on each sward offered alone, as well as when the horses had a choice between two sward heights.

2. Material and methods

The experiment was done at the experimental farm of the French National Stud (Chamberet, France, 01°43′14″–45°35′03″, 440 m) from May to June and then from September to October 2006. Nine, 2-year-old female saddle horses (Anglo-Arab and French Saddle horses) were used for the experiment after being accustomed to the experimental measurements during the month prior to the tests. These females were selected from a group of eleven 2-year-old saddle females on the basis of their liveweight; they were all bred and kept together at pasture from spring to autumn and received the same diet in individual stables during winter. The permanent pasture used throughout the experiments (9.5 ha) contained 23 species of plants: grass species accounted for 60% of the vegetation, dicotyledons and legumes respectively 23 and 17%. The pasture was dominated by rough bluegrass (*Poa trivialis*), perennial rye-grass (*L. perenne*), white clover (*Trifolium repens*) and dandelion (*Taraxacum* spp.); these were evenly distributed through the pasture and accounted for 90% of the plant biomass.

2.1. Experimental design and procedure

The experiment followed a Latin-square design with three groups, three treatments and three test periods (Table 1). The three groups of three horses were balanced for their liveweight (LW = 514 kg ± 6 S.E.) throughout the experiment, and the individuals in each group were changed for each period (Table 1). Horses are highly social ungulates organised in dominance hierarchies, and the diet of the dominant horse may be of a higher quality (Duncan, 1992). Re-grouping was done to prevent the establishment of a strong hierarchy, and to avoid confounding the period effect with a possible group effect which might affect the horses' feeding behaviour. The animals were treated against

Table 1
Experimental design of the tests. Each period of the Latin-square design was composed of three different tests of 1 week long each, which were proposed to three groups of three individual horses (the composition of the groups was changed among periods).

Period	Individuals (no.)	1st week: experimental trays	2nd week: swards offered alone	3rd week: pair-wise choices
P1	7, 8, 9	Short	Short	Intermediate–Tall
	4, 5, 6	Intermediate	Intermediate	Short–Tall
	1, 2, 3	Tall	Tall	Short–Intermediate
P2	1, 4, 7	Short	Short	Intermediate–Tall
	2, 5, 8	Intermediate	Intermediate	Short–Tall
	3, 6, 9	Tall	Tall	Short–Intermediate
P3	3, 4, 8	Short	Short	Intermediate–Tall
	1, 5, 9	Intermediate	Intermediate	Short–Tall
	2, 6, 7	Tall	Tall	Short–Intermediate

infestation by gut parasites in mid-April (ivermectin) and in mid-August (pyrantel). The first two periods lasted from 29th April to 09th June 2006. A 1-month drought between mid-May and mid-June (only 3.2 mm of rain fell during the preparation of the swards for the third period; data from MeteoFrance) affected grass regrowth and made it necessary to postpone the third period to 16th September–06th October 2006.

Three vegetative swards of different availabilities (height and biomass) and similar quality were prepared by mowing mechanically at 4 cm and allowing regrowth: 3 days for the short sward (S), 11 days for the intermediate sward (I) and 19 days for the tall sward (T). Sward height in the S, I and T patches was 6, 11 and 17 cm, respectively. Each period of the Latin-square design was composed of 3 weeks of tests: 1 week during which the horses were offered indoors vegetation turfs of one of the three sward heights, cut out of the pasture and presented in experimental trays; 1 week during which the horses grazed daily the same sward offered alone at pasture; and the last week during which the horses were offered a pair-wise choice between the two other swards at pasture (see details in Table 1). The animals were weighed on the first day of each week.

2.1.1. Experimental trays for bite mass measurements

The bite masses of the individual horses were determined on the three sward types using experimental trays. Each group was offered vegetation turfs of a single sward type (S, I or T) on three successive days indoors. The dimensions of the tray (112 cm × 72 cm × 10 cm) were established to allow the horses to take 20 bites without depletion affecting bite mass (a method reviewed by Laca et al., 1992a; adapted for horses by Fleurance et al., 2009). Each tray was composed of four sub-trays (56 cm × 36 cm × 10 cm), which were made up using turfs including 10 cm of soil and roots, cut out of the pasture on the morning of the tests and wedged in the plastic trays with two horizontal metal bars (5 mm diameter) on the soil surface to prevent the horses from pulling the swards out of the trays. We presented the trays to the horses on a metal table in the stable (70 cm high) to prevent trampling. The horses were fasted for 5 h before the test in order to standardize their motivation to feed, and kept in stables with water available. The bite masses measured were therefore probably close to the maximum values permitted by each sward height (Newman et al., 1994).

2.1.2. Swards offered alone

During the second week, each group of horses was allowed to graze each day (24 h day^{-1}) a single sward type (S, I or T; Table 1) presented as a rectangular plot bounded by an electric fence. The fence was moved every morning at 08.00 h to allow the animals' access to a new plot each day. As the pasture was slightly sloping, all the plots were parallel with the slope so as to have similar conditions for the different treatments. The sizes of the plots were chosen so that the total amount of forage available was similar among the three sward heights (S, I, and T). The amount of herbage dry matter (DM) offered was the maximal intake level measured for growing horses (31 g DM kg LW^{-1} day^{-1}); Ménard et al., 2002) multiplied by two to allow for trampling (Ferrer Cazcarra et al., 1995). Using biomass data from previous studies on similar sward types (S, 60 g DM m^{-2}; I, 150 g DM m^{-2}; T, 240 g DM m^{-2}; Mesochina, 2000; Fleurance et al., 2009), the areas offered daily to each group of three horses were 1600, 640 and 400 m^2 for the S, I and T swards, respectively. During this week, individual bite and chew rates, daily grazing time and voluntary intake were quantified on each sward.

