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Feeding behaviour and diet choices of cattle with physical and temporal constraints on forage accessibility: an indoor experiment

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Abstract

An indoor choice experiment was conducted to assess the extent to which heifers offered two forages of different quality will attempt to consume the better quality forage when the weight/number of constraints applied on its harvesting increase. The experiment involved six Salers heifers, a leafy (L) and a coarse (C) hay, and two combined or single accessibility constraints. A physical constraint consisted of reducing the prehensibility of L by covering the trough with a steel grid of either 4 cm or 6 cm mesh size (L4 or L6 v. L∞ for no grid). A temporal constraint limited the daily access time to both hays to 4 v. 24 h. The hays were either offered alone or together over 2-week periods. Dry-matter intake and feeding time were recorded daily.

As expected, the physical constraint (only L4 was efficient) made the heifers decrease their choice (proportion of feeding time or intake) for L regardless of access time, whereas the temporal constraint had no significant effect on choice. The heifers greatly modulated their intake rate of L even under strong physical constraint (L4), and then unexpectedly managed to ingest L faster than C. This emphasizes their motivation to keep ingesting the better quality forage, and underlines the difficulties in comparing diet choices with the optimal foraging theory predictions based on the relative values of a behavioural component subject to large variation, i.e. intake rate. In a very constraining situation (L4 and 4-h access), heifers made a choice that allowed them to increase their total daily digestible organic matter (DOM) intake compared with L4 or C offered alone because of an inverse relationship between feeding time and intake rate on L4. They did not however maximize their total daily DOM intake in a less constraining situation (L∞ or L6 and C, with 4-h access), since they did not consume L exclusively and showed a marked preference for a mixed diet.

Keywords: *cattle, feeding behaviour, food intake, food preferences.*

Introduction

Experiments conducted indoors involving artificially-modified foods (Kyriazakis and Oldham, 1993; Kenney and Black, 1984), reconstructed swards (Black and Kenney, 1984; Laca *et al.,* 1992) or devices creating spatial heterogeneity (Dumont and Petit, 1995; Scott and Provenza, 1998) have proved to be useful tools for dealing with issues on herbivore grazing behaviour. On the more specific topic of diet choices, indoor experiments carry many advantages. They allow good control of the relative quality of offered forages over time, accurate measurement of intakes and intake rates on each forage, and precise evaluation of the animals' behavioural adjustments under constraints (such as change of intake rate).

This experiment makes reference to the context of extensive grazing, where the low grazing pressure leads to a mosaic of often-grazed short/low-biomass vegetative patches and tall/high-biomass maturing reproductive patches (Willms *et al.,* 1988; Coughenour, 1991). This confronts herbivores with a trade-off between long term rate of energy assimilation (implying sufficient rate of passage, i.e. quality) and short term rate of food intake (quantity) (Gordon and Illius, 1992; Newman *et al*., 1995; Wilmshurst *et al.,* 1995).

To mimic indoors the low height of a vegetative sward, we constrained the availability of a good quality (leafy) hay by covering the trough with a steel grid of variable mesh size, and we offered this hay in a choice situation with another hay of lower quality (coarse) but freely available. Moreover, as increasing feeding time is a known compensatory mechanism of a reduced intake rate due to low forage accessibility (Allden and Whittaker, 1970; Penning, 1986; Penning *et al*., 1991), including in choice situations (Ginane *et al*., 2003), we also constrained the daily available feeding time. One original aspect of this study lies in combining two accessibility constraints -one physical, one temporal- and testing their effects on heifers' ingestive and choice behaviours between two forages of different quality. Many previous experiments have investigated the effects of a temporal constraint on the ingestive behaviour of ruminants offered only one forage (Hidari, 1981; Iason *et al.,* 1999 (sheep); Romney *et al.,* 1996 (goats); Suzuki *et al*., 1970; Chilibroste *et al.,* 1997 (cattle)), but few have tested the effects of a temporal constraint on diet choice (Laca *et al*., 1997 (sheep)), especially between forages differing in stage of maturity (Ginane and Petit (2005) (cattle)).

The aim of the study was to assess the extent to which heifers will attempt to maintain their choice for the leafy hay, when the weight of constraints applied on its harvesting increases. We predicted that (i) with zero or low physical constraint, the choice would be almost exclusively in favour of the leafy hay, all the more as the access time is restricted, and that it would decrease with the application of the physical constraint, (ii) the restriction of access time would then increase the choice for the leafy hay when freely available (no grid), whereas it would decrease with the most constraining grid, and (iii) consequently, the lowest choice for the leafy hay would be when the constraints are combined. These hypotheses are in accordance with the theoretical optimization approach stating that animals are supposed to prefer the food providing the highest rate of energy (digestible organic matter) intake (Stephens and Krebs, 1986).

