Reprod Nutr Dev (1997) 37, 517–528

Original article

Effects of intake level of a mixed diet on chewing activity and on particle size of ruminated boli, ruminal digesta fractions and faeces of steers

PL Kovács[1], K-H Südekum*, M Stangassinger[2]

Institut für Tierernährung und Stoffwechselphysiologie, Christian-Albrechts-Universität, 24098 Kiel, Germany

(Received 24 October 1996; accepted 5 September 1997)

Summary – This study evaluated the effects of intake of a mixed diet on chewing activity during eating and rumination and the relationship between the chewing activity and the particle size of the ruminated boli, ruminal digesta fractions and faeces in steers. Six ruminally cannulated steers received a mixed forage/concentrate diet (68:32, dry matter basis). The diet was offered twice daily at approximately 1, 1.5 and 2 times the estimated maintenance energy requirements (low, medium and high intake, respectively) in a repeated 3 × 3 Latin square design. The rumens were emptied manually and samples of the ruminated boli and of the ruminal upper strata were collected at four different times throughout the day. The dry matter weight distribution of the total amount of recovered particles was determined by a wet-sieving procedure. Numerically, the effect of intake on the mean particle sizes of the different materials was small. However, the mean particle size was reduced by almost nine tenths from their size at intake of the mixed diet (4.78 mm) to defecation (0.51 mm). The total number of minutes chewing and eating and ruminating increased as the intake level increased. When related to 1 kg of dry matter intake, only the eating and chewing times were significantly longer for the high as compared to the medium intake. Rumination patterns were examined using a cosinor model. Data indicated that the average amount of time spent ruminating also increased as the intake level increased. The overall pattern of rumination was not impaired by higher intake levels. The amount of large (≥ 4 mm) particles that escaped per minute of rumination time between 3 and 7.5 h postfeeding was similar for all the intake levels. It was concluded that an active breakdown process occurred in the rumen which could cope with the higher intake levels of the mixed diet over the range of 1 to 2 times the maintenance energy requirement level.

chewing / particle size / rumen / intake level / mixed diet

* Correspondence and reprints
Tel: (49) 431 8802538: fax: (49) 431 8801528; e–mail: suedekum@aninut.uni–kiel.de
[1]Permanent address: Debreceni Agrártudományi Egyetem, Állattenyésztéstani Tanszék, Böszörményi út 138, 4032 Debrecen, Hungary
[2]Present address: Institut für Physiologie, Physiologische Chemie und Tierernährung, Ludwig–Maximilians–Universität, Veterinärstr. 13, 80539 München, Germany

Résumé – Influence du niveau de l'ingestion d'une ration mixte sur la mastication et sur la taille des particules du bolus ruminé, des fractions de digesta dans le rumen et des fèces chez les bovins. Dans cette étude, les effets de l'ingestion d'une ration mixte sur la mastication pendant la prise de nourriture et la rumination, ainsi que sur la taille des particules du bolus ruminé, des différentes fractions de digesta dans le rumen et des fèces chez des bovins ont été évalués. Six bovins porteurs d'une canule du rumen ont reçu un ration mixte composée de 68 % (par rapport à la matière sèche) d'ensilage et de 32 % d'aliment concentré. La ration mixte était distribuée deux fois par jour et fournissait approximativement 100, 150 ou 200 % des besoins énergétiques d'entretien (ingestion faible, moyenne ou élevée, respectivement). L'étude a été conduite suivant le modèle des carrés latins répétés 3 × 3. Les rumens étaient vidés manuellement et des échantillons des boli ruminés et de la couche supérieure du rumen étaient recueillis à quatre moments différents de la journée. La taille des particules a été déterminée par lavage des différentes fractions sur tamis. La répartition du poids de matière sèche des particules a été calculée sur la base des fractions recueillies. L'effet du niveau d'ingestion sur la taille des particules des différents composés s'est avéré négligeable. En revanche, la taille moyenne des particules a diminué de presque 90 % entre le bolus ruminé (4,78 mm) et les fèces (0,51 mm). Les durées journalières d'ingestion, de mastication et de rumination ont augmenté parallèlement à la quantité d'aliment ingérée. Seules les durées unitaires (min/kg MS) d'ingestion et de mastication ont été significativement plus élevées avec le niveau haut d'ingestion par rapport au niveau moyen. L'analyse *cosinor* de la rumination a confirmé que le temps moyen par jour consacré à la rumination augmentait avec la quantité d'aliment ingérée. La répartition de l'activité au cours de la journée n'a pas été affectée par le niveau d'ingestion. La quantité de particules dites larges (≥ 4 mm) échappant à la rumination par minute entre 3 et 7,5 h après la distribution des aliments n'a pas été influencée par la quantité ingérée. Les résultats de l'étude présentée nous permettent de conclure que la dégradation de particules larges ne constitue pas un facteur limitant lors de l'ingestion d'une ration mixte couvrant d'une à deux fois les besoins énergétiques d'entretien chez le bœuf.

