

Changes in factors affecting the rate of digesta passage during pregnancy and lactation in sheep fed on hay

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Summary – The objective of this study was to assess feed intake and digesta passage characteristics in five Blackhead ewes fed hay ad libitum during pregnancy [I: d 60–80 post conceptionem (p conc); II: d 105–125 p conc; III: d 128–148 p conc] and lactation [IV: d 10–30 post partum (pp); V: d 35–55 pp]. During pregnancy, feed intake and rumination activity increased. The rumen fluid volume and the daily number of A-cycles did not change significantly. The mean retention time (MRT) of the fluid and particle markers in the reticulorumen (RR) and distal to the RR decreased by 14–32%. During lactation, the rumen fluid volume increased as compared to pregnancy by about 15%. Daily feed intake peaked during period V (83.7 g DM/kg BW^{0.75}). The MRT of particle markers in the RR increased as compared with late pregnancy. Both during pregnancy and lactation, the increased passage rate of digesta was achieved predominantly by an increased amount of digesta passing through the reticulo-omasal orifice during each opening. Sieving of forestomach contents and faeces revealed that the breakdown rate of large feed particles did not limit digesta passage.

digesta passage / feed intake / reticulorumen / rumination / roughage / pregnancy / lactation / sheep

Résumé – **Modifications des facteurs affectant la vitesse de transit des digesta pendant la gestation et la lactation chez des brebis nourries au foin.** Le but de l'étude était de déterminer les caractéristiques de la consommation d'aliments et du transit digestif chez cinq brebis Blackhead nourries ad libitum pendant la gestation et la lactation. Pendant la gestation, la consommation alimentaire et l'activité ruminale ont augmenté. Le volume de liquide du rumen et le nombre journalier de cycle A n'ont pas été significativement modifiés. Le temps moyen de rétention (MRT) des marqueurs des glucides et des particules dans le réticulo-rumen et après le réticulo-rumen a diminué de 14–32 %. Pendant la lactation, le volume de fluide du rumen a augmenté de 15 % par rapport au volume pendant

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la gestation. La consommation alimentaire journalière a atteint un pic (83,7 MS/kg BW^{0.75}) pendant la période 35–55 jours post-partum. Le MRT des marqueurs particuliers dans le réticulo-rumen était plus élevé que dans la période de fin de gestation. L'augmentation de la vitesse de passage des digesta était toujours principalement obtenue par une augmentation de la quantité de digesta passant à chaque ouverture par l'orifice réticulo-omasal. Le tamisage des contenus du pré-estomac et des fèces a montré que la destruction des grosses particules alimentaires ne limitait pas le passage des digesta.

transit digestif / consommation d'aliments / réticulo-rumen / rumination / fourrage / gestation / lactation / mouton

INTRODUCTION

The regulation of roughage intake in ruminants is the subject of controversial discussion. A new theory suggests that feed intake is adjusted to maximize the efficiency of oxygen utilization (Ketelaars and Tolkamp, 1992; Tolkamp and Ketelaars, 1992). In contrast, the prevailing concept implies that the intake of roughage is primarily limited by digesta turnover from the reticulorumen (RR). This is determined by rumen fill, rate of digesta passage, particle breakdown processes and the microbial activity in the rumen. These parameters are markedly influenced by the physical attributes of the feed. Plant cell wall contents have been identified as a major restrictive determining factor in forage intake (Mertens, 1973; Osbourn et al, 1974; Van Soest, 1994). The direct relation between cell wall intake and rumination time indicates that rate of particle comminution due to rumination may play an important role as a factor limiting roughage intake. In addition to the physical characteristics of the feed, the feed intake and the parameters determining digesta turnover from the RR are influenced markedly by the physiological status of the animal (Doreau and Rémond, 1982; Kennedy et al, 1986; Rémond, 1988; Forbes, 1995). However, it is unclear to what extent the parameters influencing digesta passage rate can be changed when animals fed exclusively roughage are confronted with an increased energy requirement.