Material and methods

The experiment was carried out at the experimental farm in Laqueuille (Puy-de-Dôme, France) from mid February to mid June 2000.

Animals and forages

We used six 18-month-old Salers heifers weighing 432 (s.d. 15) kg at the beginning and 449 (s.d. 7) kg at the end of the experiment. From 15 days before the beginning of the experiment, the heifers were housed in individual pens, isolated from each other by barriers that allowed social contacts. The bedding was made up of non-edible conifer wood shavings. Animals always had free access to water and salt blocks.

The forages used were two first-cut cocksfoot (*Dactylis glomerata*) hays, one leafy (L) and one coarse (C), harvested at two different stages of maturity (early and late cut). Their chemical characteristics, determined from samples collected throughout the experiment, are given in Table 1. In this table, values of organic matter digestibility refer to measurements made on sheep in pens with *ad libitum* feeding.

Experimental design and procedure

Each heifer had access to two adjacent troughs connected to a data processing system (Ingrand *et al*., 1998). The heifers were equipped with a halter carrying an electronic sensor indicating whether the animal's head was over the trough. The presence or absence of the heifer at the trough was checked automatically six times per minute. The troughs were placed on scales that were linked to a data processing system allowing the evolution of trough weight and thus the increase in intake over the day to be assessed. The weight of each trough was measured every minute, regardless of whether the animal's presence at the trough was detected or not.

We applied two constraints, one of physical accessibility to the leafy hay, and the other of temporal accessibility to both hays (daily access time to troughs). The physical constraint consisted in placing on the leafy hay a square weld mesh (bare steel grid) designed to constrain hay prehensibility by reducing bite size, in order to mimic the low height of a sward at pasture. The grid size was adjusted to the upper dimensions of the trough (90 × 44 cm). The diameter of the wires forming the mesh was 5 mm. The grid, placed on the surface of the food, was allowed to fall as the food was consumed. Tighteners fixed at each corner of the trough prevented the grid from being removed while the heifers were feeding. The grid was either absent or set at one of two different mesh sizes, i.e. 6 × 6 or 4 × 4 cm. These treatments are designated L∞, L6 and L4 (L by reference to the leafy hay), respectively. The temporal constraint consisted in limiting the daily access time to the troughs and was applied on both hays. The daily access time was either free (24 h/day) or restricted to 4 h/day (from 09:00 to 13:00 h). These two constraints were combined in a 3 × 2 factorial design to form six treatments : L∞-24 h, L6-24 h, L4-24 h, L∞-4 h, L6-4 h and L4-4 h.

The experiment comprised eight 2-week-long periods (Table 2). Six of the periods were divided into two 1-week subperiods, the leafy hay being offered alone for the 1st week (with a given mesh size and access time, according to the treatment under study) then in choice with the coarse hay for the following week. The two other periods (nos. 1 and 5, Table 2) consisted of offering the coarse hay alone, with or without the time constraint, according to the following time procedure. We allocated the six treatments to animals according to two successive 3 × 3 designs instead of one 6 × 6 Latin-square design, as shown in Table 2. Each 3 × 3 Latin square corresponded to a single access time so that each heifer successively experienced the different grids

Table 1 *Chemical characteristics of experimental hays (average±s.d. over periods)*

	Leafy hay (L)		Coarse hay (C)	
	Mean	s.d.	Mean	s.d.
Dry matter (DM) (g/kg fresh weight)	872	7·5	882	15·2
Organic matter (OM) (g/kg DM)	907	3·4	935	7·6
Crude protein (g/kg DM)	107	2·9	61	4·5
Neutral-detergent fibre (g/kg DM)	623	5·7	689	16·5
Acid-detergent fibre (g/kg DM)	327	6·5	371	13·3
OM digestibility †	0·657	0·0388	0·533	0·0313

† Measured on sheep in pens and given food *ad libitum* (s.d. between sheep) (no. = 6).

Table 2 *Succession of treatments for all heifers throughout the experiment†*

Animal	Heifer 1	Heifer 2	Heifer 3	Heifer 4	Heifer 5	Heifer 6
Access time	4 h/day			24 h/day		
Period 1 (2 weeks)	C	C	C	C	C	C
Period 2						
week 1	L∞	L6	L4	L∞	L6	L4
week 2‡	L∞/C	L6/C	L4/C	L∞/C	L6/C	L4/C
Period 3						
week 1	L4	L∞	L6	L4	L∞	L6
week 2‡	L4/C	L∞/C	L6/C	L4/C	L∞/C	L6/C
Period 4						
week 1	L6	L4	L∞	L6	L4	L∞
week 2‡	L6/C	L4/C	L∞/C	L6/C	L4/C	L∞/C
	24 h/day			4 h/day		
Period 5 (2 weeks)	C	C	C	C	C	C
Period 6						
week 1	L∞	L6	L4	L∞	L6	L4
week 2‡	L∞/C	L6/C	L4/C	L∞/C	L6/C	L4/C
Period 7						
week 1	L4	L∞	L6	L4	L∞	L6
week 2‡	L4/C	L∞/C	L6/C	L4/C	L∞/C	L6/C
Period 8						
week 1	L6	L4	L∞	L6	L4	L∞
week 2‡	L6/C	L4/C	L∞/C	L6/C	L4/C	L∞/C

