Feeding behaviour and intake of heifers fed on hays of various quality, offered alone or in a choice situation

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Original article

Feeding behaviour and intake of heifers fed on hays of various quality, offered alone or in a choice situation

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Abstract — We studied the feeding behaviour of cattle offered unconstrained choices between two hays of either different or similar nutritive values, and linked these choices to their behaviour when the same forages were offered alone. Over successive 10-day periods, six 15-month-old Aubrac heifers received three hays (a leafy one, G, and two late cut ones, C1 and C2, of very similar nutritive value), ad libitum, alternately alone and associated two by two. As expected, the heifers ate more G than C1 or C2 when the hay was offered alone, and preferred G in choice trials. They displayed a similar behaviour towards C1 and C2 when they were given alone, and also when they were independently associated with G (C1 and C2 making up 18% and 17% of the total intake and 21% and 17% of total feeding time, respectively) or when they were offered together (each accounting for nearly 50% of the total intake or feeding time). The choices could be related to the daily intakes of the forages given alone, which could thus be a good predictor of relative daily intakes under choice conditions. Heifers always showed partial choices, which could be seen as the research of the maintenance of optimal ruminal conditions, the result of sampling behaviour and/or the pleasure associated with the diversity of the diet. Their tendency to diversify the diet was also supported by the reaction to the recent diet by temporarily increasing their preference for the hay that had not been offered during the previous no-choice sub-period. Finally, all the choice situations raised the daily dry matter intake, which could be seen as the result of their motivation to eat due to the diversity of the offer.

feeding choice / intake / cattle / hay

Résumé — Comportement alimentaire et ingestion chez des génisses alimentées avec des foins de qualité variable, distribués seuls ou deux par deux. Nous avons étudié les choix alimentaires de bovins entre deux foins de valeurs alimentaires similaires ou différentes, et nous avons relié ces choix au comportement d'ingestion des animaux lorsque chaque fourrage leur a été proposé seul. Au cours de périodes successives de 10 jours, six génisses Aubrac âgées de 15 mois ont reçu trois foins (un foin

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de regain G et deux foins tardifs C1 et C2 de valeurs alimentaires similaires) à volonté, alternativement distribués seuls ou associés deux par deux. Les génisses ont ingéré G en plus grande quantité que C1 ou C2 lorsque les foins étaient distribués seuls et l'ont préféré en situation de choix. Elles ont eu des comportements similaires vis-à-vis de C1 et de C2 distribués seuls, mais également lorsqu'ils étaient offerts avec G (C1 et C2 représentant respectivement 18 % et 17 % des quantités ingérées totales, et 21 % et 17 % du temps d'ingestion) ou lorsqu'ils étaient distribués ensemble (chaque foin représentant environ 50 % des quantités ingérées et du temps d'ingestion). Les choix étaient en accord avec l'ingestibilité des fourrages distribués seuls, qui pourrait donc être un bon critère de prévision des quantités ingérées relatives en situation de choix. Les génisses ont toujours montré des choix mixtes, ce qui peut être interprété comme la recherche d'un maintien de conditions ruminales optimales, le résultat d'un comportement d'échantillonnage et/ou du plaisir associé à un régime diversifié. Leur tendance à diversifier le régime s'est également exprimée lors du passage d'une situation de non choix à une situation de choix, par l'augmentation temporaire de leur préférence pour le foin qui n'avait pas été distribué précédemment. Enfin, la situation de choix a significativement stimulé l'ingestion quels que soient les foins offerts, pouvant traduire une augmentation de la motivation à ingérer liée à la diversité de l'offre.

choix alimentaire / ingestion / bovin / foin

1. INTRODUCTION

In extensive grazing systems, where forages are highly variable, knowledge of what determines a herbivores' feeding choices is necessary to work out the efficient use and management of pastures. The forages differ mostly in nutritive value (digestibility, N content, etc.), and herbivores will usually select the most nutritive patches, plants or plant parts [10, 25].

In the literature, the studies on choices between forages of different quality are relative to only one difference in quality, that is in choice trials between rye-grass and clover [1, 21, 23] or between vegetative and reproductive swards [6], or when one of the two forages is pelleted [3, 18].