2.1.3. Pair-wise choices

Each group was offered a binary choice (S/T, I/T, S/I; during 7 days, 24 h day^{-1}, a new plot being provided every day by moving the electric fence): a plot for 1 day consisted of four strips of one of the sward types alternated with four strips of the other sward type. All the plots were parallel with the pasture slope so as to have similar conditions for the different treatments. Strip dimensions were determined from the area calculated for each sward type, in order to provide the same amount of herbage DM from each sward (S/T: 1600 + 400 m^2, I/T: 640 + 400 m^2, and S/I: 1600 + 640 m^2; see Fig. 1) and so that the horses could graze either the shorter sward alone, or the taller alternative all day, without being limited in available total herbage (Ginane et al., 2003). Grazing ruminants are known to show a preference for the sward not recently grazed (*e.g.* Parsons et al., 1994). Whether horses also show this behaviour is unknown but to prevent any bias, the swards offered in the pair-wise test to each group of horses were different from the sward offered alone the week before (Table 1). During the week when pair-wise choices were conducted, short-term preferences (first 30 min), daily preferences, daily grazing time and voluntary intake were measured.

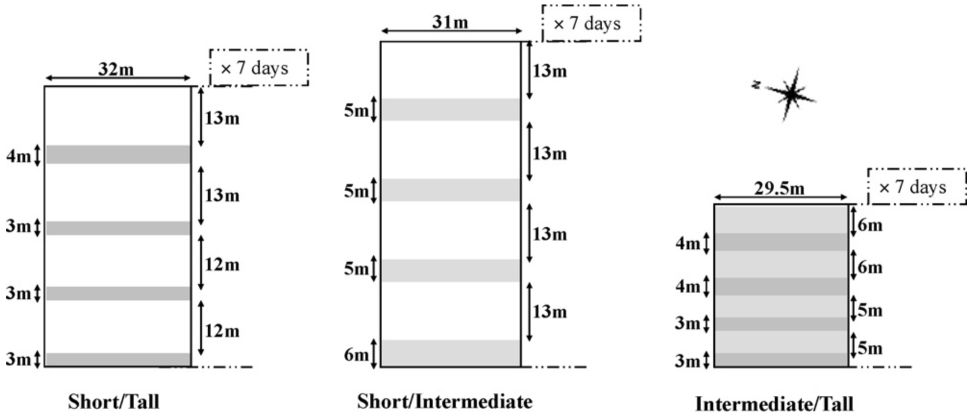

Fig. 1. Design of a 1-day plot (×7 days and ×3 periods) and stripe dimensions for the three pair-wise choices; in white the short swards, in light grey the intermediate swards and in dark grey the tall swards.

2.2. Vegetation

Sward height and herbage biomass were measured each day of the tests. At pasture, sward height was measured every day before grazing (at 08:00 h, $N = 40$ per sward × 7 days) and after grazing (24 h later, $N = 40$ per sward × 7 days) using a sward stick (*i.e.* a sliding square of polystyrene 100 cm^2, 2.7 g; Stewart et al., 2001). To check whether sward heights remained different among the three sward types during the test despite sward depletion due to grazing, heights were measured every 6 h over one (randomly chosen) of the 7 days of pair-wise tests ($N = 20$ per sward at 14:00, 20:00 and 02:00 h). For swards offered in experimental trays, the heights were measured just before the turfs were cut out of the pasture ($N = 20$ per sward × 3 days). Herbage biomass (in g DM m^{-2}) was measured before grazing from grass samples cut at ground level in a 25 cm × 25 cm cell ($N = 8$ per sward × 3 days for trays and ×7 days for swards offered alone; $N = 6$ per sward × 7 days for pair-wise choices) and dried at 60 °C to constant weight. Grass samples ($N = 4$ taken at random in the grass collected for biomass measurements, except for S swards in trays where $N = 2$ because of the small amount of grass collected) were then analysed for ash (after incineration for 6 h at 550 °C; Jarrige, 1988), crude protein (CP; Kjeldahl method $N \times 6.25$) and fibre (NDF: neutral detergent fibre; Goering and Van-Soest, 1970).

2.3. Animal behaviour and voluntary intake

The first day of each week at pasture (pair-wise choices and tests where swards were offered alone) was used to accustom the animals to the new sward conditions: the horses were offered a plot with the same characteristics as the ones offered the following days but no behavioural measurements were made. Patch choice on a daily scale and daily grazing time were determined using scan sampling (one observation/individual each 15 min, involving 96 observations per individual over 24 h; Altmann, 1974) during eight 3 h sessions spread over days 2–4 for practical reasons. The observer, using a lamp at night, noted whether the horses were grazing (searching, biting, chewing or swallowing food; and where the animals were grazing in pair-wise choices), resting, moving (foraging overriding walking if both occurred simultaneously) or doing other activities (from Duncan, 1983). The horses were very tame and the observer was extremely careful never to alarm the animals, or to make them move away from their chosen feeding patches. Patch choice was quantified from the proportion of grazing time spent foraging on each sward type. We also assessed the short-term preferences of the horses during the first 30 min of test (on days 2–4) before any grass depletion and trampling could occur. The same notation was used as for the 24 h observations, using scan sampling at more frequent intervals (one observation/individual each 30 s, so 120 observations/individual × 3 days).

Bite and chew rates (number of bites and chews per minute on each sward type) were recorded at pasture on day 2, during the 3 h following the horses' arrival in the test areas (*i.e.* when patch heights were similar to those offered on the trays): 3–4 measurements were made per individual. Bite mass (in g of DM) was estimated on 3 consecutive days by weighing the experimental trays offered indoors, before and after the horses had taken 20 bites. The weight loss was corrected for evapo-transpiration losses by weighing non-grazed trays kept in the test area during the measurements of bite masses. Instantaneous intake rates (IIR) were then calculated for each individual on each sward from its mean bite mass measured on trays and mean bite rate at pasture (Fleurance et al., 2009). From the chew rate (chews min^{-1}), bite rate (bites min^{-1}) and bite mass (g DM $bite^{-1}$) measurements, the number of chews per g DM (chews $bite^{-1}$/bite mass) was estimated.