† L and C represent leafy and coarse hays; ∞, 6 and 4 represent the mesh size of the grid (no grid, 6-cm wide mesh or 4-cm wide mesh).
‡ On week 2 of periods 2, 3, 4, 6, 7, and 8, animals were offered a choice between L and C.

for one given access time, then the same grids for the other access time, in order to prevent them from changing access time too often; this allowed them to anticipate the available time and adjust their behaviour accordingly. This experimental design was validated by the results of the first and fifth periods : when animals experienced a modification of access time, they needed about 5 to 6 days to stabilize intake. These first and fifth periods, when the coarse hay was offered alone for 2 weeks, allowed heifers to adapt to the new access time they were going to experience for the three following 2-week periods (each without, then with, choice).

The hays were distributed *ad libitum* once a day, at 09:00 h, their place in the troughs being alternated daily. A minimum of 2 kg of fresh matter of each hay was given each day, and proportionately 0·20 refusals were allowed when intake approached or exceeded 2 kg.

Behavioural measurements and sample collection

The electronic detection system installed at the troughs enabled us to assess the total daily feeding times and their distribution throughout the day. Similarly, the electronic trough weighing system allowed us to follow the evolution of intake over the day. Daily intakes were also measured manually, by daily weighing of hay offered and refused, which allowed us to regularly check the reliability of the electronic weighing system. Individual intake data were adjusted linearly to a 450 kg heifer, by multiplying intake per kg of heifer weight at the considered period by 450. Intake and feeding-time data allowed the preference for the leafy hay to be expressed as a proportion of total intake or total daily feeding time (choice ratios).

The hays offered were sampled on each of the last 4 days of each week. These samples were then bulked by week to be analysed for dry and organic matter, crude protein (Kjeldahl N × 6·25), neutral-detergent fibre (NDF) and acid-detergent fibre (ADF, Komarek *et al*., 1994). These chemical characteristics are given in Table 1.

We also collected samples of heifers' faeces on the same days. Faeces were grouped by heifer and by week and analysed for their nitrogen content (Nf) in order to assess diet organic matter digestibility (OMD) using the equation proposed by Peyraud (1998) and given below:

$$OMD = 0{\cdot}975 - 0{\cdot}00633/Nf$$

(Nf expressed as a proportion of faecal organic matter).

The OMD of the leafy and the coarse hays (in the specific situation where there was neither a choice nor a constraint) thus obtained made it possible to estimate the digestible organic matter (DOM) intakes considered below.

Statistical analyses

We used the GLM procedure in the SAS statistical software package (Statistical Analysis Systems Institute, 1999). The situations of no choice and choice were analysed separately as they were not conducted on the same experimental weeks. Similarly, when there was not a choice, we first analysed the results obtained only with the leafy hay as the coarse hay was not offered at the same periods. However, since with several of the variables studied, the period had no effect, and for others its effect did not mean a progressive evolution with time, we repeated the data analysis by including the coarse hay without testing the period effect. Similarly, in order to compare the no choice and choice situations, we repeated the data analysis including another factor, which was the situation (no choice or choice).

The data analysed were daily dry matter (DM) and DOM intakes, daily feeding times, DOM intake rates on each hay, diet digestibility estimated from faecal N content and, when there was a choice, the choice ratios (proportion of DM and DOM intake and feeding time). These ratios were angular transformed (arcsinus) to stabilize variance. Whether or not there was a choice, we tested the effect of grid mesh size, access time, and their interaction, period and heifer.

Results

Whether the analysis concerned the situation where there was or was not a choice, we did not detect any effect of the 6-cm mesh size compared with the no grid situation, whatever the studied variables. Therefore, it is not the grid itself but only the reduced size of its mesh that constituted a constraint to animals. Furthermore, for all studied variables, a first interesting result is that the interaction between the physical and the temporal constraints was never significant.