Therefore, the present study focused on the behaviour and intake of cattle faced with a choice between two long forages that either differed greatly or were very similar in nutritive value. These forages were offered ad libitum without a constraint over several days. The absence of a constraint contrasts with most experiments where the accessibility of the preferred forage varied in order to manipulate the relative intake rate of the forages [4, 6, 8, 19], which has been shown to influence the choices both at pasture [4, 13] and indoors [7, 16], as predicted by the Optimal Foraging Theory [26]. When the relative intake rates (IR) and choices are measured without a constraint, choices are usually recorded in short-term tests [13, 17, 21]. However, measurements over several days are assumed to take better account of the post-ingestive effects of individual foods that influence choice [3, 11].

In addition, foraging herbivores encounter successions of foods, the nature of which is able to modulate diet selection in favour of the forage not previously encountered, as observed within a few days on cattle by Parsons et al. [23]. Therefore each choice between the two forages was preceded by a no-choice period during which one of them was given as the sole forage. This allowed to compare the preferences for either the forage given previously or that which was not given. By these no-choice and choice successions with the same forages, we also evaluated the behavioural adaptation of cattle to choice situations (intake, feeding behaviour, duration of eating bouts).

2. MATERIALS AND METHODS

This trial was carried out from March to May 1999 at the experimental farm of Laqueuille (Puy-de-Dôme, France).

2.1. Animals and forages

We used six 15-month old Aubrac heifers, which came from a herd reared at INRA, housed in individual pens and isolated from each other by open-work fences. They weighed 395 kg (s.d. 19) at the beginning and 425 kg (s.d. 19) at the end of the experiment. The litter was made up of non-edible conifer wood shavings. The animals had free access to water and salt blocks. They were accustomed to the experimental conditions and were fed hay for at least 15 days before the start of the experiment. No concentrate was fed to the animals during the whole experimental period.

We used three different hays, obtained from a re-growth of a natural pasture: a first late cut of cocksfoot and a first late cut of tall fescue, designed as good (G), coarse 1

(C1) and coarse 2 (C2) respectively. They were all harvested in good climatic conditions. The two late cut hays were chosen with a similar chemical composition (Tab. I). Since intake rates (IR) are often considered as determinants of choice, we also measured the dry matter (DM) intake rate of each hay in standardised conditions, for over 5 minutes with the Aubrac heifers after 14-hour fasting. Such IR were therefore very high and could be considered as potential IR of the hays by these heifers. We named them short-term IR. C1 and C2 were also similar in short-term IR and were ingested more slowly than G. The digestibility estimated from the N-content of the heifers' faeces were also determined for the hays (Tab. I).

2.2. Experimental design and procedure

Each heifer had two adjacent mangers connected to a data processing system [14]. The heifers were equipped with a halter carrying an electronic sensor to tell whether the animal's head was over the manger. The

Table I. Chemical composition and digestibility of the three hays offered.

Hay	Good (G) Regrowth from natural pasture	Coarse 1 (C1) First cut of cocksfoot *Dactylis glomerata*	Coarse 2 (C2) First cut of tall fescue *Festuca* sp.
Dry matter content (DM) † (g·kg⁻¹ fresh matter)	874	875	879
Organic matter content (OM) (g·kg⁻¹ DM)	886	936	931
Crude protein (g·kg⁻¹ DM)	174	63	72
NDF (g·kg⁻¹ DM)	581	676	679
ADF (g·kg⁻¹ DM)	266	358	372
OM digestibility ‡	0.769	0.567	0.573
Intake rate (g DM·min⁻¹) §	54	44	44

† In all tables, DM = dry matter.
‡ Estimated from the N content of the heifers' faeces.
§ Measured independently over a few minutes on fasted heifers.

Table II. Succession of treatments for all heifers throughout the experiment.

Heifers	Period 1 (20 days)		Period 2 (20 days)		Period 3 (20 days)	
	no choice	choice	no choice	choice	no choice	choice
1	C1	GC1	G	GC2	C2	C1C2
2	G	GC1	C1	C1C2	C2	GC2
3	G	GC2	C2	C1C2	C1	GC1
4	C2	GC2	G	GC1	C1	C1C2
5	C2	C1C2	C1	GC1	G	GC2
6	C1	C1C2	C2	GC2	G	GC1

† In all tables, G, C1 and C2 are respectively Good, Coarse 1 and Coarse 2 hays.

presence or absence of the heifer was checked automatically every 11 seconds. We calculated the daily feeding time for each hay, considering whether the heifer stopped eating when it left the trough for longer than one minute (5 successive checks).