mastication / taille des particules / rumen / taux d'ingestion / ration mixte

INTRODUCTION

Ruminal digesta constituents can escape from the rumen by absorption of microbial fermentation products through the rumen wall or by the passage of undigested feeds, microbial mass and fermentation products to the omasum. The probability of particle passage from the rumen increases with decreasing particle size (Poppi et al, 1980). Reduction in the size of consumed forage particles must occur before they can pass through the reticulo-omasal orifice (Welch, 1982). Digesta particle size can be reduced by chewing during eating and rumination and by microbial action or detrition (McLeod and Minson, 1988). Microbial digestion decreases the dry matter (DM) contents of the ruminal digesta but has little effect on particle size reduction (Welch, 1982) including large particle breakdown (Ulyatt et al, 1986). It does, however, facilitate particle breakdown by weakening the cell-wall structures (Wilson et al, 1989a, b). These findings show that chewing during eating and rumination are the major factors contributing to particle size reduction, and thus chewing efficiency is an important factor influencing the voluntary intake of forages.

Several authors have examined the relationship between intake and chewing activities (Welch and Smith, 1970; Balch, 1971; Sudweeks et al 1980; De Boever et al, 1993a, b), but only a few studies have investigated the quantitative relationships between ingestive and ruminative mastication and breakdown of large forage particles in the rumen at different intake levels (Luginbuhl et al, 1989a). The present study examined the effects of intake level of a mixed diet on chewing during eating and rumination and the relationships between chewing activ-

ities and the particle sizes of ruminated boli, ruminal digesta fractions and faeces in a group of steers. A preliminary report including parts of the study has been published previously (Kovács et al, 1996).

MATERIALS AND METHODS

Details concerning the animals and diets and the experimental design have been previously described (Kovács et al, 1997). Briefly, six ruminally cannulated steers received a mixed diet consisting, on average, of (as a percentage of DM) 43% Italian ryegrass silage, 25% maize silage, 30% concentrate and 2% mineral–vitamin mix. The experimental design was a repeated 3 × 3 Latin square with 21-day periods. The diet was offered twice daily (0700 and 1900 hours) at approximately 1, 1.5 and 2 times the estimated maintenance energy requirements according to the Agricultural Research Council (1980), and the different diets are hereafter referred to as low, medium and high intakes, respectively. The daily DM intakes at the low, medium and high intake level, respectively, were 6.22, 9.03 and 12.04 kg.

Sample collection

Representative samples were obtained for each dietary ingredient and composited for each period. These were stored (silage at –20 °C) for the subsequent analyses. Ruminated boli were collected at approximately 3 and 7.5 h after the beginning of the morning and evening feeding time, respectively, on days 9 and 10. Two boli were collected on each occasion. Because of the small size and the almost liquid consistency of the reswallowed boli, which made representative sampling at the cardia difficult, the ruminated boli were collected from the oral cavity after approximately the 20th chewing motion. Samples of the ruminal upper strata (RUS) were collected manually 3 and 6 h after the beginning of the morning and evening feeding time, respectively, on days 9 and 10 by taking samples (approximately 2 kg) from the top of the ruminal raft in the central, cranial and caudal regions of the dorsal ruminal sac. Total reticulo-ruminal contents were removed manually at 1430 hours (day 13), 1000 hours (day 14), 0230 hours and 2200 hours (day 18). This schedule provided samples at 3 and 7.5 h after the beginning of the morning and evening feeding time, respectively. Because of the time required to empty six steers, emptyings were started 45 min before these times and finished 45 min after. The order of animals was changed at each emptying using a blocking system. All ruminal contents that could be removed by hand were emptied into a rectangular, insulated tub. This material was referred to as mat. Material not removable by hand was bailed into an insulated plastic barrel. This material was referred to as bailable liquids (BL) (Robinson et al, 1987). Both fractions were weighed, mixed thoroughly, subsampled (mat, 2–3 kg and BL, 1 kg) and then liquids were returned to the rumen followed by mat. Total faecal collections were made over 5 days. The faecal collecting started and finished at 0700 hours. The faeces were collected in plastic pans. Wet faeces were weighed twice daily to the nearest 10 g and mixed. An aliquot of 5% was transferred to an accumulative sample container. Ruminated boli, ruminal digesta materials and faeces were immediately stored at –20 °C until analysis. Starting at 0700 hours on day 15, the chewing activity of the steers was estimated by visual observation every 5 min for 2 × 24 h. This schedule has been reported to give extremely reliable estimates (Lehner, 1979). It was assumed that the eating or ruminating activity observed at 5-min intervals occurred for the entire 5 min preceding the observation. Rumination after 10 min of other activity was considered a separate period of rumination. Chewing activities were expressed as time per kilogram of DM intake and denoted eating index (EI), ruminating index (RI) and total chewing index (CI) (De Boever et al, 1993b).