When there was not a choice

As expected, the 4-cm mesh size significantly reduced DOM intake rates on the leafy hay ($P<0{\cdot}001$) whatever the access time (Figure 1d). However, heifers did not compensate by increasing their daily feeding time in 24-h access ($P>0{\cdot}05$) (Figure 1b). When given 4-h access, animals spent between 0·88 and 0·92 of the allowed time feeding according to the physical constraint, and actual daily feeding times were reduced by about 0·40 compared with free access time ($P<0{\cdot}001$). This significant reduction was accompanied by a significant increase in intake rates on L ($P<0{\cdot}001$), whatever the physical constraint (Figure 1d). We observed that on L4 from 24-h to 4-h access, heifers managed to increase their intake rate nearly as much as on L6 or L∞, which represents a proportionately greater increase (0·40 *v.* 0·31). The 4-cm mesh size significantly reduced DM and DOM intakes ($P<0{\cdot}001$) by about 0·25, whatever the access time (Figure 1a and c). Despite the intake rate adjustments made by heifers, the access time constraint also reduced daily DM and DOM intakes ($P<0{\cdot}001$), by 0·14 on L∞ and L4 and by 0·22 on L6. Lastly, the grid slightly reduced the OMD of the diet ($P<0{\cdot}01$), even at the 6-cm mesh size and whatever the access time (Table 3), possibly due to it being more difficult for animals to sort the better elements within the leafy hay when a grid was in place. The temporal constraint did not affect diet OMD ($P>0{\cdot}05$) (Table 3).

With the coarse hay included in the analysis, it appears that, as on L, the reduction of access time led on C to an increase in intake rate ($P<0{\cdot}01$) (Figure 1d) and to a decrease in intake ($P<0{\cdot}001$) (Figure 1a and c). Whatever the access time, the heifers, as expected, ingested C at a significantly lower rate than L∞ or L6 ($P<0{\cdot}001$), but at a similar rate to L4 ($P>0{\cdot}05$) (Figure 1d). DM intake on C was significantly lower than on L∞ or L6, especially with 4-h access, and higher than on L4 ($P<0{\cdot}001$) (Figure 1a). However, DOM intakes were similar on C to those on L4 and lower than on L∞ and L6, regardless of access time ($P<0{\cdot}001$) (Figure 1c).

