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Note

Fill effect of concentrates in the rumen of sheep

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Summary — In an experiment based on a 4 x 4 latin square design with eight sheep, of which four were fistulated, the effects of four diets (H: hay alone; HB: hay + barley; HW: hay + wheat; HP: hay + beet pulp) were studied on daily dry matter (DM) intake, rumen content and the physicochemical characteristics of rumen content. The supplies of 700 g of concentrate were equivalent, on average, to 32% of total DM intake of the diets. Intake of hay alone was 66 g/kg$W^{0.75}$ and the rates of substitution of roughage by concentrate were 0.48, 0.42 and 0.63 for diets HB, HW and HP, respectively. At the end of the main meal, fresh digesta contents in the rumen were the same with all the diets, consistent with a physical effect on intake. The estimated residence times of the digestive residues of the concentrates were 8, 4 and 9 h, with the value for barley probably including an increase in residues from hay. At the end of the night, rumen fill tended to be lower when animals were receiving concentrates; thus, digestive residues of concentrates may not have limited intake between large meals.

concentrate / digestion / rumen / sheep

Résumé — Effet d'encombrement des aliments concentrés dans le rumen du mouton. *Dans un essai en carré latin avec huit moutons, dont quatre fistulés du rumen, l'effet de quatre rations (H = foin seul ; HB = foin + orge ; HW = foin + blé ; HP = foin + pulpe de betterave) a été étudié sur les quantités de MS ingérées par jour, la quantité de contenu ruminal et les caractéristiques physicochimiques du contenu ruminal. Les apports de 700 g de concentré ont été équivalents à 32%, en moyenne, de la MS totale ingérée des rations HB, HW, et HP. L'ingestion de foin seul a été égale à 66 g de MS/kg $P^{0.75}$ et les taux de substitution fourrage/concentré ont été égaux respectivement à 0,48, 0,42 et 0,63. A la fin du grand repas, les quantités de contenus ruminaux frais ont été identiques quelle que soit la ration (13,1 kg pour des moutons de 70 kg), en liaison avec un effet physique du concentré dans l'arrêt de l'ingestion. Les temps de séjour estimés des résidus digestifs des concentrés ont été respectivement de 8, 4 et 9 heures, la valeur pour l'orge incluant probablement une augmentation des résidus issus du foin. En fin de nuit, il a été observé une tendance à ce que le rumen soit moins rempli lorsque les animaux recevaient des aliments concentrés. Il est donc peu probable que les résidus digestifs des concentrés aient ensuite limité l'ingestion entre les grands repas.*

concentré / digestion / rumen / mouton

INTRODUCTION

There is extensive documentation of the effect of the substitution of roughage by concentrate (Blaxter et al, 1961) in ruminants. It has often been measured to predict roughage intake (Dulphy et al, 1987; Faverdin et al, 1991). The $\Delta F/\Delta C$ substitution rate varies widely. The main factors of variation are known: forage ingestibility, nature of concentrate, proportion of concentrate and animal energy requirements (Guerin and Dulphy, 1984; Berge and Dulphy, 1985). In contrast, the mechanisms involved in the variations are not well understood. In many of the explanations put forward they have been ascribed to digestive phenomena: improvement in the digestion rate of low grade roughages by nitrogen supply in concentrates and decrease in the digestion rate of other forages due to the presence of starch and soluble carbohydrates in the concentrates. It has also been suggested that marked changes in the physicochemical characteristics of reticulo-rumen content are responsible for intake modifications and, with large concentrate supplies, a metabolic control of appetite via animal requirements.

The aim of this study was to examine how physical regulation of intake is implicated when a diet of forage and concentrate is given to sheep. This mechanism of regulation probably accompanies short-term effects of palatability and nutrients coming from digestion (Faverdin et al, 1995).

Study of repletion level in the reticulorumen (Aitchison et al, 1986; Dulphy et al, 1992) is very helpful in understanding the effects of these mechanisms. This was performed with sheep receiving hay with and without concentrate. In addition, because substitution rates differ according to the nature of concentrate, three were compared: barley, wheat and beet pulp.

The fill effects of the different feeds were evaluated by comparing the average amounts of digesta in the reticulorumen to dry matter (DM) intake. A fill index was calculated in this way. It is emphasized that this concept is very different from the fill value of Jarrige et al (1986) which is an expression of the ingestibility, and includes all the mechanisms controlling intake.