Analytical procedures

The analytical methods for proximate constituents and detergent fibre fractions of the feedstuffs have been described previously (Kovács et al, 1997). Dry matter weight distribution of the total recovered particles of the mixed diet, ruminated boli, ruminal digesta fractions and faeces was determined by a wet-sieving procedure (Kovács et al, 1997) and used to partition each material among percentages of large (≥ 4.0 mm), medium (< 4.0 mm and ≥ 1.0 mm), and small (< 1.0 mm and ≥ 0.063 mm) particles. The mean particle size, derived from the sieving data, was estimated by fitting the percentage of cumulative

weight (DM) oversize from each sieve to an exponential model (Fisher et al, 1988) using the non-linear model procedure of SAS (1988). The only modification of the procedure of Fisher et al (1988) was that all particles were assumed to pass through a sieve with a square aperture twice that of the largest sieve that was used during the sieving procedure of the different materials. The interval from 0.063 mm to double the aperture of the largest sieve (L) was then numerically integrated by division into 1 000 intervals:

$$\text{step} = (L - 0.063)/\ 1\ 000 \quad [1]$$

and mean size was calculated as

$$\frac{\sum_{i=1}^{1\,000} \text{step} \times R' \times (0.063 + i \times \text{step})}{\sum_{i=1}^{1\,000} \text{step} \times R'} \quad [2]$$

where R' = the first derivative of cumulative percent weight oversize.

Rumination data were separately evaluated for the day (0700 to 1900 hours) and night (1900 to 0700 hours) intervals. Data were analysed according to the cosinor model of Halberg et al (1967) using the non-linear model procedure of SAS (1988). This model uses the equation

$$F = C_0 + C \cos(\omega t + \psi) \quad [3]$$

where the fraction of time spent ruminating (F) is a function of: C_0, the level or fitted mean (average proportion of time spent ruminating); C, amplitude (maximal difference from C_0); ω, the (fixed) angular frequency (24/12); t, time and ψ, phase (time interval from the beginning of feeding until the time when F reaches C_0). The peak time, which represents the peak of the cosinor curve (time interval from the beginning of feeding to the time when F reaches its maximal value) was also calculated.

The amount of large particles that escaped from the rumen between 3 and 7.5 h postfeeding was estimated as the difference in amount of large particle DM in the rumen between these two time points. The quantity of large particles was calculated from the DM contents of ruminal mat and BL at these time points and the DM percentage of large particles in the respective ruminal digesta fraction (Kovács et al, 1997). The time spent ruminating between 3 and 7.5 h postfeeding was used to calculate the amount of large particles that escaped from the rumen in the given time interval per minute of rumination time.

Statistical analysis

Data were analysed by the mixed model procedure of SAS (1992). The model for data of particle size distribution of ruminated boli and ruminal digesta fractions was as follows:

$$Y_{ijklm} = M + P_i + A_j + I_k + TI_l + PF_m + (I\,TI)_{kl} + (I\,PF)_{km} + (TI\,PF)_{lm} + e_{ijklm}$$

where Y_{ijklm} is the observed response; M is the overall mean; P_i is the effect of period i, i = 1–3; A_j is the random effect of animal j, j = 1–6; I_k is the effect of intake level k, k = 1–3; TI_l is the effect of time interval (day versus night) l, l = 1–2; PF_m is the effect of time postfeeding m, m = 1–2; $(I\,TI)_{kl}$ is the effect of interaction between intake k and time interval l; $(I\,PF)_{km}$ is the effect of interaction between intake k and time postfeeding m; $(TI\,PF)_{lm}$ is the effect of interaction between time interval l and time postfeeding m; e_{ijklm} is the residual error.

For each response variable, a total of 72 (six steers × three intake levels × two time intervals × two times postfeeding) observations was obtained.

The covariance structure of the repeated measurement factors (time of day and time postfeeding) was tested with types; Simple, Toeplitz and Unstructured (SAS, 1992). Because of differences in the variance structure of the particle fractions at 3 and 7.5 h postfeeding, the Unstructured type with one band was used for evaluating the data of particle size distribution of ruminated boli and ruminal digesta fractions.

For the examination of chewing patterns and the amount of large particles escaping from the rumen between 3 and 7.5 h postfeeding, the model was as follows:

$$Y_{ijkl} = M + P_i + A_j + I_k + TI_l + (I\,TI)_{kl} + e_{ijkl}$$

Food and faecal particle size data were analysed using the model:

$$Y_{ijkl} = M + P_i + A_j + I_k + e_{ijk}$$

Treatment (intake) means for all variables were analysed further with the following orthogonal

contrasts: low intake versus (medium intake + high intake) and medium intake versus high intake. Significance was declared at $P < 0.05$ unless otherwise indicated. Averaged over all intake levels, the mean size of particles at different sampling sites was compared by subtracting the related values from each other and estimating the general mean for the difference from zero.