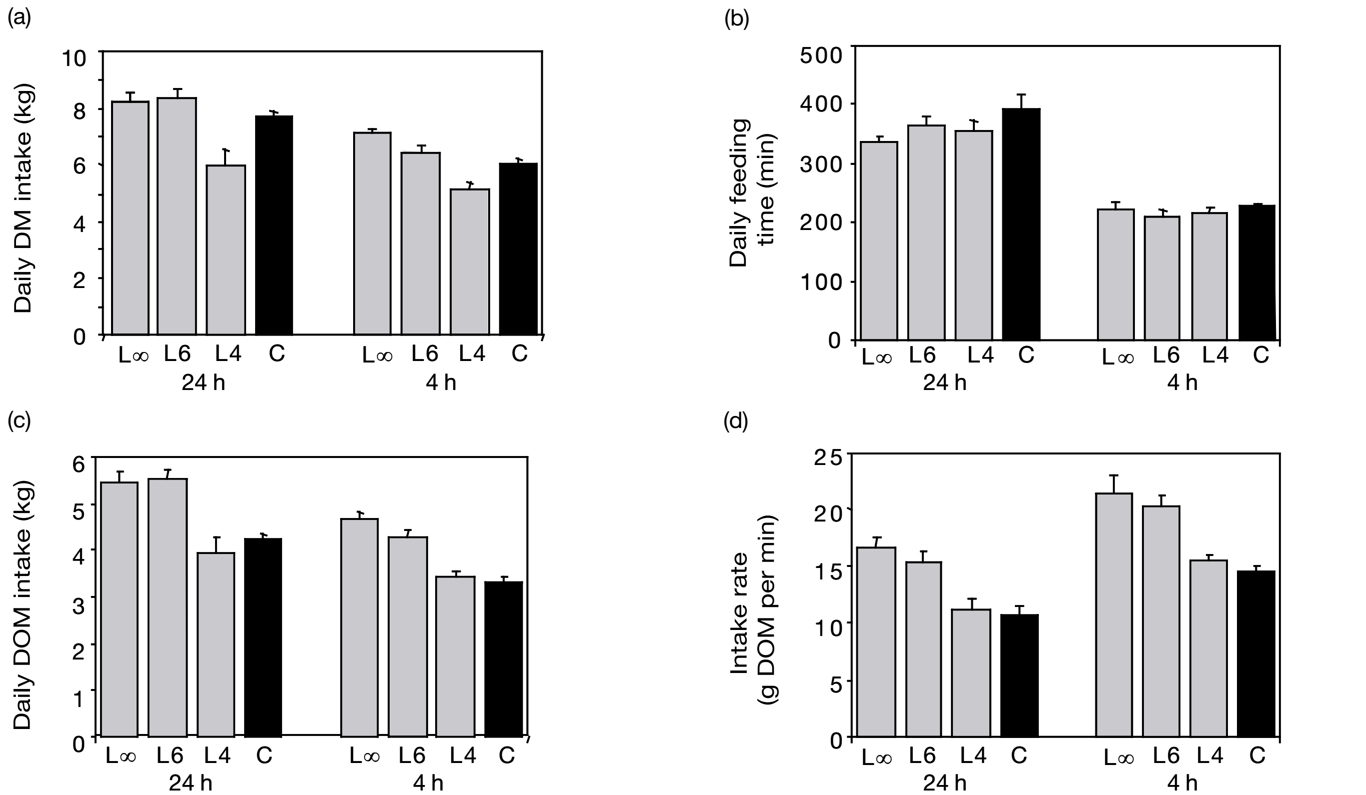

Figure 1 Daily dry matter (DM) intake (a), feeding time (b), digestible organic matter (DOM) intake (c) and DOM intake rate (d) (mean±s.e.) on leafy (L, grey bar) and coarse (C, black bar) hays when offered alone, according to physical (L∞: no grid, L6 and L4: grid with 6-cm or 4-cm mesh size, respectively) and temporal constraints (24 h or 4 h of access daily).

When there was a choice

The heifers maintained their preferences for the leafy hay with the restriction of access time, whether these choices were expressed in terms of DM or DOM intake ratio (Figure 2a and c) or feeding time ratio (Figure 2b) ($P>0{\cdot}05$). It should be noted however that preferences were slightly increased with L∞ and L6 while they were slightly decreased with L4. The temporal constraint reduced daily intake of DM or DOM ($P<0{\cdot}001$) (Figure 1a, c), but this reduction was limited to about proportionately 0·17 as the reduction of total feeding time ($P<0{\cdot}001$) (Figure 1b) was accompanied by a considerable increase in intake rate not only on the leafy ($P<0{\cdot}001$) but also on the coarse hay ($P<0{\cdot}001$) (Figure 2d). The greatest increase in intake rate was observed on L4 (proportionately +0·62) and the intake rate of C was also the highest when associated with L4 ($P<0{\cdot}01$).

The physical constraint significantly reduced the preference for the leafy hay ($P<0{\cdot}001$), by decreasing feeding time on L ($P<0{\cdot}001$) and increasing feeding time on C ($P<0{\cdot}001$), without a significant increase in total feeding time ($P>0{\cdot}05$) (Figure 2b). These modifications appeared more pronounced in 4-h than in 24-h access, despite a non-significant interaction between constraints ($P>0{\cdot}05$), as in 24-h access the decrease in feeding time on L was weak and non-significant ($P>0{\cdot}05$). Expressed as a DM or DOM intake ratio, the results were similar, except that in both 24-h and 4-h access, the intake of L was significantly lower with L4 than with L∞ or L6 ($P<0{\cdot}001$) (Figure 2a, c) due to lower intake rate on L4 than on L∞ or L6. The physical constraint significantly affected DOM intake rates, which were reduced for the leafy hay with the 4-cm mesh size ($P<0{\cdot}001$) and slightly more in 24-h ($P<0{\cdot}001$) than in 4-h access ($P<0{\cdot}01$) (Figure 2d). It is worth noting that the intake rate of L was higher in treatment L4-4 h than in L∞-24 h ($P<0{\cdot}001$). In contrast, intake rates on the coarse hay increased with the increasing physical constraint ($P<0{\cdot}05$), whatever the access time. The physical constraint to access L significantly but moderately reduced total DM and DOM intake ($P<0{\cdot}001$), whatever the access time (Figure 2a and c).

Lastly, the physical constraint, which decreased the preference for the leafy hay, reduced diet OMD ($P<0{\cdot}001$) by 0·015 in 24-h access and by 0·034 in 4-h access (Table 3). Conversely, the temporal constraint, which did not modify the choice for L, did not significantly modify diet OMD ($P>0{\cdot}05$), despite the slight decrease for L4 (-0·015) (Table 3).

Comparison of situations where there was or was not a choice

Whatever the intensity of the physical constraint, the heifers lengthened their total daily feeding time when there was a choice compared with when there was not (L alone), whenever they had the opportunity to do so (24-h access) (situation × access time, $P<0{\cdot}01$).

In treatments L∞ and L6, animals decreased their feeding time on L when there was a choice ($P<0{\cdot}001$) in both 4-h and 24-h access, without substantially and significantly increasing their intake rate on this leafy hay ($P>0{\cdot}05$). They devoted a non-negligible part of their feeding time to the coarse hay, which was ingested at a slightly lower rate in the