We conducted the experiment during three 20-day periods, divided into two 10-day sub-periods. During the first sub-period only one hay was given, alternately in the two mangers. During the second sub-period the animals had a choice between two hays, each being distributed alternately in each manger. For each sub-period we used the Latin square procedure, as shown in Table II. In addition, the two hays given during a choice sub-period were offered alone in the previous no-choice sub-period to one heifer out of the two. This enabled us to study the effect of the recently eaten hay on further choices.

Hays were given once a day at 8:30 am, and remained available for 24 hours. A minimum of 4 kg of hay was given each day, and 15% of the refusals were allowed when intake approached or exceeded 4 kg. Offer and refusal of hays were weighed each day for all heifers. They were sampled daily during the last 5 days of each sub-period, for dry matter (DM) content measurements and chemical analyses (ash, N, NDF and ADF contents). We also took faeces

samples from each heifer during the last 5 days to estimate the organic matter digestibility (OMD) of the diet from the N content of the faeces (N_f, % of OM), using the equation proposed by Peyraud [24]: $OMD = 0.975 - (0.633 / N_f)$. The daily DM intake (DMI) of the hays was calculated per kg of the actual live weight of each animal, then it was adjusted to a 400-kg heifer. For each diet, we also calculated the digestible organic matter intake (DOMI).

2.3. Behavioural data computing

Choice ratios were expressed in the usual way [2, 16] as the ratio of the DMI of G by the total DMI in the case of GC1 and GC2 choices, and we chose the ratio of DMI of C1 by total DMI for the C1C2 choice. In the same way, we calculated a choice ratio expressed as feeding time. We also calculated a feeding time choice ratio for the first hour of eating after the food distribution, which could be interpreted as the spontaneous preference.

To better describe the choices, we first recorded the daily number of switches between hays. Then we estimated the number and duration of eating bouts for each hay, two eating bouts being considered as distinct when the heifer was away from the manger for more than one minute, or when

it switched between hays. The bouts were also classed by duration into three groups: the first class corresponded to one detection of the animal's head over the manger, i.e. a very short visit (less than 22 seconds). The second class grouped bouts that were between 22 seconds and 5 minutes long. The third one comprised bouts that were longer than 5 minutes.

2.4. Statistical analyses

We used the SAS software GLM procedure [27]. We first analysed the effect of day on DM intake within each sub-period. Since DMI stabilised sufficiently after 5 days, we considered for all variables their means over the last 5 days of each sub-period. The choice ratios (in DMI and in feeding time) were converted to arc-sinus to stabilise variance.

In each situation (no choice and choice) we tested the effect of the treatments (nature of hay and choice between hays respectively), periods and heifers by analysis of variance. The analyses of choice ratios included the effect of hay given previously in the no-choice situation. We also compared the choice and no-choice situations for the total daily intake (of dry matter or digestible organic matter) and total feeding time, for the daily intake of each hay and daily intake rate. For this purpose we used the nonparametric test of Wilcoxon for paired data, averaged over the last 5 days of each sub-period. Since the animals behaved similarly

with the two coarse hays, we pooled the results obtained with them and considered only two types of hays: good (G) and coarse (C). This gave six paired data for each of three types of no choice – choice succession: G then $G + C$; C then $G + C$; C then $C + C$.

We also used the Wilcoxon test for paired data to compare the choice ratios (in feeding time) observed over the whole day and during the first hour of eating. We compared the distribution between the 3 classes of the eating bout duration, between the two hays of each type of choice (GC and CC), by the chi-squared test. Since this distribution was similar between the heifers, we summed the number of bouts of all heifers per type of choice and class for each hay.

3. RESULTS

3.1. Intake

The daily DMI increased during the experiment by close to one kg, resulting in a period effect in a choice ($P < 0.001$) and in a no-choice situation ($P < 0.001$). Total daily DMI did not differ significantly between the heifers, nor did the proportion of each hay in the choice situation ($P > 0.05$).

In the no-choice situation, the daily intake of G was greater than those of the two other hays. As expected, total DMI in the choice situation was higher when G was present, and heifers preferred G (Tabs. III and IV).

Table III. Feeding behaviour of heifers according to the forage in a no-choice situation.