RESULTS

Intake affected the mean size of particles at all sampling sites with the exception of those of the ruminated boli (table I). The magnitude of the changes related to intake in mean particle size was only small, however. The mean size of the ruminal mat and BL particles and faecal particles was smaller at the low intake level than at the medium and high intake ones. The mean size of the RUS particles decreased as the intake increased from medium to high intake.

Averaged across intakes, the particle sizes at the different sampling sites were different from each other (fig 1) with the exception of similar particle sizes in the ruminated boli and RUS. The highest values were observed for the mixed diet and the lowest values for faecal particles. Ruminated boli and ruminal digesta materials had intermediate values for mean particle size. The value in the mixed diet was almost tenfold that of the faeces.

Eating, ruminating and hence total chewing time increased as the intake level increased (table II). The increase in time spent ruminating was caused by an increase in both the number of rumination periods and the duration of the periods. Eating time was not influenced by time interval. There was no difference between day and night in the number of rumination periods but the duration of the rumination periods was greater during the night. This resulted in a longer time spent ruminating during the night at the low and medium intakes. The EI increased with increasing intake, whereas RI stayed almost constant. As a result, CI differed between the medium and high intake levels (table II). The time interval (day versus night) influenced RI. The animals ruminated more per kg DM at night. Because the chemical composition of the diet was constant at the three intake levels,

Table I. Mean particle size of the mixed diet and of materials collected at different sites of the digestive tract.

	Intake[a]			*Effect (P)*	*Contrasts (P)*		*SE*
	L	*M*	*H*	*Intake*	*L versus (M+H)*	*M versus H*	
Mixed diet	4.80	4.75	4.79	0.07	0.07	0.11	0.01
Ruminated boli	2.41	2.57	2.74	0.31	0.23	0.44	0.18–0.26[b]
Ruminal digesta							
Upper strata	2.70	2.83	2.60	0.03	0.57	0.01	0.08–0.14
Mat	1.82	1.89	1.87	0.01	0.01	0.20	0.02
Bailable liquids	1.58	1.64	1.62	0.05	0.02	0.41	0.02–0.03
Faeces	0.49	0.52	0.52	0.01	0.01	0.89	0.02

[a]L, low; M, medium; H, high; [b]because of missing values the range of SE is given.

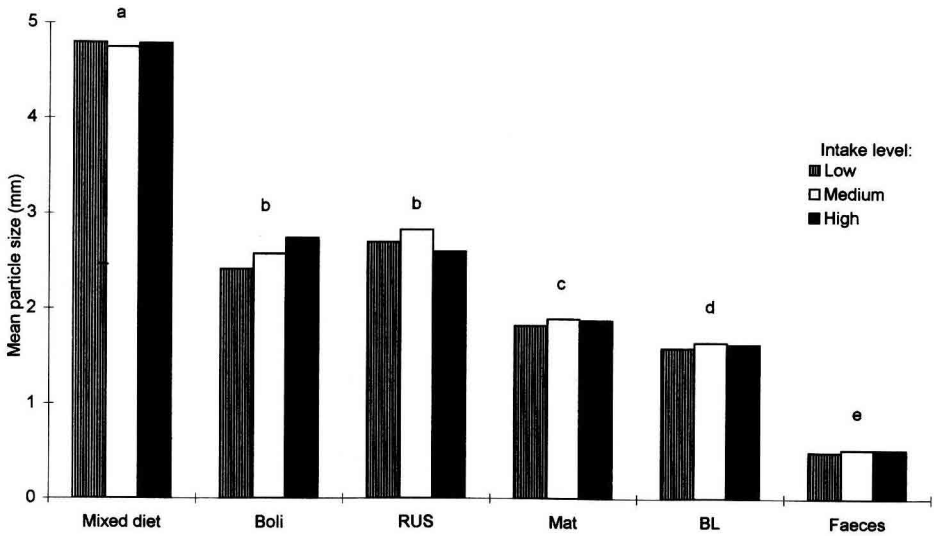

Fig 1. Mean particle size of materials from different sampling sites in steers fed a mixed diet at three intake levels. Across the different intake levels, different letters indicate significant ($P < 0.05$) differences between sampling sites. Boli, ruminated boli; RUS, ruminal upper strata; Mat, ruminal mat; BL, ruminal bailable liquids.

we observed identical results regardless of whether the time of chewing or rumination was related to the intakes of DM, NDF or forage NDF (data not shown).