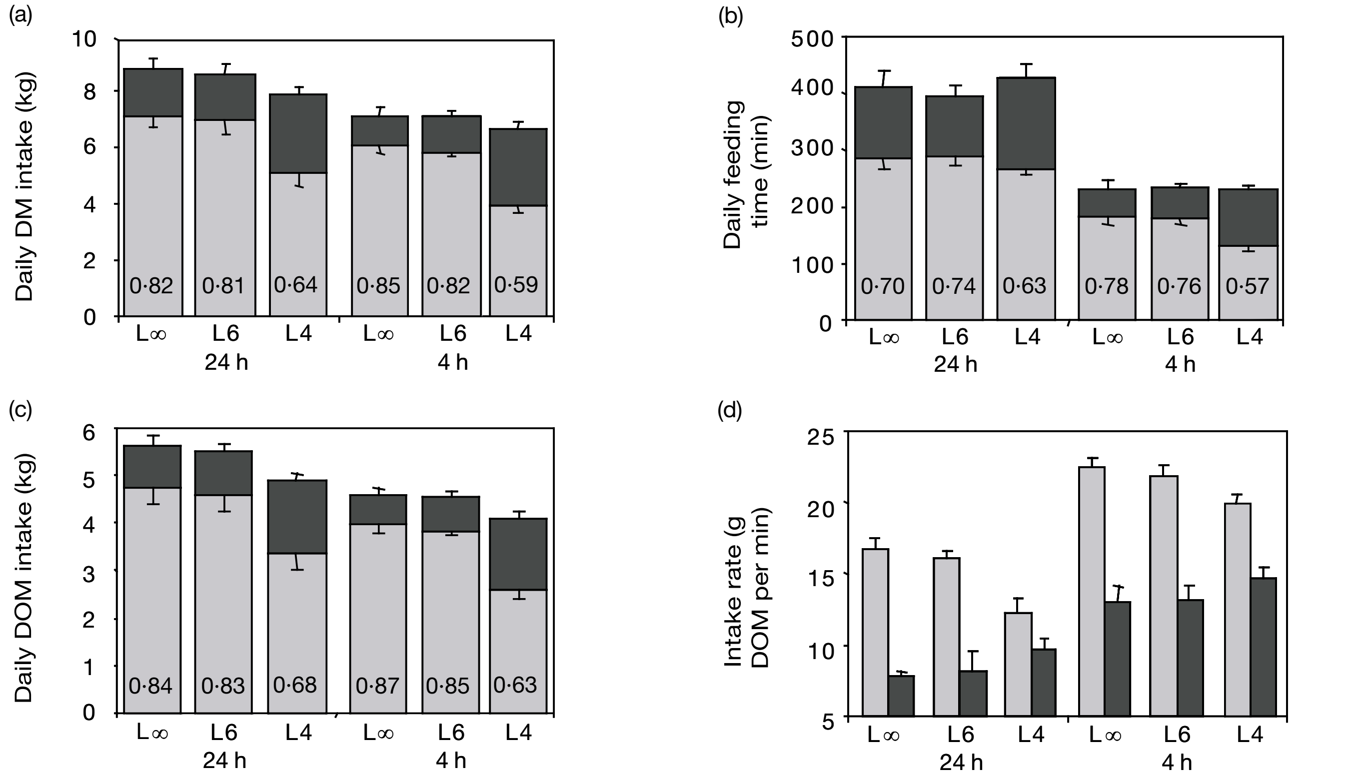

Figure 2 Daily dry matter (DM) intake (a), feeding time (b), digestible organic matter (DOM) intake (c) and DOM intake rate (d) (mean±s.e) on leafy (L, grey bar) and coarse (C, black bar) hays when offered in a choice situation, according to physical (L∞: no grid, L6 and L4: grid with 6-cm or 4-cm mesh size, respectively) and temporal constraints (24 h or 4 h of access daily).
Choice ratios for L (proportion of total intake or total feeding time) are indicated within the bars in (a), (b) and (c).

Table 3 *Organic matter digestibility (mean±s.e.) of the diet when the hays (leafy (L) and coarse (C)) were offered either alone or in a choice situation according to physical and temporal constraints*†

	Free access time (24 h)				Restricted access time (4 h)			
	L∞	L6	L4	C	L∞	L6	L4	C
No choice	0·739 (0·0015)	0·733 (0·0060)	0·717 (0·0073)	0·588 (0·0069)	0·736 (0·0042)	0·720 (0·0030)	0·724 (0·0055)	0·589 (0·0094)
Choice‡	0·710 (0·0065)	0·707 (0·0066)	0·695 (0·0045)	- -	0·714 (0·0082)	0·704 (0·0062)	0·680 (0·0024)	- -

† Physical constraints: L∞, no grid; L6 and L4, grid with 6-cm and 4-cm mesh size, respectively. Temporal constraints: 24 h or 4 h of access daily.
‡ In the choice situation, the digestibility is that of L and C combined.

choice than in the no choice situation (P<0·05). Therefore, total DM and DOM intakes were not significantly increased by giving choice when the constraint on L was absent or weak (L∞, L6) (P>0·05), whatever the access time, contrary to the most constraining treatment (L4, see below) (situation × grid, P<0·01).