Daily intake was estimated individually by total faecal collection, when each sward was offered alone and when the swards were offered in pair-wise choices, with digestibility estimated from faecal crude protein concentrations (Mesochina et al., 1998). During the whole experiment, the faeces were individualised by giving each horse 60 g of small coloured plastic balls (one colour per horse) in 140 g of oats, every morning starting the first day of the tests. The faeces were collected twice a day (09.00 and 16.00 h) during days 5–7 of the week, when it could be expected that the horses were fully acclimatised to their diet.

2.4. Statistical analyses

The individual animals were treated as replicates for statistical analyses as the design of the plots (see Fig. 1) allowed them to graze swards of different heights while staying in a group, in which line of sight among the three animals was never broken (see also Dumont et al., 1995; Illius et al., 1999; Ginane et al., 2002). The characteristics of the sward types were compared using the ANOVA procedure of SAS (Statistical Analysis System, 1999). We tested the differences of 'heights', 'biomasses' or 'quality' (NDF or CP) among 'sward' types (S, I, and T), 'period' (P1, P2, and P3) and their interaction.

For daily feeding time, bite and chew rates, bite masses and intake rates, the Mixed Procedure of SAS was used (Mixed Models with the Residual Maximum Likelihood algorithm), to test the effect of the 'sward' types (S, I, and T) or of the 'pair-wise choice' (S/T, S/I, I/T; only for daily feeding time). The consequence of the re-grouping of horses among periods was that all the horses did not experience all the treatments. Mixed linear models allow the analysis of repeated measures data, by taking into account both the variations between animals and the covariation within animals. In addition, some missing measures do not cause all data for an animal to be ignored (Littell et al., 1998). To prevent the variance due to potentially confounding factors being inaccurately incorporated in the error term of the analysis, the 'period' and 'individual' effects were integrated as random variables. For intake levels, as the herbage biomasses obtained were slightly different from those expected (see Table 2), the total amount of DM daily offered to the horses differed (S: 113 kg DM ± 5 S.E., I: 82 kg DM ± 3 S.E., T: 85 kg DM ± 3 S.E.; S/T: 174 kg DM ± 3 S.E., I/T: 142 kg DM ± 2 S.E., S/I: 196 kg DM ± 3 S.E.). We therefore integrated a 'food supply' factor and its interaction with 'sward' in the fixed effects of the mixed model, since the total amount of DM available could have affected intake levels. For each of these models, pair-wise *t*-tests were performed to compare sward types or pair-wise choices, with the Bonferroni adjustment for *p*-values (Miller, 1981).

In the pair-wise choices the animals could select between two options only (A or B), so the proportion of the grazing time spent on A (pA) plus the proportion of the grazing time spent on B (pB) was equal to 1. To assess the preferences of the horses, these data were therefore treated as non-independent compositional data (Aitchison, 1986) and the logarithm of the ratio of the grazing time spent on each treatment (pA/pB) was used (Illius et al., 1999). Where only one resource was exploited (*i.e.* pA = 1 and pB = 0), the calculation of the correct log ratio was impossible, so these zeros were substituted by the smallest amount observed in the resource use, which was 0.01 in our study (Elston et al., 1996). We then tested whether the degree of preference differed among pair-wise choices using the same type of mixed model as previously ('pair-wise choice' as a fixed effect, 'period' and 'individual' as random effects), and we checked whether these preferences (log of the ratio (pA/pB)) differed from 0 with a Student's *t*-test.

To test whether the short-term choices (proportion of 30 first min of test grazing taller sward; y) were influenced by intake rates, a regression analysis was performed using the non-linear (NLIN) procedure of SAS on the average values of the short-term preferences for each individual over the 3 days in each period ($N = 27$). The model (from Dumont et al., 1998; Ginane et al., 2002) was:

$$y = A(1 - \exp(-b(\text{IIR ratio})^c))$$

The IIR ratio was calculated for each pair-wise choice as the instantaneous intake rate on the taller sward divided by that realised on the shorter sward. As the composition of the groups was changed among periods, IIRs were not measured for each individual on each sward (see Table 1). We consequently used the estimated IIR from the fitted functional response (individual IIRs—from bite rate measured during the first 3 h at pasture × bite mass measured on trays—as a function of grass height on the trays).

Finally, the 24 h observation period was divided into four 6 h intervals (8:00–14:00; 14:00–20:00; 20:00–2:00; 2:00–8:00 h) to assess the dynamics of the switches

Table 2
Characteristics of the Short, Intermediate and Tall swards for each test (pair-wise choices, swards offered alone or experimental trays) during the three periods (mean ± S.E.).