The cosinor analysis revealed that the average proportion of time spent ruminating (C_0, level), mean rumination time and the amplitude (C) increased as intake level increased (table III). The overall pattern of rumination, however, as described by peak time and phase (Woodford and Murphy, 1988), was not affected by intake level.

As intake level increased, the amount of large particle DM that escaped from the rumen was higher and the steers ruminated longer between 3 and 7.5 h postfeeding (fig 2). The quantity of large particles that escaped from the rumen per minute of rumination, however, was not affected by intake level.

DISCUSSION

Among the different intake levels, numerical differences in the mean particle size of the ruminated boli, ruminal mat and BL, and of RUS and faeces were small. The mean particle size differed largely, however, between the different sampling sites, indicating that active particle breakdown processes occurred at all intake levels. Based on mean faecal particle size as a measure of the mean size of particles that can escape the reticulum (Ulyatt et al, 1986), we could conclude that, on average, particles of the mixed diet had been broken down to almost one tenth of their original size.

The mean size of RUS particles, the ruminal digesta fraction representing the least degraded particles in the rumen, was only half that of the mixed diet. The magnitude of this difference points to a marked

Table II. Chewing activities of steers fed a mixed diet at three levels of intake[a].

	Time interval										
	Day			*Night*			*Effect (P)*[b]		*Contrasts (P)*		*SE*
Intake[c]	*L*	*M*	*H*	*L*	*M*	*H*	*Intake*	*Interval*	*L versus (M+H)*	*M versus H*	
Eating											
min/12 h	19.2	32.1	60.4	22.1	27.9	51.3	<0.01	0.22	<0.01	<0.01	4.4
min/kg DMI[d]	6.2	6.7	10.0	6.1	6.8	8.8	<0.01	0.45	<0.01	<0.01	0.90
Rumination											
min/12 h	68.3	99.2	163.8	82.1	123.3	160.4	<0.01	0.08	<0.01	<0.01	7.59
min/kg DMI	22.0	22.2	25.8	27.1	27.9	27.2	0.59	0.02	0.47	0.46	3.60
periods/12 h	6.08	8.25	10.17	6.42	7.83	8.83	<0.01	0.44	<0.01	0.06	0.73
min/period	11.2	11.7	16.7	12.7	15.7	18.5	<0.01	<0.01	<0.01	<0.01	0.95
Total chewing											
min/12 h	87.5	131.9	224.1	104.2	151.3	211.7	<0.01	0.09	<0.01	<0.01	10.9
min/kg DMI	28.1	28.9	35.8	33.9	34.1	35.8	0.03	0.02	0.11	0.03	4.14

[a]Values are the average of two consecutive 24-h observations; [b]no significant intake × time interval interactions occurred; [c]L, low; M, medium; H, high; [d]dry matter intake.

Table III. Cosinor analysis of rumination data.

	Time interval										
	Day			*Night*			*Effect (P)*[a]		*Contrasts (P)*		*SE*
Intake[b]	*L*	*M*	*H*	*L*	*M*	*H*	*Intake*	*Interval*	*L versus (M+H)*	*M versus H*	
Mean rumination time	1.31	1.67	2.53	1.33	2.01	2.67	<0.01	0.23	<0.01	<0.01	0.24
Peak time (hours)	1238	1324	1339	0042	0124	0044	0.25	0.44	0.11	0.64	0.45
Level (C_0)	0.109	0.139	0.211	0.111	0.168	0.223	<0.01	0.22	<0.01	<0.01	0.02
Amplitude (C)	–0.006	–0.058	–0.103	0.001	–0.046	–0.019	0.03	0.07	0.01	0.67	0.03
Phase (ψ)	1.99	1.64	2.12	0.72	1.18	0.75	0.99	0.07	0.90	0.97	0.64

[a]No significant intake × time interval interactions occurred; [b]L, low; M, medium; H, high.