MATERIALS AND METHODS

Animals and diets

Eight castrated Texel rams were used, of which four were fitted with a rumen fistula, 75 mm in diameter. All the animals were kept in individual pens. They had an average weight of 70 (+/–3) kg.

Table I. Mean characteristics of feeds used (g/kg DM).

	Crude protein	*Ashes*	*Neutral detergent fiber*	*Lignin without ashes*
Hay	88	88	663	52
Barley	113	66	181	8
Wheat	120	28	98	6
Beet pulp	92	86	480	18

Four diets, corresponding to four treatments, were supplied twice daily at 0830 and 1630 hours: H: hay alone; HB: hay + barley; HW: hay + wheat; HP: hay + beet pulp.

Table I gives the characteristics of each feed. Refusals were removed at 0800 hours. The animals were then given hay ad libitum (10% refusals) and 700 g of concentrates daily, 15 min before the hay. The concentrates had been ground and pelleted and the hay was chopped. The animals had free access to water and salt blocks.

The experiment was based on a 4 x 4 latin square design with two replications (one with normal sheep, one with fistulated sheep). The order of the treatments was always the same (given earlier), with an abrupt change of diet between two periods. Each period lasted 3 weeks. Digesta in the reticulorumen were studied only with the fistulated sheep.

Measurements

The amounts of hay DM offered and refused were weighed daily to calculate intake. Total N content, ashes, total cell walls and lignin (Goering and Van Soest, 1970) were then analyzed for the four feeds.

The fill effect of the hay and concentrates was estimated from the reticulorumen contents. These contents were manually removed before (0800 hours) and after (1030 hours) the main meal in the morning and weighed at 3 day intervals during the third week, once hay intake had become stable (see Chiofalo et al, 1992). Thereafter, it was assumed that the mean of the two values obtained was a good evaluation of the average content amounts during a 24 h cycle (Dulphy et al, 1988).

Some characteristics of the contents were determined: total cell walls and lignin of the dry phase, pH, volatile fatty acids (VFA) and osmotic pressure of the liquid phase. All these analyses have been described previously by Chiofalo et al (1992).

Statistical analyses

The general linear model procedure (SAS, 1985) was used to perform analysis of variance of the different parameters. The model was:

$$Y_{ijkp} = S_i + A_j + P_k + T_p + £_{ijkp}$$

where S_i = effect of square i (1 degree of freedom [df]) (only for intake, table II); A_{ij} = effect of animal j in the square i (6 df for intake, 3 df for digesta); P_k = effect of period k (3 df); T_p = effect of treatment p (3 df).

Table II. Dry matter (DM) intake by the eight sheep.

	Hay alone	*Hay + barley*	*Hay + wheat*	*Hay + pulp*	*RSD*
Animal live weight (kg)	68.6 [b]	69.6 [ab]	70.8 [a]	71.0 [a]	1.9
DM intake (g/day)					
Hay	1 563 [a]	1 271 [b]	1 302 [b]	1 184 [b]	108
Concentrate	0	610	615	604	23
Substitution rate	–	0.48	0.42	0.63	–
Forage DM intake (g/kgW$^{0.75}$)	65.7 [a]	52.7 [b]	53.4 [b]	48.4 [c]	4.0

[abc] Values on the same line followed by same letter are not significantly different.

RESULTS

Intake

The hay used was highly ingestible (66 g of DM/kgW$^{0.75}$). With concentrate supply, there was a decrease in hay intake, which was greater with the beet pulp (table II). However, there was no significant difference in hay intake among the three diets with concentrate (51.5 g DM/kgW$^{0.75}$). The substitution rates for wheat and barley were comparable and that for pulp a little higher (table II).

Concentrate supplementation always lowered hay intake during the main meal between 0830 and 1030 hours, slightly with wheat, but markedly with barley and pulp. During small meals animals receiving barley had a higher intake (table III).

Table III. Influence of the diet on the reticulorumen contents (four sheep).