Test		Heights (cm)		Biomasses (g DM)	Quality	
		Start	End	Start	Fibre NDF (% DM)	Crude protein (% DM)
Choice S/T	Short	5.9 ± 0.1^a	5.2 ± 0.1^a	61.4 ± 2.4^a	48.5 ± 1.9^a	18.8 ± 0.9^a
	Tall	17.2 ± 0.2^b	7.6 ± 0.3^b	186.8 ± 7.1^b	47.4 ± 1.9^a	18.6 ± 0.5^a
Choice S/I	Short	5.8 ± 0.1^a	5.4 ± 0.1^a	63.1 ± 2.2^a	51.3 ± 0.9^a	17.8 ± 0.9^a
	Intermediate	12.1 ± 0.1^b	6.9 ± 0.1^b	132.8 ± 3.4^b	50.2 ± 0.8^a	18.6 ± 0.7^a
Choice I/T	Intermediate	10.3 ± 0.1^a	6.3 ± 0.1^a	99.5 ± 3.1^a	51.3 ± 0.9^a	20.4 ± 0.6^a
	Tall	17.5 ± 0.2^b	8.9 ± 0.2^b	188.9 ± 5.0^b	52.4 ± 1.3^a	17.6 ± 0.7^b
Swards alone	Short	6.5 ± 0.1^a	5.0 ± 0.1^a	71.1 ± 2.5^a	48.5 ± 1.8^a	17.6 ± 0.7^a
	Intermediate	10.4 ± 0.1^b	5.7 ± 0.1^b	124.2 ± 3.1^b	49.4 ± 1.9^a	19.8 ± 0.8^a
	Tall	17.5 ± 0.2^c	6.8 ± 0.1^c	199.1 ± 5.1^c	45.4 ± 2.6^a	17.8 ± 0.6^a
Trays	Short	5.9 ± 0.1^a	NA	59.4 ± 4.2^a	50.7 ± 2.6^a	15.3 ± 1.3^a
	Intermediate	11.5 ± 0.2^b	NA	112.3 ± 4.2^b	49.1 ± 1.7^a	21.2 ± 0.7^b
	Tall	21.5 ± 0.4^c	NA	246.5 ± 11.2^c	46.2 ± 2.1^a	15.8 ± 1.1^a

[a,b,c]Different letters within a column indicate significant differences within each test ($p < 0.05$).

between the two sward types offered in the preference tests. The mean number of switches per hour of grazing was compared for each pair-wise choice among these four 6 h intervals, with the 'period' and 'individual' factors being taken as random effects. The mean number of switches per hour of grazing on a daily basis was also compared among pair-wise choices.

3. Results

3.1. Sward characteristics

The mean height of the swards for the S, I and T treatments was 6.1 cm ± 0.1, 11.0 cm ± 0.1 and 17.7 cm ± 0.1 (mean ± S.E.) respectively, and the differences were significant ($p < 0.001$) for height and biomass. Depletion occurred over the day, and sward heights decreased for all treatments ($p < 0.05$). However, sward heights were significantly different ($p < 0.05$) among sward types until the end of the day (Table 2). Nutrient quality was similar among treatments (mean values were 49.2% NDF ± 0.5 S.E. and 18.3% CP ± 0.3 S.E.). However, the protein content of the I sward was higher than that of the other two swards in the I/T choice and for the trays (Table 2).

The characteristics of the swards differed significantly ($p < 0.05$) among periods (height: P2 < P1 < P3; biomass: P1 = P2 > P3; NDF: P1 < P2 < P3; CP: P1 < P2 < P3), so 'period' was included as a random variable in the remaining analyses. For each period taken alone, single sward types (S or I or T) had very similar heights among the tests (trays, swards offered alone and pair-wise choices): the mean sward heights never differed by more than 3 cm (17%) for the tall sward, 2.7 cm (24%) for the intermediate sward and 1.7 cm (28%) for the short sward. For the measures of grass quality, the interaction 'sward × period' was significant ($p < 0.05$) for CP content, but the differences among swards were minor. In particular there were no significant differences in quality (neither NDF, nor CP) between any two swards offered simultaneously. For each period taken alone, few of the differences in quality (NDF or CP) for a particular sward type (S or I or T) were significant ($p < 0.05$), and were always small. The worst case was for the S trays that were of a lower quality than the S sward in the S/T choice in period 1 (S trays being 8.7% lower in NDF and 4.0% lower in CP, $p < 0.05$) and than the S sward offered alone in period 2 (S trays being 8.4% higher in NDF and 3.9% lower in CP, $p < 0.05$).

3.2. Daily dry matter intake and grazing time

The mean ingestion per horse was 20.8 g DM kg LW^{-1} day^{-1} (±3.0 S.E), with no significant effects of tests (swards offered alone or pair-wise choices) or sward types (S, I, T; S/T, S/I, I/T). There were no significant effects of the 'food supply' variable (total amount of DM offered) or its interaction with 'sward' type. The average intake of the individual horses varied between 14 and 32 g DM kg LW^{-1} day^{-1}, but the differences were not significant. The grazing time of the horses averaged 14:05 h day^{-1} ± 28 min, and was not significantly different among periods and individuals.

3.3. Preferences and instantaneous intake rate characteristics

The horses selected the taller patch in the first 30 min of the pair-wise tests (Table 3). Bite rates, measured at pasture during the first 3 h, were significantly lower on the taller grass ($p < 0.001$) while the mean bite mass, measured on the trays, were at least twice as great on the tall sward compared with the other two heights ($p < 0.01$; Table 4). As sward height increased, the horses chewed significantly less per unit of DM intake (Table 4). Instantaneous intake rates differed among patches, being significantly higher for the tallest ones (Table 4).

The functional response, the relation between instantaneous intake rate (IIR) and grass availability measured as sward height (in cm), is asymptotic in the range considered here:

$$\mathrm{IIR} = \frac{2.45 \times \text{sward height}}{1 + 0.027 \times \text{sward height}} \qquad (p < 0.001, R^2 = 0.56, N = 27) \tag{1}$$

The animals' selectivity, expressed as the proportion of the first 30 min of test spent grazing on the taller sward (y), was regressed on the ratio of the IIRs of the swards estimated from regression (1) on the swards offered (x = IIRA/IIRB; sward A being the taller one). The model was:

$$y = 0.94(1 - \exp(-0.19(x)^{5.85})) \qquad (p < 0.001, N = 27). \tag{2}$$

This non-linear regression accounted for 64% of the corrected sum of squares (Fig. 2). When the intake rate on the taller sward was 1.6 times than that on the shorter

Table 3
Proportion of grazing time (p) spent on the taller sward for each pair-wise test during the first 30 min of tests and at a daily scale, and logarithm of the ratio (pA/pB) where A is the taller sward and B the shorter.