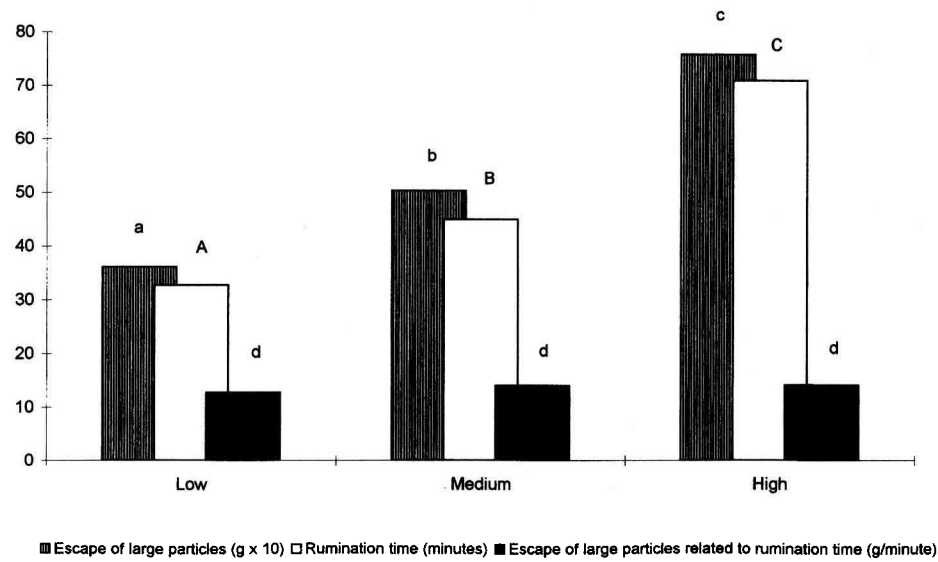

Fig 2. Ruminal escape of large particles and rumination time between 3 and 7.5 h postfeeding in steers fed a mixed diet at low, medium and high intake levels. Within a given variable, columns bearing different superscripts indicate significant differences ($P < 0.05$) between the orthogonal contrasts of low intake versus (medium + high intake) and medium versus high intake.

effect of the initial chewing on large particle breakdown. In sheep fed chopped ryegrass hay, Faichney et al (1989) found that chewing during eating accounted for 9.8% of the comminution of dietary particles between the mouth and the pylorus. It was expected that, after 20 chewing movements, the mean particle size of the ruminated boli was smaller than that of RUS. Luginbuhl et al (1989b) indicated that a portion of the regurgitated boli was selected from the upper region of the rumen. The values for the mean particle size of these two materials, however, were similar. Compared with RUS, the particles of ruminated boli could have undergone alterations in their physical and chemical properties that are not reflected by the size distribution. Part of the fermentation gas may be removed by rumination and the anatomical structure of the forage particles can be changed through rumination. These combined actions may then increase the (functional) specific gravity of particles of ruminated boli without causing concomitant changes in the particle size. They may also increase the probability of passage out of the rumen.

A comparison of the mean particle size of ruminal digesta materials, ie, RUS, mat and BL, illustrated the stratification of the ruminal contents and the enrichment of large undigested ruminal digesta particles in the RUS. Also, these data supported the hypothesis that ruminal BL are a starting pool for digesta passage from the reticulo-rumen (Kovács et al, 1997), although the mean size of BL particles was three times that of the faecal particles and careful digesta collection

from the ventral reticulum is required to clarify this (Shaver et al, 1988).

De Boever et al (1990) have reviewed factors influencing chewing activity and have listed animal species, physiological stage, time of access to feed, protein content of the ration, forage to concentrate ratio, feeding level, body weight and individual variations as the main factors. Out of these factors, only intake level and individual variations were relevant in our study. Duration of eating and rumination increased as intake level increased. It seems that at higher intake levels both the increased duration and the number of rumination periods accounted for the increased rumination time. This explanation was also supported by the cosinor analysis. The average proportion of time spent ruminating (C_0, level) sharply increased as the intake level increased. Our data supported that of Murphy et al (1983), who assumed that animals fed two equal meals daily would have two distinct cosine patterns during the day. The synchronizer or forcing oscillation which entrains a biological rhythm (Bünning, 1973) has become feeding time. This synchronized rhythm was obviously not impaired by higher intake levels. The variables of overall pattern of rumination, peak time and phase, were not affected by intake level. It seems that animals ruminated in similar rhythms during the day and the night. Because steers were quieter at night, as indicated by the observations of physical activity (data not shown), they could ruminate longer per rumination period.

Balch (1971) introduced CI as a measure of fibrousness characteristic for forages. Bae et al (1981) and Beauchemin et al (1994) reported that the NDF content was closely related to chewing time. Because the NDF content of the mixed diet was constant across all the intake levels, we only evaluated EI, RI and CI. The increase in EI with the higher intake levels has already been observed in cattle fed forages (Freer et al, 1962; Bae et al, 1981). Freer et al (1962) assumed that the faster eating rate at lower intake levels was probably associated with the smaller digesta load of the reticulorumen. At the high intake level, the steers had 112 min/day of eating activity as compared to only 41 min/day at the low intake level. Faverdin (1985) (quoted by Dulphy and Faverdin 1987) observed that the rate of eating declined as a large meal proceeded, from 120 to about 50 g/min owing to longer pauses in actual chewing as the meal progressed.