	Hay	*Hay + barley*	*Hay + wheat*	*Hay + pulp*	*RSD*
DM intake on previous day (g)					
Hay	1 464 [a]	1 217 [ab]	1 272 [ab]	1 120 [b]	144
Concentrate	0	601	616	593	33
DM intake during the main meal (0830/1030 hours)					
Hay (g)	619 [a]	404 [b]	538 [a]	421 [b]	66
Concentrate	0	301	308	302	12
Hay DM intake during small meals (g)	226	409	196	278	–
Digesta at 0830 hours (g)					
Fresh	11 920 [a]	10 240 [a]	9 670 [a]	10 200 [a]	1 374
Dry	1 229 [a]	1 129 [ab]	1 021 [ab]	963 [b]	135
NDF	885 [a]	799 [ab]	728 [ab]	675 [b]	102
NDS	344 [a]	330 [a]	293 [a]	288 [a]	35
ADL	121 [a]	99 [ab]	92 [b]	91 [b]	16
Digesta at 1030 hours (g)					
Fresh	13 300 [a]	12 660 [a]	12 640 [a]	13 830 [a]	986
Dry	1 673 [a]	1 673 [a]	1 717 [a]	1 710 [a]	111
NDF	1 201 [a]	1 131 [a]	1 170 [a]	1 173 [a]	100
NDS	472 [a]	542 [b]	547 [b]	537 [b]	21
ADL	145 [a]	119 [b]	118 [b]	145 [a]	13
Total DM turnover (%)	4.2	5.4	5.7	5.3	–
Retention time (h)					
Total DM	23.9 [a]	18.7 [b]	17.4 [b]	18.7 [b]	1.9
Conc DM (estimated)	–	8	4.4	9.3	–
Total NDF	25.9 [a]	25.8 [a]	25.2 [a]	21.6 [a]	2.7
Total ADL	42.2 [a]	39.5 [a]	39.2 [a]	41.2 [a]	5.2

DM: dry matter; NDF: neutral detergent fiber; NDS: neutral detergent soluble; ADL: acid detergent lignin.
[ab] Values on the same line followed by same letter are not significantly different.

In comparison with hay intake in diet H, proportions of hay intake in the other diets were, respectively, 81, 83 and 76% for the eight sheep and 83, 87 and 76% for the four fistulated sheep. It can therefore be considered that the four fistulated sheep were representative of the whole group, even if their total intake was 7% under that of normal sheep.

The abrupt changes in diet had several interesting effects (fig 1a–d). There was an immediate fall in hay intake after barley supplementation (fig 1a) which became more pronounced on the second and third days, but thereafter intake rose again slightly and remained stable. Substituting wheat for barley (fig 1b) had no effect. When pulp was substituted for wheat (fig 1c), hay intake immediately dropped but then stabilized. Finally, hay intake rose sharply (fig 1d) when pulp was suppressed.

Rumen fill and DM turnover

At 0830 hours, just before feed distribution, the fresh digesta contents in animals receiving wheat and pulp concentrates were slightly lower than those of the other two diets, but overall there was no significant difference among diets (table III).