	Pair-wise choice (B–A)	Proportion of grazing time spent on A (pA)	Logarithm of the ratio (pA/pB)	t-Test p-value
First 30 min	Short–Tall	0.92 ± 0.02	1.30 ± 0.10[a]	<0.001
	Short–Intermediate	0.96 ± 0.01	1.65 ± 0.10[b]	<0.001
	Intermediate–Tall	0.75 ± 0.03	0.57 ± 0.10[c]	<0.001
Daily scale	Short–Tall	0.65 ± 0.02	0.27 ± 0.06[a]	<0.01
	Short–Intermediate	0.76 ± 0.03	0.53 ± 0.06[b]	<0.001
	Intermediate–Tall	0.61 ± 0.03	0.20 ± 0.06[a]	<0.01

[a,b,c]Different letters within a column indicate significant differences ($p < 0.05$) among pair-wise choices.

Table 4
Bite rate measured at pasture on swards offered alone, bite mass measured on experimental trays offered indoors and the instantaneous intake rate (IIR, calculated from bite rate × bite mass) for the three swards (mean ± S.E.). Chews (N g DM^{-1}) were calculated from chew rates measured at pasture on swards offered alone and IIR.

Swards	Bite rate (N min^{-1})	Bite mass (g DM)	Chews (N g DM^{-1})	Measured IIR at start (g DM min^{-1})
Short	42.2 ± 1.6^{a}	0.34 ± 0.08^{a}	5.3 ± 0.6^{a}	13.5 ± 3.3^{a}
Intermediate	43.1 ± 1.6^{a}	0.51 ± 0.08^{a}	4.1 ± 0.6^{b}	21.9 ± 3.3^{a}
Tall	30.3 ± 1.7^{b}	1.06 ± 0.08^{b}	2.9 ± 0.6^{c}	32.5 ± 3.3^{b}

^{a,b,c}Different letters within a column indicate significant differences among swards ($p < 0.05$).

sward, the animals spent about 90% of their time on the taller one, and as the rates of intake became more similar (*i.e.* the value of the ratio decreased) the time spent grazing the taller sward declined. At the scale of a day, the preferences were less pronounced than during the first 30 min of grazing but the horses always selected the taller swards (Table 3).

The mean number of switches between sward heights per hour of grazing is represented in Fig. 3 for each of the pair-wise tests and for the four 6 h intervals. The number of switches increased between the beginning and the end of the tests for the S/T and S/I choices ($p < 0.05$), but remained high and constant for the I/T treatment. The daily mean number of switches per hour of grazing was significantly higher ($p < 0.01$) on the I/T treatment (1.55 ± 0.1 S.E.) than on the S/I one (1.06 ± 0.1 S.E.), the value for the S/T choice was intermediate (1.27 ± 0.1 S.E.).

4. Discussion

The swards differed significantly for both height and biomass, but were similar in nutritional quality based on NDF and CP contents, particularly when the swards offered in pair-wise choices or alone within each period are considered. Therefore, quality differences were unlikely to have affected preference or daily intake. Though the height of the swards decreased as the horses grazed, the differences in grass height among the patches remained significant until the end of the tests. In addition, the horses defecated homogeneously over the stripes of different heights into the plots (N. Edouard, pers. observations) so the presence of faeces is unlikely to have affected the horses' feeding behaviour.

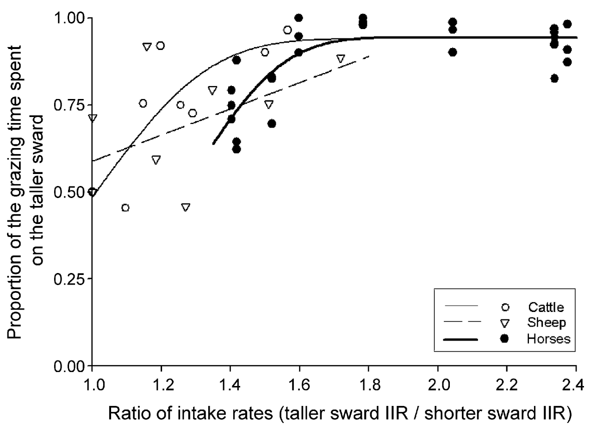

Fig. 2. Relationship between the proportion of grazing time (during the first 30 min) spent on the taller grass in pair-wise choice situations and the ratio of the instantaneous intake rates realised on the two swards, for cattle, sheep (Illius and Gordon, 1990) and horses (present study).