	Forages				Significance
	G	C1	C2	s.e.	of effect
Daily DM intake (kg)	6.2	5.4	5.7	0.10	***
Daily feeding time (min)	271	235	264	10.0	
Number of bouts	30	62	54	6.5	*
Daily intake rate (g DM·min^{-1})	23.0	23.7	22.3	0.69	

Table IV. Feeding behaviour of heifers in a choice situation, according to the type of choice.

	Choices				Significance
	GC1	GC2	C1C2	s.e.	of effect
Dry matter intake ratio †	0.82	0.83	0.51	0.071	**
Feeding time ratio †	0.79	0.83	0.54	0.053	*
Total DM intake (kg)	6.9	6.8	6.2	0.12	**
Total feeding time (min)	291	307	227	22.3	(‡)
Total number of bouts	57	49	93	2.8	**
Bouts ratio †	0.62	0.62	0.53	0.069	
Number of switches	20	26	28	2.9	

† Dry matter intake ratio, feeding time ratio and bouts ratio represent the proportion of the total daily intake, total daily feeding time and total daily number of eating bouts on G for GC1 and GC2, and on C1 for C1C2.
‡ Feeding time is significant ($P < 0.05$) between associations with the Mann-Whitney test.
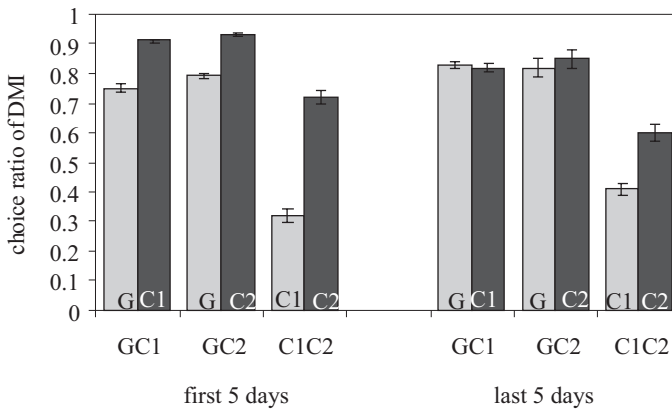

Figure 1. The effect of the hay previously offered alone (stated in the columns) on the choice ratios of DMI (means ± s.e.) during the first and last 5 days of the choice subperiods (for definition of choice ratios, see footnote of Tab. IV).

Heifers ingested C1 and C2 in the same amounts in the no-choice situation. In C1C2, they had no preference for either hay, with a good balance between them. They also ingested the same quantity of C1 and C2 in GC1 and GC2, either in absolute terms or relative to total DMI (Tabs. III and IV).

The preferences were largely influenced during the first 5 days of choice sub-periods by the nature of the forage distributed during the previous no-choice sub-periods ($P < 0.01$), and it was in favour of the other one. It was the more pronounced for C1C2: the preference in favour of C1 was 33% when it was given before and 73% when it

was not given. The effect of the previous diet decreased during the choice sub-period and was absent (GC1, GC2) or non significant (C1C2) during the last 5 days ($P > 0.05$, Fig. 1).

The choice situation stimulated the total DMI in all situations, for all heifers, as indicated by the comparison of paired data of each sub-period (last 5 days) ($P < 0.05$): this was the case not only from C1 or C2 to GC1 or GC2 (+23%), but also from C1 or C2 to C1C2 (+11%), and from G to GC1 or GC2 (+10%) (Fig. 2). In this latter case, the increase in total DMI (+0.65 kg, from 0.15 kg to 1.1 kg according to the heifer) was matched with a decrease in DMI of G by all the heifers (–0.5 kg on average, $P < 0.05$), although among animals the extent of this decrease varied widely and there was no relationship between the increase in total DMI and the decrease in DMI of G. The increase in intake in the choice persisted steadily throughout the 10-day sub-period.

Expressed as digestible organic matter, the total intakes were evidently higher with GC1 or GC2 (4.5 kg) than with C1 or C2 (2.9 and 3.0 kg respectively: +52%, $P < 0.05$). They were also slightly but significantly higher with C1C2 (3.3 kg)

than with C1 or C2 alone (+10%, $P < 0.05$). This was, however, not the case with GC1 or GC2 compared with G alone (4.2 kg: +6%, $P > 0.05$), because of the decrease in the G intake and of the variations in the preference between the heifers.