When there was a significant physical constraint (L4), giving choice also decreased the feeding time on L whatever the access time, as in treatments L∞ and L6, but at the same time increased intake rate on L (P<0·01), particularly in 4-h access. The heifers devoted a great part of their feeding time to the coarse hay and ingested it nearly as fast as when it was offered alone (P>0·05). Therefore, they ingested more DM and DOM when offered a choice, whatever the access time (P<0·001).

Whatever the physical constraint, the ingestion of both hays in choice led to a decrease in diet digestibility (P<0·001) compared with the situation where only L was offered (Table 3).

Discussion

In this indoor experiment, we used a grid to reduce the accessibility of the leafy hay, in order to mimic the low height of vegetative sward at pasture. We combined this constraint with a temporal constraint to test the motivation of heifers to keep ingesting the leafy hay, which they preferred, when it was offered with another lower quality but physically more accessible hay. We used the optimal foraging theory (Stephens and Krebs, 1986) as a theoretical framework, as the optimization approach enables quantitative prediction of choices and provides a reference for comparison with observed diet choices.

The grid to reduce intake rates

One of the main currencies considered to be maximized by herbivores is the energy intake rate (EIR) of forages (Stephens and Krebs, 1986). Our predictions supposed that we managed to make EIR lower on L with the finest grid mesh size (L4) than on C, to create a trade-off between short-term rate of food intake (i.e. ‘quantity’, by selecting C) and long-term rate of energy assimilation (i.e. ‘quality’, by selecting L).

The finest mesh size (L4) managed to reduce the intake rate of L, and in line with the predictions, choice for L decreased when the smallest mesh size was applied. However, we did not manage to make EIR on L4 lower than on C because the animals demonstrated an interesting capacity to modulate their intake rate on this hay despite the grid. A width of 4 cm would nevertheless represent about half of the estimated incisor arcade breadth of 450-kg body weight cattle (Illius and Gordon, 1987), and it appears that the 4-cm-wide mesh did indeed constrain the animals. The clearest evidence for this is that total daily intake in an absence of choice was lower on L4 than on L∞ or L6, whatever the access time. It seems that animals ‘get tired’ of collecting the leafy hay through this grid, as shown by the fact that (i) in 24-h access they did not extend their feeding time on L when the physical constraint was intensified and the intake rate went down, while the reverse is often observed with other physical constraints such as short grass height (Penning, 1986; Penning *et al.,* 1991; Rook *et al.,* 1994; Ginane *et al.,* 2003), and (ii) the preference for L in treatment L4-4 h progressively declined from 0·80 to 0·45 over the 4 hours. This indicates that a physical constraint may not be expressed solely in terms of a decrease in intake rate but also in terms of a loss of animal motivation, more difficult to assess, but which was here made evident with the smallest grid mesh size.

Indeed, heifers greatly modified their absolute and relative intake rates of forages according to the measurement conditions (choice or no choice, measurement time scale, etc.). For example, when there was not a choice, on the basis of the allocated 4 or 24 h, L4 was ingested at the same rate as C, but over the 1st hour of feeding it was ingested faster (+5·8 g DOM per min in 24-h access and +4·5 g/min in 4-h access). Again, intake rate on L4 ranged from 11·1 g DOM per min when there was no choice with 24-h access to 15·5 g/min with 4-h access, then up to 19·9 g/min in choice with 4-h access. Intake rate was then higher with maximal than minimal constraints (L∞ or L6 with 24-h access), and very close to the value of 22·4 g DOM per min expressed while L was freely accessible with 4-h access in choice. Intake rate on L4 even reached 25·4 g DOM per min during the first hour of feeding in choice with 4-h access. This great flexibility of heifers in increasing their intake rate on L was probably made possible by the fact that the leafy structure of L required few mastication cycles during eating. Either way, this underlines their motivation to favour the better quality forage, including when it was offered in choice while they could consume the freely accessible coarse hay. In comparison, the coarse hay was ingested at the same rate whether or not there was a choice (with L4), under 4-h access. This great flexibility in behaviour stresses the limit of using the notion of fixed constraints when they are expressed by means of behavioural variables, as pointed out by Illius and Gordon (1999), and may make comparison difficult between observed diet choices and predictions from a theory based on these behavioural variables (relative energy intake rates between forages).