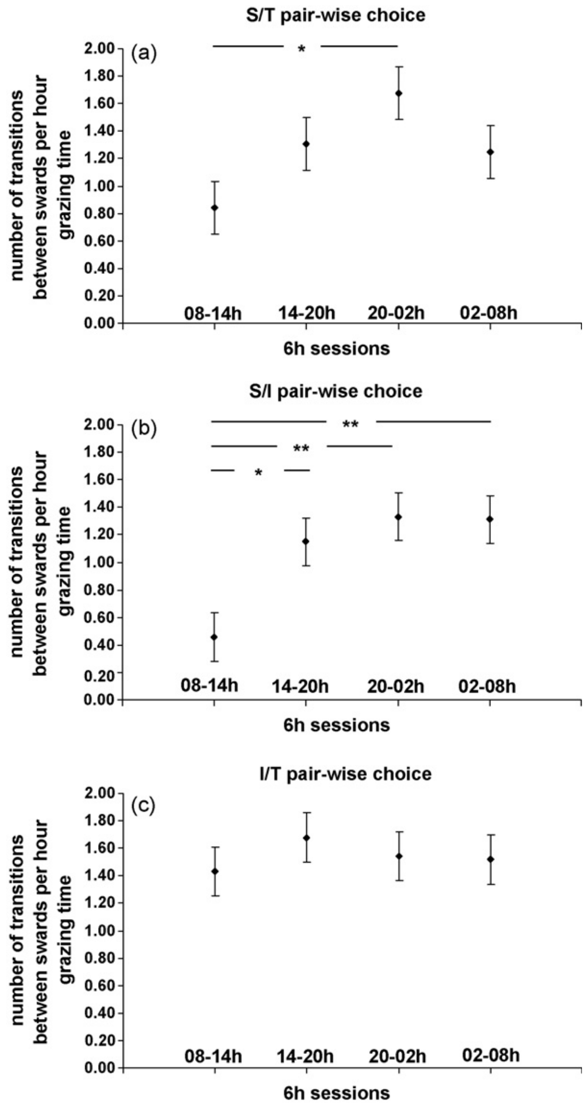

Fig. 3. Mean number of switches per hour of grazing (±S.E.) between the two swards offered simultaneously in pair-wise choices during the experiments (the 24 h were divided into four 6 h intervals); a, Short/Tall choice; b, Short/Intermediate choice; c, Intermediate/Tall choice; $^{*}p < 0.05$, $^{**}p < 0.01$.

4.1. Daily intake

The horses grazed 14 h per day, which is typical for horses at pasture (12–16 h; Duncan, 1992, for a review). Intake averaged 21 g DM kg LW^{-1} day^{-1}. Neither intake nor feeding time was influenced by sward height, by the nature of test (pair-wise choices or swards offered alone) or by the period. The digestibility of the ingested grass (mean: 61% DMD) was independent of sward type and test conditions, so diet quality remained similar.

Daily intake has been well documented for horses fed with hays indoors (Duncan, 1992, for a review) but little information is available on intake at pasture and the causes of the large variations observed are not understood (Fleurance et al., 2001; Ménard et al., 2002). In a review of experiments on the same site as in the present study, Mesochina (2000) found similar levels of intake by 2-year-old horses (saddle breeds), with a mean of 21 g OM kg LW^{-1} day^{-1} ($\pm$3 S.E.; OM = organic matter) *vs.* a mean of 25 g OM kg LW^{-1} day^{-1} ($\pm$3 S.E.) in the present study. These intake levels are low compared with other studies in the literature for horses with similar requirements: using the same method, Ménard et al. (2002) measured daily intakes ranging from 25 to 41g DM kg LW^{-1} day^{-1} on wet grasslands stocked with growing draught horses. Experiments in controlled conditions are therefore necessary to better understand how vegetation characteristics and animal factors affect voluntary intake in horses.

In our study, the total amount of food available ('food supply'), which was about twice as high in pair-wise choices as in the swards offered alone, had no measurable effect on intake levels. The amount of DM available for horses at start of the test (biomass in g DM m^{-2} $\times$ surface in m^2) decreased throughout the day due to trampling, lying, and defecation. The amount of wasted herbage was affected by the vertical distribution of biomass and was partly compensated by the grass biomass produced by regrowth, so the losses were smaller in the short swards because of the larger area available for regrowth. This could explain why sward height showed the greatest decrease in the tallest swards (Table 2). Nonetheless, the differences in sward height among swards were maintained all through the day and the voluntary intake by the horses allowed them to meet their nutritional requirements whatever the situation. The horses ingested a mean of 1200 g of digestible CP and 16 Mcal of net energy per day which is more than the recommended allowances according to the INRA standards for growing horses (Martin-Rosset, 1990). These intake levels allowed rapid growth: the daily liveweight gains were 570–740 g day^{-1}.

4.2. Patch choice

When offered a choice between patches differing in height, the horses expressed strong preferences in the short-term for the tallest ones. This behaviour is consistent with the observations made by Naujeck et al. (2005) for horses grazing swards ranging from 3.5 to 15 cm. However, in their experiment, no data on grass quality were available and it was not possible to determine how sward height and nutritive value were related. In the present study, the swards offered in binary choices had similar NDF and CP content except for the choice I/T where CP was lower in the tall sward. However, the horses did not choose the I sward which suggests that this difference in CP content between swards did not affect the selection of feeding sites. The result here is consistent with previous work on cattle (Distel et al., 1995; Griffiths et al., 2003) and sheep (Black and Kenney, 1984; Bazely, 1990): when the same sward was offered at two different heights, the taller one was preferred.

The horses modified their ingestive behaviour in response to a decrease in sward height by increasing the bite rate as bite mass declined. This response is consistent with other results on horses (Naujeck and Hill, 2003; Fleurance et al., 2009), and ruminants (Laca et al., 1992b; Gross et al., 1993; Prache, 1997). The horses also made fewer chews per unit of DM intake on the tallest swards, implying lower energy costs when harvesting taller vegetation. Their preference for taller patches is consistent with the Optimal Foraging Theory, that the animals should prefer patches where DM and nutrient intake rates are highest, and feeding costs are minimised. This result has been reported for ruminants at least for short-duration tests (Black and Kenney, 1984; Illius et al., 1999; Griffiths et al., 2003). This is the first time that it has been demonstrated in horses using grass patches of similar nutritive values.

In a study comparing the selection of food plants by Red deer (*Cervus elaphus*), Highland cattle (*Bos taurus*) and Konik ponies (*Equus caballus*) in a forest environment, selectivity was also explained by intake rate maximisation (DOMIR: digestible organic matter intake rate), though it was suggested that the ponies may have been less sensitive to the instantaneous intake rate constraint than the two ruminant species (only 52% of the diet composition explained by the DOMIR maximisation for ponies, 65% for the two ruminants; Van Wieren, 1996). The differences between this experiment and ours in the strength of response by horses may result from the contrasting nutritional environments mainly caused by inclusion of woody species, which had low DOMIR values but high P and Ca content, in Van Wieren's study.