3.2. Feeding behaviour and intake rate

In the no-choice situation, the daily feeding times were not statistically different between the forages (though half-an-hour shorter for C1), and the daily DM intake rates were the same (Tab. III). In the choice situation, the heifers spent 64 and 80 min less time eating C1C2 than GC1 and GC2 respectively (Tab. IV). Since the variance was greater in GC2, due to one heifer that had a 2-hour longer feeding time than the others, these differences between the types of choice were evaluated by the Mann-Whitney test for low data numbers. It indicated that total feeding time was lower with C1C2 than with the other choices ($P < 0.05$). The total feeding time was increased significantly from the no-choice C1 or C2 to the choices GC1 or GC2 (+56 or +43 min; $P < 0.05$, for paired data), and was similar in the other cases.
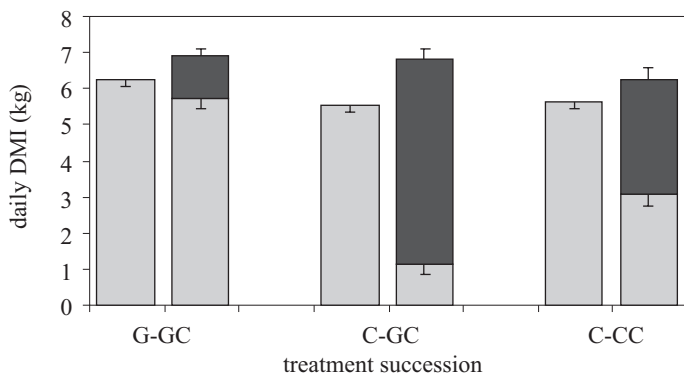

Figure 2. Total dry matter intake (DMI, means ± s.e.) according to the no-choice (first column) and choice (second column) situation. In choice, the grey area represents the DMI of the hay previously offered alone, and the black area the DMI of the associated hay.
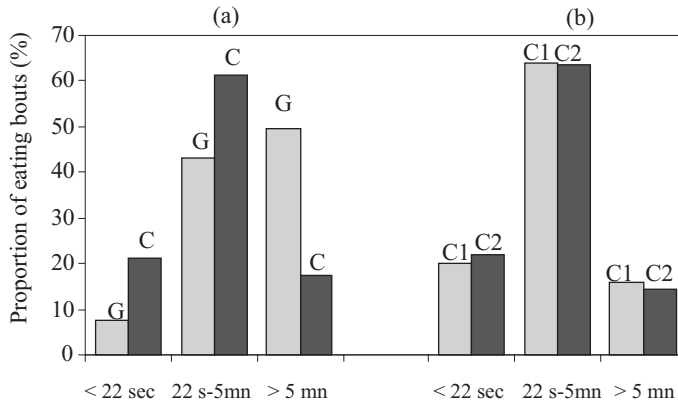
Figure 3. Proportions of eating bouts with different durations for each hay with a choice between a good (G) and a coarse hay (C) (a), and between two coarse hays (C1 and C2) (b).

The preferences expressed in feeding time ratios were the same as those expressed in DMI (Tab. IV). However, they were more pronounced in the first hour after food distribution than over the whole day, the difference being significant (Wilcoxon test) for GC1 and GC2 (0.96 and 0.95 vs. 0.79 and 0.83 in favour of G; $P < 0.05$), but not for C1C2 (0.60 vs. 0.54 in favour of C1). No significant variation between the animals ($P > 0.05$) was observed on feed preferences.

Intake rates of hays could vary largely according to the situation (choice vs. no-choice, analysed by the paired data test within periods) and to the nature of the associated forage in choice situations (s.e. 1.99 g DM·min^{-1} from global variance analysis). This was manifested for C1 and C2 hays. When they were given alone, the intake rates of C1 and C2 (23.7 and 22.3 g·min^{-1} respectively) were higher than when associated with G (19.7 and 17.0 g·min^{-1} respectively, $P < 0.01$), and slightly (but not significantly) slower than when offered together (27.6 and 27.1 g·min^{-1} respectively, $P > 0.05$). In choice situations, intake rates of C1 and C2 were lower when associated with G than when offered together ($P < 0.05$). The DM intake rates of

G did not vary between the no-choice (23 g DM·min^{-1}) and choice situation nor with C1 or C2 (24.1 and 23.8 g respectively, $P > 0.05$).