The L4-C choice : the benefit of having choice
While foraging, herbivores are confronted with diverse constraints and are supposed to make choices resulting from the balance of costs and benefits. In the present study, it appears that the intake of L4 was constrained by its cropping cost (lower daily DM intake on L4 than on C offered alone) as was the one of C by its rates of chewing and digestion (lower digestibility of C than of L), with similar daily DOM intakes with either L4 or C at the end of the day. Thus, the heifers may have maximized either diet quality or DM intake by mainly selecting L4 or C respectively, with a similar resulting DOM intake. In fact, the choice expressed in terms of proportion of feeding time was slightly in favour of L (about 0·6 whatever the access time). This behaviour is interesting because it enabled heifers to ingest more DOM all in all than when L4 or C were offered alone (4·9 kg in choice *v.* 3·9 and 4·2 kg with 24-h access, and 4·1 *v.* 3·4 and 3·3 kg with 4-h access). The increase in intake in the choice situation has already been shown in different contexts, with sheep grazing grass and clover (Champion *et al.,* 2004) or with heifers feeding on hays of different quality (Ginane *et al*., 2002). Here, it is mainly the result of an inverse relationship between decreasing time spent feeding on L4 and increasing intake rate on this hay. While spending less time feeding on L in choice than in no choice, the heifers ingested it much faster, especially when the access time was restricted (12·3 *v*. 11·1 g DOM per min with 24-h access and 19·9 *v*. 15·5 g/min with 4-h access), while intake rate on C remained stable (9·8 *v*. 10·8 g/min and 14·7 *v*. 14·5 g/min with 24-h and 4-h access respectively). Thus, even if heifers showed a great interest in L, in a very constraining situation (L4-4 h) they did not prioritize their diet quality by ingesting L in great amounts. Rather, they chose to divide their feeding time between the two hays and to manage their intake rate so that they increased their total DOM intake in the choice situation, with a resultant diet digestibility between those obtained with either L4 or C offered alone. These results therefore agree with the conclusions rising from a growing body of grazing experiments stating that the observed diet choices of ruminants faced with heterogeneous swards with low availability of good forages would have to provide a maximal daily DOM intake (WallisDeVries and Daleboudt, 1994; Wilmshurst *et al.,* 1995; Hirata *et al.,* 2002).

Mixed diets : the case of L∞-C and L6-C
When L∞ or L6 and C were presented together, the optimal choice must have been mainly or indeed exclusively in favour of L, as the heifers could maximize both diet quality and DM or DOM intake by feeding only on L. However, the heifers always deliberately included C in their diet in non-negligible proportions. With 24-h access, the increase in total feeding time when there was a choice allowed heifers to maintain DOM intake compared with when the leafy hay was offered alone. Unexpectedly, the restriction of access time only slightly increased the choices for L, but the higher intake rates of both hays on 4-h than on 24-h access allowed DOM intakes with 4-h access to be similar when there was or was not a choice. Mixed diets are a general rule in ruminant feeding behaviour, and various theories, some linked to the animal's cognitive abilities, have been put forward to explain this deviation from optimal choice.

The leafy and the coarse hays were different in chemical composition, digestibility and probable sensorial characteristics. Therefore, the observed diet diversity may result from the will to maintain an adequate ruminal and/ or nutritional balance (Westoby, 1978; Cooper *et al.,* 1995 and 1996). The need to regularly sample foods to update information (Illius and Gordon, 1990; Provenza and Balph, 1990) must have had a lower influence as animals were used to the hays and treatments for several days before data were recorded. Finally, the observed mixed diets can also be interpreted as the pleasure of ingesting diversified foods with different sensorial characteristics (Rolls, 1986). We can only speculate on the respective influences of these theories in explaining the observed mixed diets. They may all have contributed to the deviation from predictions, resulting in the great proportion of feeding time and intake recorded on C.

The results showed that in a very constraining situation where daily intake may be very low (L4-4 h), the heifers when offered a choice shared their feeding time among both hays and managed their intake rates in such a way that they were able to increase their total daily DOM intake compared with when either of the hays were offered alone. In a less constraining situation (L∞ or L6-4 h), the heifers expressed a clear intent to mix their diet and did not maximize their total daily DOM intake.

It appeared difficult to mimic indoors, with the grid, a physical grazing constraint such as sward height. The small mesh size of the grid constrained animals (by decreasing their motivation), but was not expressed, as has been shown to be the case outdoors, by a clear drop in intake rate compared with the more accessible alternative forage of lower quality. This may stem from the fact that on short grass, the necessity for the grazer to walk and move its head between small bites probably prevents it from compensating the small bite mass by increasing bite rate as much as on the finest-size mesh grid. The indoor experiment nevertheless carries many advantages as it can easily provide useful data to explain choices (e.g. intake, intake rate and feeding time recorded when the food options are offered alone) and provide information on the relative weights of behavioural adaptations (intake rate, feeding time) in constraining situations. In the present experiment, it notably revealed the heifers' capacity to modulate their intake rate on L, to keep ingesting this hay of better quality and to increase their total daily DOM intake in a very constraining situation. Therefore, indoor studies represent useful complements to grazing studies for understanding the behavioural mechanisms involved in ruminant food selection and ingestion at pasture.

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