In their review of the constraints on diet selection in mammalian herbivores, Illius and Gordon (1990) referred to an experiment that was very close to the present one, in which the short-term preferences of cattle and sheep between vegetative grass patches of different height were observed, together with the instantaneous intake rate achieved on each of the swards (Clark et al., unpublished). The information available on the quality of the swards suggests that they did not differ greatly, so their data are directly compared with ours in Fig. 2. Cattle and horses selected the taller sward more consistently than sheep, probably because the IIR of the two larger species was more strongly constrained on the short swards than for sheep due to their larger body size (Illius and Gordon, 1987) and perhaps to other differences in their feeding habits (*e.g.* use of the tongue by cattle). Both cattle and horses were highly selective, spending 90% of their grazing time on the sward where they achieved the highest intake rate, as long as the intake rate ratio was above 1.6.

However, horses may have been less sensitive to sward height than cattle when the intake rate ratio was around 1.4 (Fig. 2): more data are necessary to prove this point.

4.3. Underlying processes

The horses never spent 100% of their grazing time on the most profitable patch (where the DM intake rate was higher; Fig. 2): like ruminants, the horses realised sub-optimal, rather than strictly optimal choices (Dumont et al., 1998; Illius et al., 1999; Ginane et al., 2002). Since the alternatives were of high and similar nutritional value, the penalty for expressing sub-optimal choices resulting in partial preferences between high quality swards was small. Switches between the two swards increased during the day for the S/T and S/I choices. Even if we cannot exclude the possibility that the horses switched more often in the afternoon and the night because of decreasing motivation to eat (satiety), the constant number of switches between I and T swards throughout the day suggests that other constraints were more important. The resulting mixed diet could indeed reflect the increasing difficulty for the animals to discriminate between alternatives and their need to re-evaluate regularly the value of each sward (sampling behaviour), as well as the declining gain from feeding on the tallest swards as the result of their depletion (Illius et al., 1999; Prache et al., 2006) or more generally that the alternatives were of similar value (Dumont et al., 1995). Additionally, information gained during short periods of grazing could be used by the animals together with pre-consumption cues. This could be particularly true in the case of I/T association, where differences in sward height may have been more difficult to discriminate from the beginning of the day since the two swards were characterised by a higher variability of leaf length (11 and 19 days of regrowth for I and T swards respectively) compared with the short sward (3 days of regrowth). More switches between I and T swards were indeed observed for the I/T experiment (Fig. 3).

5. Conclusion

We show for the first time that sward height affects patch selection and ingestive behaviour in horses, independently of variations in the nutritive value of forages. This demonstrates that diet selection in horses is consistent with the predictions based on the maximisation of dry matter instantaneous intake rate, and therefore provides evidence to support the use of optimal foraging models for predicting the choices made by horses between patches of a similar and high quality. The animals realised sub-optimal choices rather than strictly optimal ones, which could be the consequence of partial preferences or sampling behaviour.

In spring, on high quality pastures, horses are thus expected to graze taller swards which can be eaten faster. Further research will now have to explore how the horses may be constrained by the maturation of swards, and how they adapt their feeding behaviour when there is a trade-off between intake rates and diet quality.

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References

Aitchison, J., 1986. The Statistical Analysis of Compositional Data. Chapman and Hall, London, UK.

Altmann, J., 1974. Observational study of behaviour: sampling methods. Behaviour 49, 227–267.

Bazely, D.R., 1990. Rules and cues used by sheep foraging in monocultures. In: Hughes, R.N. (Ed.), Behavioural Mechanisms of Food Selection. Springer-Verlag, Berlin, pp. 343–367.

Black, J.L., Kenney, P.A., 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. Aust. J. Agric. Res. 35, 565–578.

Distel, R.A., Laca, E.A., Griggs, T.C., Demment, M.W., 1995. Patch selection by cattle: maximisation of intake rate in horizontally heterogeneous pastures. Appl. Anim. Behav. Sci. 45, 11–21.

Dumont, B., Dutronc, A., Petit, M., 1998. How readily will sheep walk for a preferred forage? J. Anim. Sci. 76, 965–971.

Dumont, B., Petit, M., D'Hour, P., 1995. Choice of sheep and cattle between vegetative and reproductive cocksfoot patches. Appl. Anim. Behav. Sci. 43, 1–15.

Duncan, P., 1983. Determinants of the use of habitats by horses in mediterranean wetland. J. Anim. Ecol. 53, 93–111.

Duncan, P., 1992. Horses and Grasses: The Nutritional Ecology of Equids and their Impact on the Camargue. Springer-Verlag, New York.

Edwards, P.J., Hollis, S., 1982. The distribution of excreta on New Forest grassland used by cattle, ponies and deer. J. Appl. Ecol. 19, 953–964.

Elston, D.A., Illius, A.W., Gordon, I.J., 1996. Assessment of preference among a range of options using log ratio analysis. Ecology 77, 2538–2548.

Ferrer Cazcarra, R., Petit, M., D'Hour, P., 1995. The effect of sward height on grazing behaviour and herbage intake of three sizes of Charolais cattle grazing cocksfoot (*Dactylis glomerata*) swards. Anim. Sci. 61, 511–518.

Fleurance, G., Duncan, P., Mallevaud, B., 2001. Daily intake and the selection of feeding sites by horses in heterogeneous wet grasslands. Anim. Res. 50, 149–156.

Fleurance, G., Duncan, P., Fritz, H., Cabaret, J., Gordon, I.J., 2005. Importance of nutritional and anti-parasite strategies in the foraging decisions of horses: an experimental test. Oikos 110, 602–612.

Fleurance, G., Duncan, P., Fritz, H., Cabaret, J., Cortet, J., Gordon, I.J., 2007. Selection of feeding sites by horses at pasture: testing the anti-parasite theory. Appl. Anim. Behav. Sci. 108, 288–301.