In no-choice situations, heifers produced more eating bouts with the coarse hays than with G ($P < 0.05$, Tab. III). Similarly, the total number of bouts was higher for the C1C2 choice than for the other two that included G ($P < 0.01$, Tab. IV). The total daily number of switches between hays was high (20 to 28 according to choice) and not statistically different between the choices (Tab. IV). The proportion of eating bouts for G in GC1 and GC2 was not significantly different from that of C1 in the C1C2 association. The number of eating bouts was well balanced between C1 and C2 in C1C2 (53% of the bouts were realised on C1), and only slightly (but significantly) in favour of G (62%) in GC1 and GC2 ($P < 0.05$). The chi-squared analysis of the distribution of bout duration showed significant differences between G and coarse hays in GC1 and GC2 ($P < 0.001$), with a greater proportion of short bouts (less than 22 s) and a lower proportion of long bouts (more than 5 min) for the coarse hays (Fig. 3a). On the contrary in C1C2, the distributions were identical between the two hays (Fig. 3b).

4. DISCUSSION

4.1. Intake rates, voluntary intake and diet choices

Relative potential energy intake rates of forages are considered as a good predictor of choices [10]. These potential intake rates are calculated on a short time scale and are considered to characterise the forages by representing the maximum rate at which they can be ingested by the animals. The potential intake rates of digestible OM of G, C1 and C2, calculated from potential DM intake rates and OM digestibility (Tab. I), were 36.5, 23.4 and 23.5 g digestible OM·min^{-1} respectively. All observed choices were in accordance with these relative intake rates of hays and therefore with predictions of the Optimal Foraging Theory [26]. However, these intake rates of digestible OM, obtained from short term tests on fasted heifers, do not integrate all the post-ingestive effects of forages that could act on diet choices on a daily basis, such as the rate of passage [22] and of fermentation [3]. In this respect, the relative voluntary daily DM (or digestible OM) intakes of forages when given alone, which integrate these parts of digestive processes, may represent a better predictor of choices. A comparison of Tables III and IV indicates that daily intakes of heifers were also in good accordance with their choices. It is particularly noticeable that heifers which behaved similarly towards the two coarse hays when they were offered alone (intake, feeding time), were also exactly doing so when these hays were offered in a choice situation, either together or with the good hay. These observations would thus indicate that daily DM intakes of hays could be predictors of relative daily intakes in choice as well as short-term digestible OM intake rates.

4.2. Partial choices

Although the heifers largely preferred the better hay, they also consumed a significant amount of the associated coarse hay, up to nearly 20% of total intake, even though it had a far lower nutritive value. Partial choices have been widely observed indoors [2, 5, 16] or in grazing conditions [13, 28, 30].

Partial choices have been assumed to result from sampling behaviour, i.e. the need to regularly re-evaluate the qualitative characteristics of the different foods, even as here with familiar foods in a familiar environment [25]. The high daily number of switches between hays (20 to 28 according to the choice), and the high number of short bouts on the coarse hays when given with the better one, could support such sampling behaviour. However, the need to re-evaluate regularly the relative values of hays is unlikely in GC choice, as the preference for G was near absolute during the first hour after feed distribution.

Partial choices could also result from difficulties in discriminating between the characteristics of each food [12, 30]. This would not be the main reason here because the temporary higher preference for the hay which was not given before the choice sub-period indicates that the heifers were able to discriminate well between the hays and in particular between the two coarse ones.

Cooper et al. [3] showed that the diet choices of sheep were consistent with the maintenance of optimal ruminal conditions. Maintenance of chemical or physical balance of the digestive process may be evoked in the present study, because the coarse hays, richer in fibre, could have a favourable effect by slowing down the high rate of fermentation and the rate of passage of constituents from the leafy regrowth hay. This would be in accordance with the postingestive regulation of choice [2, 25] and the hypothesis that animals adjust diet choice and intake to maximise comfort [9]. Introducing other nutrient constraints like minerals were found to improve the prediction of diet choice by optimal foraging models [29].

Moreover, we cannot exclude the pleasure associated with the change of food,

which could be viewed as a hedonistic process, notably in the C1C2 treatment in which ingesting both hays cannot be related to the research of some digestive comfort. This would be consistent with the observed increase in total DM intake in the choice situation, including when the two forages were of a similar value.