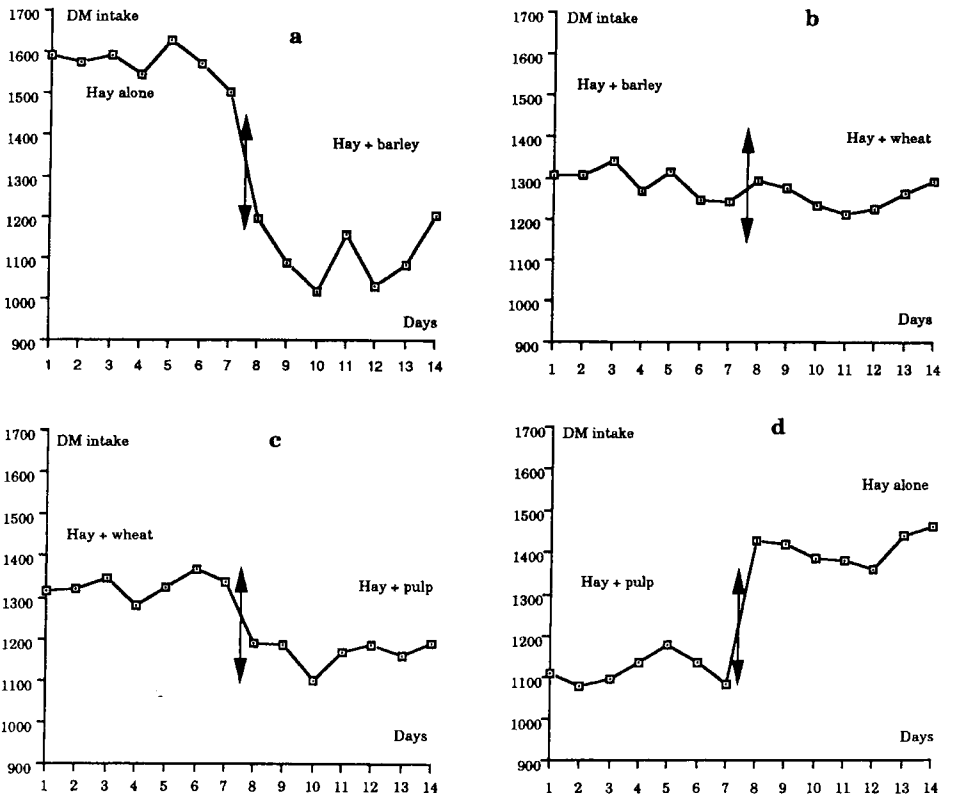

Fig 1. Effect of changing the diets on hay intake (g/day). **a.** Diet H to HB. **b.** Diet HB to HW. **c.** Diet HW to HP. **d.** Diet HP to H.

At 1030 hours, just after the end of the first main meal, the fresh digesta contents were closely similar with all four diets while in the dry digesta contents there was practically no difference. Unsurprisingly, the proportion of plant cell walls in the content was lower when animals were receiving concentrates.

Comparison of the increases in the dry digesta content and DM intake during the corresponding main meal shows a DM disappearance of about 160 g with hay alone and hay given with barley or wheat. In contrast, no disappearance was observed when the animals received pulp (table IV). Missing DM was composed of cell wall (neutral detergent fiber [NDF]) and cell content (neutral detergent soluble [NDS]) for hay, but mainly all of NDS for diets HB and HW. There was a small gain of NDF for diets HW and HP and nearly no loss of NDS for diet HP.

The DM disappearance rate out of the reticulorumen (transit + absorption) was 4.2%/h with hay, ie, an average residence time for the digesta of 23.7 h. In these conditions, the mean digesta content over 24 h would be 99% of DM ingested as hay, corresponding to a fill index of 0.99. If we consider this value to be constant for all the diets, then the residence times of digesta would be 8, 4 and 9 h with barley, wheat and pulp, respectively, giving a fill effect of 0.33, 0.18 and 0.38.

Characteristics of rumen contents

The characteristics of reticulorumen contents are given in table V. The DM content was lower with the pulp diet at 0830 hours. At 1030 hours, DM content with the pulp diet was again (but not significantly) lower than with the other two concentrate diets, but there was no difference with hay alone.

At 0830 hours, ie, 16 h after the evening distribution of concentrates, pH values were practically identical. At 1030 hours, there

Table IV. Estimation of matter disappearing (–) from the rumen during the main meal (120 min) (by comparing content before the meal and content after the main meal).

g	*Hay*	*Hay + barley*	*Hay + wheat*	*Hay + pulp*
Dry matter				
Before + intake	1 848	1 834	1 867	1 686
After	1 673	1 673	1 717	1 710
Variation	–175	–161	–150	+24
NDF				
Before + intake	1 295	1 121	1 115	1 099
After	1 201	1 131	1 170	1 173
Variation	–94	+10	+55	+74
NDS				
Before + intake	553	713	752	587
After	472	542	547	537
Variation	–81	–171	–205	–50

See table III for abbreviations.

was no change in pH with hay alone, but a decrease of 0.46 with pulp and 0.8 with wheat and barley. Osmotic pressure was modified neither by the diet nor by digesta sampling time (265 mOsm).

At 0830 hours, VFA content was similar with all four diets. However, at 1030 hours, VFA content was much higher with the three concentrates, and at comparable levels, than with hay alone. There was little difference between the diets in the proportion of propionic acid but this increased between 0830 and 1030 hours. The proportion of acetic acid was lower after concentrate supply and decreased between 0830 and 1030 hours, particularly with wheat and barley supplementation.