Several studies have shown that chewing during eating and rumination may compensate for each other, ie, total chewing time per kilogram of consumed DM remained constant at increasing intake levels (Freer et al, 1962; Bae et al, 1981; Andrieu et al, 1986). In our trial, RI was constant across the different intake levels, whereas CI slightly increased at the high intake level. Deswysen et al (1987) stated that no compensation occurs at higher intakes between duration of ingestive and ruminative chewing owing to an increased proportion of manipulative movements during eating. The number and type of chews per minute during eating or per minute of rumination should thus be measured to get more accurate information on this topic. Deswysen et al (1987) suggested that the chewing time required by animals fed a given amount of forage is of limited use because chewing time is influenced by the potential level of intake the animals received. At ad libitum intakes a reduction in CI was observed (Shaver et al, 1988), which may also increase the size of particles leaving the reticulum (Van Soest, 1994).

The threshold size of particles for passage out of the rumen was reported to range from 1 to 4 mm (Poppi et al, 1980; Grenet, 1984; Shaver et al, 1988; Ulyatt et al, 1986). Particles greater than 4 mm have a very small probability of leaving the rumen. Changes in the amount of this fraction may

be due to intake level or breakdown caused by chewing and rumination. Because the animals ingested their meals within 3 h post-feeding, except for two animals at the high intake level, who had 5 and 10 min, respectively, of initial chewing activity between 1000 and 1430 hours, it was assumed that the escape of large particles from the rumen between 3 and 7.5 h after feeding predominantly occurred by rumination. Evaluated per minute of rumination time, the same quantity of large particles escaped from the rumen at each intake level, which indicates that rumination efficiency was not impaired at the higher intake levels.

On the basis of the present findings it was concluded that, over the intake range of 1 to 2 multiples of maintenance energy requirements, the latter being near to a voluntary intake level, an active breakdown process occurred in the rumen, which could cope with the higher intake level. The stability of the breakdown process appeared to be due to the constant efficiency and patterns of rumination. The average daily rumination time at the high intake level was only 5.2 h, which was far below the maximal rumination time of 8 to 10 h/day (Welch, 1982; Bosch, 1991). This finding indicates that for regimens, whose intake level is at the low end of requirements for mature steers, other factors than physical structure control feed intake.

ACKNOWLEDGMENTS

We thank C Lewin for his care of the steers and H Rothfuß, P Schulz and K Voigt for their unremitting help during the animal trials. PLK received a DAAD (Deutscher Akademischer Austauschdienst) scholarship.

REFERENCES

Agricultural Research Council (ARC) (1980) *The Nutrient Requirements of Ruminant Livestock.* Commonwealth Agric Bureaux, Farnham Royal, Slough

Andrieu J, Demarquilly C, Korea A (1986) Influence du niveau d'alimentation sur le comportement alimentaire du mouton au cours du premier cycle de végétation. *2ièmes Journées sur la Nutrition et l'Alimentation des Herbivores.* INRA, Paris, 19–20 mars, 2 pp

Bae DH, Welch JG, Smith AM (1981) Efficiency of mastication in relation to hay intake in cattle. *J Anim Sci* 52, 1371–1375

Balch CC (1971) Proposal to use time spent chewing as an index of the extent to which diets for ruminants possess the physical property of fibrousness characteristic of roughages. *Br J Nutr* 26, 383–392

Beauchemin KA, Farr BI, Rode LM, Schaalje GB (1994) Optimal NDF concentration of barley based diets for lactating dairy cows. *J Dairy Sci* 77, 1013–1030

Bosch MW (1991) Influence of stage of maturity of grass silages on digestion processes in dairy cows. PhD dissertation, Agric Univ Wageningen

Bünning E (1973) *The Physiological Clod,* 3rd English ed. Springer, New York, NY, 107–110

De Boever JL, Andries JI, De Brabander DL, Cottyn BG, Buysse FX (1990) Chewing activity of ruminants as a measure of physical structure – a review of factors affecting it. *Anim Feed Sci Technol* 27, 281–291

De Boever JL, De Brabander, DL, De Smet AM, Vanacker JM, Boucqué CV, (1993a) Evaluation of physical structure. 2. Maize silage. *J Dairy Sci* 76, 1624–1634

De Boever JL, De Smet AM, Vanacker JM, Boucqué CV (1993b) Evaluation of physical structure. 1. Grass silage. *J Dairy Sci* 76, 140–153

Deswysen AG, Ellis WC, Pond KR (1987) Interrelationships among voluntary intake, eating and ruminating behaviour and ruminal motility of heifers fed corn silage. *J Anim Sci* 64, 835–841

Dulphy JP, Faverdin P (1987) L'ingestion alimentaire chez les ruminants: modalités et phénomènes associés. *Reprod Nutr Dev* 27 (1B), 129–155

Faichney GJ, Poncet C, Boston RC (1989) Passage of internal and external markers of particulate matter through the rumen of sheep. *Reprod Nutr Dev* 29, 325–337

Fisher DS, Burns JC, Pond KR (1988) Estimation of mean and median particle size of ruminant digesta. *J Dairy Sci* 71, 518–524