4.3. Effect of recent diet on choices

The behaviour of heifers in diversifying their diet is also supported here by the temporary higher preference for the hay that was not given alone before the choice situation, compared to the final preference at the end of the choice sub-period. This result confirmed those obtained on grazing sheep by Newman et al. [21] in short duration tests and by Parsons et al. [23] in a few days, and showed that diet selection by cattle is also modulated by the nature of their recent diet. As in Parsons' experiment, we observed that this effect decreased with time, being non significant after five days. At least five days seemed necessary for the animals to balance their diet in a choice situation. This has to be taken into account when measuring daily intake and preferences in choice situations. Newman et al. [21] proposed two reasons for the effect of a recent diet: a possible wish to restore the level of a component of the diet, and an attractive effect of novelty. This last reason should be more important when the nutritive values of forages offered in a choice situation are closed, and in our trial the effect was greater with the association of C1 and C2. When the difference in quality between the forages is more marked, their own nutritional characteristics could mask this effect of attraction for novelty.

4.4. Stimulation of intake in the choice situation

The choice situation significantly increased the daily dry matter intake of the heifers in comparison with the no-choice situation whatever the choice tested. This was surprising for the choice situation between the two coarse hays, since they had similar values and can be supposed to have no associative effect from a digestive or nutritional point of view. This indicated a possible importance of the motivation to eat due to the diversity of the offer besides the digestive mechanisms in regulating feed intake. Furthermore, when animals moved from good hay alone to a choice situation between good and coarse hays, the increase in total DM intake was accompanied by a decrease in the DM of G, resulting in a non-significant increase in total digestible OM intake, on the contrary to the other choices. In this case, the increase of dry matter intake in a choice situation was thus not due to energy considerations, but was rather the result of motivation enhanced by the diversity of the offer.

In rangeland conditions, it is argued that the motivation to eat and total intake are increased when plant diversity reaches an optimum [20]. From our results, as from those obtained indoors with pellets [18] and outdoors with adjacent monocultures of clover and grass [1], it appears that a binary choice could be sufficient to stimulate intake. The present systems of prediction of forage intake [15] ignore the possible effect of diversity on voluntary intake. It would be useful to extend the present results to more long term situations and to other types of herbivores (species, physiological stages and nutrient requirements), and to know whether the animals could obtain benefit from a choice situation, or whether they would become gradually accustomed to the choice situation and no longer increase their daily intake.

5. CONCLUSION

Faced with choices between two hays of either very similar or very different quality, heifers seemed to behave in close

accordance with the relative short-term intake rates but also with relative daily voluntary dry matter intakes of the forages when they were given alone. This could thus be a predictor of relative daily intakes under choice conditions. Due to great knowledge of the ingestibility of the forages, this could provide a useful basis for predicting preferences.

In the present study, giving the animals a choice between two hays stimulated their daily DM intake by at least ten per cent compared with what was eaten when the same forages were offered alone. Despite this increase, when the hays differed, the intake of the forage with a lower value was largely at the expense of the better one. These results emphasize the possible importance of the motivation to eat due to the diversity of the offer and the motivation of the heifers to diversify their diet.

This motivation for diversifying the diet was confirmed by the increased preference for the hay not offered during the previous no-choice period, and by the partial choices always expressed whatever the forages offered. This could result from the search for maximum digestive comfort, sampling behaviour, or associated pleasure.

ACKNOWLEDGEMENTS

REFERENCES

[1] Champion R.A., Rutter R.J., Orr R.J., Penning P.D., Costs of locomotive and ingestive behaviour by sheep grazing grass and clover monocultures or mixtures of the two species, in: Veissier I., Boissy A. (Eds.), Proceedings of the 32nd Congress of the International Society for Applied Ethology, Clermont-Ferrand, France, 1998, p. 213.

[2] Cooper S.D.B., Kyriazakis I., Nolan J.V., Diet selection in sheep: the role of the rumen environment in the selection of a diet from two feeds that differ in their energy density, Brit. J. Nutr. 74 (1995) 39–54.

[3] Cooper S.D.B., Kyriazakis I., Oldham J.D., The effects of physical form of feed, carbohydrate source, and inclusion of sodium bicarbonate on the diet selections of sheep, J. Anim. Sci. 74 (1996) 1240–1251.

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

[5] Dumont B., Petit M., An indoor method for studying the preferences of sheep and cattle at pasture, Appl. Anim. Behav. Sci. 46 (1995) 67–80.

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

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

[8] Dumont B., Maillard J.F., Petit M., The effect of the spatial distribution of plant species within the sward on the searching success of sheep when grazing, Grass For. Sci. 55 (2000) 138–145.