DISCUSSION

The first noteworthy feature is that hay intake was high, primarily owing to its composition (Dulphy et al, 1990), but also perhaps because the trial was performed over long-day periods (Michalet-Doreau and Gatel, 1983). The substitution rates, which on average were 0.51, were comparable to the val-

Table V. Mean characteristics of reticulorumen contents (four sheep).

		Hay	*Hay + barley*	*Hay + wheat*	*Hay + pulp*	*RSD*
DM content (g/kg)	0830	103[a]	109[a]	106[a]	94[b]	4
	1030	121[a]	132[a]	134[a]	124[a]	12
NDF content (g/kg DM)	0830	721[a]	708[ab]	712[ab]	700[b]	11
	1030	718[a]	675[b]	680[b]	686[b]	17
pH	0830	6.71[a]	6.73[a]	6.71[a]	6.75[a]	0.10
	1030	6.73[a]	5.93[c]	5.91[c]	6.29[b]	0.13
Osmotic pressure (mOsm/L)	0830	269[a]	263[a]	270[a]	266[a]	16
	1030	255[a]	266[a]	272[a]	262[a]	17
Total VFA (mmol/L)	0830	83[a]	86[a]	81[a]	83[a]	9
	1030	94[b]	122[a]	119[a]	118[a]	10
Acetic acid (%)	0830	71[a]	69[ab]	67[c]	68[bc]	1.4
	1030	69[a]	64[b]	64[b]	67[ab]	2.1
Propionic acid (%)	0830	17[ab]	17[b]	19[a]	18[a]	0.8
	1030	20[a]	20[a]	21[a]	21[a]	1.5
Butyric acid (%)	0830	8.5	10.8	11.1	9.9	1.3
	1030	8.8	12.8	12.0	9.3	1.6

VFA: volatile fatty acids; see table III for other abbreviations.

ues reported by Guerin and Dulphy (1984) and Berge and Dulphy (1985) in experiments in which concentrate supply also accounted for 30% of the feed (see also Crabtree and Williams, 1971; Lamb and Eadie, 1979). The results of our experiment are thus consistent with other findings.

In the short term, three main factors can control intake: rumen fill, nutrients in the rumen and palatability of the feed (Dulphy and Demarquilly, 1994; Faverdin et al, 1995).

The rapidity of intake control was striking when concentrates were added or withdrawn. This observation is consistent with the results of Baumont et al (1994). In addition, period effect on intake was not significant. In this trial the possibility of metabolic control over a long period seems therefore reduced.

In our experimental conditions, the rumen seemed to be full at the end of the main meal even after distribution of concentrates; thus, differences in juice composition seem to be a consequence of intake and a possible chemical control of intake at the end of the main meals seems without importance here, in opposition to observations made with grass silage (Chiofalo et al, 1992). However, the possibility of a brief chemically mediated control of intake (by rumen chemoreceptors) after the main meal cannot be entirely ruled out, since the control of large and small meals can involve different mechanisms (Gill and Romney, 1994). A temporary reduction in appetite may occur with barley and wheat when rumen pH is low and VFA content high. Nevertheless, reported findings vary (Malestein et al, 1984; Duranton and Bueno, 1985). To determine whether this mechanism does occur, both the physicochemical conditions in the rumen after main meals and during the small meals would need to be studied. Osmotic pressure varies little during the main meal and over the day (Lemosquet et al, 1996) and, therefore, has probably no effect on intake (Carter and Grovum, 1990).

Rumen fill in animals receiving concentrates was 15% lower before the morning meal than in those given hay alone. This may be firstly due to a dislike for the associated forage (Baumont et al, 1994), as observed in previous trials when animals seemed to wait for the more palatable of two distributed forages (Gatel, 1984; Baumont et al, 1990). In addition, low volontary intake of certain forages has already been observed during experiments in which there was no choice of feed (Greenhalgh and Reid, 1971; Colucci and Grovum, 1993). However, more detailed studies on the pattern of intake during the nyctohemeral cycle and on intake rate are needed (Gill and Romney, 1994) to test this hypothesis. This may also be due to a lower state of hunger when animals are fed concentrates. The modification of this state can be rapid because the concentrates are rapidly digested.

In the literature, results on the evolution of reticulorumen content vary widely from one trial to another. With a straw-based diet, content increased by 8% after the main meal when barley was given (Dulphy et al, 1994), whereas in another study (Lemosquet et al, 1996) with a hay-based diet there was a decrease of 26% in reticulorumen content after concentrate supply. In contrast, in a study with dairy cows (Gasa et al, 1991), concentrate supply had no effect. The different possible situations are therefore numerous.