Freer M, Campling RC, Balch CC (1962) Factors affecting the voluntary intake of food by cows. 4. The behaviour and reticular motility of cows receiving diets of hay, oat straw and oat straw with urea. *Br J Nutr* 16, 279–295

Grenet E (1984) Wet sieving technique for estimating particle size in herbivore digesta. In: *Techniques in Particle Size Analysis of Feed and Digesta in Ruminants* (PM Kennedy, ed), Occasional Publ No 1, Can Soc Anim Sci, Edmonton, AB, 167

Halberg F, Tong YL, Johnson EA (1967) Circadian system phase – an aspect of temporal morphology; procedures and illustrative samples. In: *The Cellular Aspects of Biorhythms* (H von Mayersback, ed), Springer, New York, NY, 20–48

Kovács PL, Südekum K-H, Stangassinger M (1996) Untersuchungen zum Zerkleinerungsprozess von Futterpartikeln einer gemischten Ration im Verdauungstrakt von Rindern bei drei Futteraufnahmeniveaus (Abstr). *Proc Soc Nutr Physiol* 5, 100

Kovács PL, Südekum K-H, Stangassinger M (1997) Rumen contents and ruminal and faecal particle size distribution in steers fed a mixed diet at three amounts of intake. *Anim Feed Sci Technol* 64, 143–154

Lehner PN (1979) *Handbook of Ethological Methods.* Garland STPM Press, New York, NY

Luginbuhl J-M, Pond KR, Burns JC, Russ JC (1989a) Effects of ingestive mastication on particle dimensions and weight distribution of coastal bermudagrass hay fed to steers at four levels. *J Anim Sci* 67, 538–546

Luginbuhl J-M, Pond KR, Burns JC, Russ JC (1989b) Eating and ruminating behavior of steers fed costal bermudagrass hay at four levels. *J Anim Sci* 67, 3410–3418

McLeod MN, Minson DJ (1988) Large particle breakdown by eating ryegrass and alfalfa. *J Anim Sci* 66, 992–999

Murphy MR, Baldwin RL, Ulyatt MJ, Koong KJ (1983) A quantitative analysis of rumination patterns. *J Anim Sci* 56, 1236–1240

Poppi DP, Norton WB, Minson DJ, Hendrickson RE (1980) The validity of the critical particle size theory for particles leaving the rumen. *J Agric Sci* 94, 275–280

Robinson PH, Tamminga S, van Vuuren AM (1987) Influence of declining level of feed intake and varying the proportion of starch in the concentrate on rumen ingesta quantity, composition and kinetics of ingesta turnover in dairy cows. *Livest Prod Sci* 17, 37–62

SAS® Institute Inc (1988) STAT User's guide, Release 6.03. SAS Inst Inc, Cary, NC, 675–712

SAS® Institute Inc (1992) Tech Rep P–229, Release 6.07. SAS Inst Inc, Cary, NC

Shaver RD, Nytes AJ, Satter LD, Jorgensen NA (1988) Influence of feed intake, forage physical form, and forage fiber content on particle size of masticated forage, ruminal digesta and feces of dairy cows. *J Dairy Sci* 71, 1566–1572

Sudweeks EM, Ely LO, Sisk LR (1980) Effects of intake on chewing activity of steers. *J Dairy Sci* 63, 152–154

Ulyatt MJ, Dellow DW, John A, Reid CSW, Waghorn GC (1986) Contribution of chewing during eating and rumination to the clearance of digesta from the rumino–reticulum. In: *Control of Digestion and Metabolism in Ruminants* (LP Milligan, WL Grovum, A Dobson, eds), Reston Books, Englewood Cliffs, NJ, 498– 515

Van Soest PJ (1994) *Nutritional Ecology of the Ruminant,* 2nd ed. Cornell Univ Press, Ithaca, NY

Welch JG (1982) Rumination, particle size and passage from the rumen. *J Anim Sci* 54, 885–894

Welch JG, Smith AM (1970) Forage quality and rumination time in cattle. *J Dairy Sci* 53, 797–800

Wilson JR, Akin DE, McLeod MN, Minson DJ (1989a) Particle size reduction of the leaves of a tropical and a temperate grass by cattle. II. Relation of anatomical structure to the process of leaf breakdown through chewing and digestion. *Grass Forage Sci* 44, 64–75

Wilson JR, McLeod MN, Minson DJ (1989b) Particle size reduction of the leaves of a tropical and a temperate grass by cattle. I. Effect of chewing during eating and varying times of digestion. *Grass Forage Sci* 44, 55–63

Woodford ST, Murphy MR (1988) Effect of physical form on chewing activity, dry matter intake, and rumen function of dairy cows in early lactation. *J Dairy Sci* 71, 674–686