[9] Forbes J.M., Provenza F.D., Integration of learning and metabolic signals into a theory of dietary choice and food intake, in: Cronjé P.B. (Ed.), Ruminant physiology: digestion, metabolism, growth and reproduction, 2000, pp. 3–19.

[10] Illius A.W., Foraging behaviour and diet selection, in: Gudmundsson O. (Ed.), Grazing Research at Northern Latitudes, 1986, pp. 227–236.

[11] Illius A.W., Gordon I.J., Constraints on diet selection and foraging behaviour in mammalian herbivores, in: Hugues R.N. (Ed.), Behavioural Mechanisms of Food Selection, 1990, pp. 369–392.

[12] Illius A.W., Clark D.A., Hodgson J., Discrimination and patch choice by sheep grazing grass-clover swards, J. Anim. Ecol. 61 (1992) 183–194.

[13] Illius A.W., Gordon I.J., Elston D.A., Milne J.D., Diet selection in goats: a test of intake-rate maximization, Ecology 80 (1999) 1008–1018.

[14] Ingrand S., Vimal T., Fléchet J., Agabriel J., Brun J.P., Lassalas J., Dedieu B., A free-access system for the long-term monitoring of individual intake of beef cows kept in a group, in: Proceedings of the IXth European Intake Workshop, North Wyke, UK, 1998, pp. 17–20.

[15] Jarrige R., Demarquilly C., Dulphy J.P., Hoden A., Robelin J., Béranger C., Geay Y., Journet M., Malterre C., Micol D., Petit M., The INRA "Fill Unit" system for predicting the voluntary intake

of forage-based diets in ruminants, J. Anim. Sci. 63 (1986) 1737–1758.

[16] Kenney P.A., Black J.L., Factors affecting diet selection by sheep. I. Potential intake rate and acceptability of feed, Aust. J. Agric. Res. 35 (1984) 551–563.

[17] Kenney P.A., Black J.L., Colebrook W.F., Factors affecting diet selection by sheep. III. Dry matter content and particle length of forage, Aust. J. Agric. Res. 35 (1984) 831–838.

[18] Kyriazakis I., Oldham J.D., Diet selection in sheep: the ability of growing lambs to select a diet that meets their crude protein (nitrogen × 6.25) requirements, Brit. J. Nutr. 69 (1993) 617–629.

[19] Laca E.A, Distel R.A., Griggs T.C., Deo G., Demment M.W., Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilisation, in: Proceedings of the XVIIth International Grassland Congress, 1993, pp. 710–712.

[20] Meuret M., Bruchou C., Modélisation de l'ingestion selon la diversité des choix alimentaires réalisés par la chèvre au pâturage sur parcours, Renc. Rech. Rum. 1 (1994) 225–228.

[21] Newman J.A., Parsons A.J., Harvey A., Not all sheep prefer clover: diet selection revisited, J. Agric. Sci. (Camb.) 119 (1992) 275–283.

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

[23] Parsons A.J., Newman J.A., Penning P.D., Harvey A., Orr R.J., Diet preference of sheep: effects of recent diet, physiological state and species abundance, J. Anim. Ecol. 63 (1994) 465–478.

[24] Peyraud J.L., Techniques for measuring faecal flow, digestibility and intake of herbage in grazing ruminants, in: Proceedings of the IXth European Intake Workshop, North Wyke, UK, 1998, pp. 39–43.

[25] Provenza F.D., Balph D.F., Applicability of five diet-selection models to various foraging challenges ruminants encounter, in: Hugues R.N. (Ed.), Behavioural Mechanisms of Food Selection, 1990, pp. 423–460.

[26] Pyke G.H., Optimal foraging theory: a critical review, Annu. Rev. Ecol. Syst. 15 (1984) 523–575.

[27] Statistical Analysis System, SAS/STAT Guide for personal computers, Version 6, SAS Institute Inc, Cary, NC, USA, 1987.

[28] Wallis de Vries M.F., Daleboudt C., Foraging strategy of cattle in patchy grassland, Oecologia 100 (1994) 98–106.

[29] Wallis de Vries M.F., Shippers P., Foraging in a landscape mosaic: selection for energy and minerals in free-ranging cattle, Oecologia 100 (1994) 107–117.

[30] Wilmshurst J.F., Fryxell J.M, Hudson R.J., Forage quality and patch choice by wapiti (Cervus elaphus), Behav. Ecol. 6 (1995) 209–217.