The repletion levels of the reticulorumen in this study were therefore similar at the end of the main meal for all diets and so it is likely that, at that time, physical control of appetite was preponderant. Fill effect can be divided into an immediate effect (end of main meal) and a postprandial effect in which the impact decreases with time. The estimations made here concern this second effect. However, in order to be entirely accu-

rate it would be necessary to evaluate continuously rumen digestive residues from both the hay and the concentrates distributed. This technique is needed in combination with the nylon bag method of Michalet-Doreau and Sauvant (1989) giving the digestion rate of fed concentrates. The approach with the nylon bags has been tried by Madsen et al (1994) with forages. Such studies should evidence a slowing down of the digestion rate of hay in the presence of concentrate. This phenomenon, which very likely enhances the fill effect of hay, has been widely documented (Henning et al, 1980; Mertens and Loften, 1980; Miller and Muntifering, 1985; Aitchison et al, 1986; Hoover, 1986; Pienaar et al, 1990; Gasa et al, 1991 and others). Two ways can be implicated: an increase of the lag time and/or a decrease of the digestion rate. The first way probably explains why there is no cell wall loss during main meals after concentrate intake.

A further aim of this study was to examine possible differences among the concentrates used. According to Michalet-Doreau and Sauvant (1989), barley is digested more rapidly than wheat and beet pulp more slowly than wheat. This suggests that barley would produce the lowest rumen fill, as in fact was observed by Muller and Beranger (1979) and Verité and Dulphy (1981). In contrast, our present results showed more residual digesta with barley than with wheat. This could be due to a more pronounced decrease in the digestion rate of hay (Berge, 1982), which led to a higher DM content in the rumen at 0830 hours than with the other two concentrate diets.

Wheat supplementation resulted in lower (but not significantly) rumen fill in the morning before the main meal than barley concentrate supply. In addition, the estimation of residence time of wheat in the rumen gave a low value. In this case, it is possible that the digestion rate of hay was not affected.

Beet pulp was expected to have least impact on the digestion rate of hay (Berge, 1982) and, hence, on its fill effect. In contrast, the digestion of pulp was comparatively slow and its fill index greater than that of wheat. In addition, pulp seems to have a considerable effect on satiety since, during the main meal, there was no quantifiable passage of DM through the reticulo-omasum orifice. This was perhaps because dried beet pulp strongly absorbs water (Ramanzin et al, 1994) and, above all, may decrease free water necessary for the passage of particles and soluble products. In this situation mechanisms of physical control of intake are clearly involved during the main meal.

Another aim of this work was to test a new approach in the study of concentrates. Some uncertainties are the consequence of this. For example, the results of table V are relatively imprecise because amounts of digesta, not measured on the same day, are compared. RSD of rumen contents are high and it is probable that the results, at the same hour, are variable from one day to another. Elsewhere, calculation of the fill values of concentrates would be better if more values of rumen contents had been available during the day, because the rates of digestion of concentrates are high.

A comparable trial, but with a lot of measurements of rumen contents, will be necessary to have a better idea of the fill effect of concentrates. The method to measure contents is difficult to use and, therefore, another is needed to follow precisely digesta in the rumen with markers. Nevertheless, results obtained in this trial are relatively logical.

CONCLUSION

It is clear that concentrates have a fill effect in the rumen. When the concentrate supply is not very great the effect is apparent at the end of the main meals and, very likely,

plays a short-term role in satiety. During the day concentrates lead to the presence of residue in the rumen. They could also result in an increase in the amount of residue from forage. It should not be difficult to estimate these digestive residues between ingestion of the concentrates and their disappearance. In contrast, the physical effect of these residues on animal appetite during the day seems secondary and the interpretation of observations is difficult. More accurate studies are needed on how the control of forage-based and concentrate-based diets is regulated (cf Baumont et al, 1994). Accordingly, along with the fill effect of the concentrates, two other mechanisms have to be studied: the possibility that the animals will wait for the preferred food (oropharyngeal control) and the possibility of a negative effect on hay intake of a lower state of hunger when concentrates are fed (metabolic control).

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