Fleurance, G., Fritz, H., Duncan, P., Gordon, I.J., Edouard, N., Vial, C., 2009. Instantaneous intake rate in horses of different body sizes: influence of sward biomass and fibrousness. Appl. Anim. Behav. Sci. 117, 84–92.

Ginane, C., Dumont, B., Petit, M., 2002. Short-term choices of cattle vary with relative quality and accessibility of two hays according to an energy gain maximisation hypothesis. Appl. Anim. Behav. Sci. 75, 269–279.

Ginane, C., Petit, M., D'Hour, P., 2003. How do grazing heifers choose between maturing reproductive and tall or short vegetative swards? Appl. Anim. Behav. Sci. 83, 15–27.

Goering, H.K., Van-Soest, P.J., 1970. Forage and fibre analyses. In: Agricultural Handbook, US Department of Agriculture.

Griffiths, W.M., Hodgson, J., Arnold, G.C., 2003. The influence of sward canopy structure on foraging decisions by grazing cattle. I. Patch selection. Grass Forage Sci. 58, 112–124.

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

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., 1990. Constraints on diet selection and foraging behaviour in mammalian herbivores. In: Hughues, R.N. (Ed.), Behavioural Mechanisms of Food Selection. Springer-Verlag, Berlin, pp. 369–393.
Illius, A.W., Gordon, I.J., Elston, D.A., Milne, J.D., 1999. Diet selection in goats: a test of intake-rate maximization. Ecology 80, 1008–1018.
Jarrige, R., 1988. Alimentation des bovines, ovins et caprins. INRA Publications, Versailles.
Laca, E.A., Ungar, E.D., Seligman, N.G., Ramey, M.R., Demment, M.W., 1992a. An integrated methodology for studying short-term grazing behaviour of cattle. Grass Forage Sci. 47, 81–90.
Laca, E.A., Ungar, E.D., Seligman, N., Demment, M.W., 1992b. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass Forage Sci. 47, 91–102.
Lamoot, I., Meert, C., Hoffmann, M., 2005. Habitat use of ponies and cattle foraging together in a coastal dune area. Biol. Conserv. 122, 523–536.
Littell, R.C., Henry, P.R., Ammerman, C.B., 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76, 1216–1231.
Martin-Rosset, W., 1990. L'alimentation des chevaux. INRA, Paris.
Ménard, C., Duncan, P., Fleurance, G., Georges, J.Y., Lila, M., 2002. Comparative foraging and nutrition of horses and cattle in European wetlands. J. Appl. Ecol. 39, 120–133.
Mesochina, P., 2000. Niveau d'ingestion du cheval en croissance au pâturage: mise au point méthodologique et étude de quelques facteurs de variation. PhD, Institut National Agronomique Paris-Grignon.
Mesochina, P., Martin-Rosset, W., Peyraud, J.L., Duncan, P., Micol, D., Boulot, S., 1998. Prediction of the digestibility of the diet of horses: evaluation of faecal indices. Grass Forage Sci. 53, 189–196.
Miller Jr., R.G., 1981. Simultaneous Statistical Inference. Springer-Verlag, New York.
Naujeck, A., Hill, J., 2003. Influence of sward height on bite dimensions of horses. Anim. Sci. 77, 95–100.
Naujeck, A., Hill, J., Gibb, M.J., 2005. Influence of sward height on diet selection by horses. Appl. Anim. Behav. Sci. 90, 49–63.
Newman, J.A., Penning, P.D., Parsons, A.J., Harvey, A., Orr, R.J., 1994. Fasting affects intake behaviour and diet preference of grazing sheep. Anim. Behav. 47, 185–193.
Parsons, A.J., Newman, J.A., Penning, P.D., Harvey, A., Orr, R.J., 1994. Diet preference of sheep: effects of recent diet, physiological state and species abundance. J. Anim. Ecol. 63, 465–478.
Prache, S., 1997. Intake rate, intake per bite and time per bite of lactating ewes on vegetative and reproductive swards. Appl. Anim. Behav. Sci. 52, 53–64.
Prache, S., Bechet, G., Damasceno, J.C., 2006. Diet choice in grazing sheep: a new approach to investigate the relationships between preferences and intake-rate on a daily time scale. Appl. Anim. Behav. Sci. 99, 253–270.
Putman, R.J., Fowler, A.D., Tout, S., 1991. Patterns of use of ancient grassland by cattle and horses and effects on vegetational composition and structure. Biol. Conserv. 56, 329–347.
Roguet, C., Dumont, B., Prache, S., 1998. Selection and use of feeding sites and feeding stations by herbivores: a review. Ann. Zootech. 47, 225–244.
Spalinger, D.E., Hobbs, N.T., 1992. Mechanisms of foraging in mammalian herbivores: new models of functional response. Am. Nat. 140, 325–348.
Statistical Analysis System, 1999. SAS/STAT Guide. SAS Institute Inc., Cary, NC, USA.
Stephens, D.W., Krebs, J.R., 1986. Foraging Theory. Princeton University Press.
Stewart, K.E.J., Bourn, N.A.D., Thomas, J.A., 2001. An evaluation of three quick methods commonly used to assess sward height in ecology. J. Appl. Ecol. 38, 1148–1154.
Taylor, E.L., 1954. Grazing behaviour and helminthic disease. B. J. Anim. Behav. 2, 61–62.
Van-Soest, P.J., 1982. Nutritional ecology of the ruminant: ruminant metabolism, nutritional strategies, the cellulolytic fermentation and the chemistry of forages and plant fibres. Corvallis, OR.
Van Wieren, S.E., 1996. Do large herbivores select a diet that maximizes short-term energy intake rate? Forest Ecol. Manage. 88, 149–156.