The objective of this study was to investigate the factors that enable the animal to

increase its feed intake during a period of increased energy demand and to calculate the relationships between the various parameters determining digesta turnover from the RR, which may limit feed intake. As a means of increasing the energy requirement, we chose pregnancy and lactation, for two reasons: first, pregnancy and lactation represent natural conditions of increased energy demand with which animals normally have to cope; second, in contrast to lactation, the abdominal space becomes progressively restricted during pregnancy owing to the enlarging uterus. Thus, the comparison of pregnancy and lactation makes it possible to assess the importance of the factor of restricted space in the abdominal cavity on the rate of digesta passage and feed intake.

MATERIALS AND METHODS

Five rumen-fistulated 2-year-old Blackhead ewes were adapted to an ad libitum diet of medium-quality hay. Ovulation was synchronized by applying an intravaginal sponge for 12 days (Chronogest[®], Intervet, Boxmeer, Holland) followed by an injection of PMSG (500 IE im; Intergonan[®], Vemie Veterinär Chemie, Kempen). The ewes were housed with a Blackhead ram for the following 3 days. Pregnancy was diagnosed sonographically 4 weeks later.

Experimental design

Five experimental periods (EP) lasting 20 days each were conducted: d 60–80 post conceptionem (p conc) (EP I), d 105–125 p conc (EP II), d

128–148 p conc (EP III), d 10–30 post partum (pp) (EP IV) and d 35–55 pp (EP V).

During these experiments, the sheep were kept in metabolism crates and fed long hay [first cut; *Lolium* spp; g/kg dry matter (DM): crude fibre 333 (Weende analysis), crude protein (nitrogen \cdot 6.25) 109, ash 82; 8.67 MJ metabolizable energy/kg DM] exclusively (the analysis was performed in the Department of Animal Nutrition, School of Veterinary Medicine, Hannover). Animals were fed frequently to achieve an approximately constant rumen fill, and to maximize the stimulation for intake (EP I–III: at 0800, 1200, 1600, 2000 and 0200 hours, 600 g hay/meal; EP IV, V: at 0800, 1200, 1600, 2000, 0000 and 0400 hours, 600 g hay/meal). Water and mineralized salt licks were accessible at all times. On d 149 p conc, the ewes were put together in a box for lambing. Between d 149 and d 153 p conc, three ewes gave birth to one lamb each, one ewe had twins and one ewe had triplets, one of which was dead. On d 7 pp, the ewes were again put into the metabolism crates.

The procedures were identical in all five experimental periods. Feed intake and water intake were determined from d 10–20 by weighing each refusal before the next feed was offered. Feed refusals were found regularly and were discarded. Water intake was measured once daily at 0800 hours. Body weight (BW) was determined at 0800 hours on d 6. The apparent digestibility of the organic matter (OM) was calculated by the total collection method (d 11–20). The amount of OM in a subsample of hay and a subsample of faeces (taken from the faecal output on d 3, 5 and 7) was estimated by subtracting the weight of ash (determined by heating the sample to 550 °C for 6 h) from the weight of the DM in the respective sample. The OM intake was corrected by the additional estimation of the OM of the feed refusal collected from each animal on one day during each experiment. Milk production of the ewes was determined daily from d 7 to d 60 post partum as follows: lambs were accommodated separately from the ewes. Each lamb was weighed before and after suckling, which was allowed for about 10 min six times per day in week 2 pp, four times per day in week 3 pp, three times per day in week 4 pp and twice daily from week 5 to week 8 pp. A disposable nappy was put on each lamb during suckling to avoid distortions caused by urine and faecal losses. Thereby, the amount of consumed milk as well as daily weight gain of the lambs could be calculated. The lambs did not receive

any additional concentrates, but hay was available.

The duration of feed intake, rumination and resting was measured in each sheep on 3 days between d 12 and d 18, ie, 72 h per animal. A rubber tube filled with foam rubber was attached to the halter below the lower jaw. It was connected via a polyethylene tube to a pressure transducer (Statham P23Db; H Sachs, Freiburg). The typical patterns of pressure changes during feeding and rumination were recorded on a multi-channel recorder (Watanabe WTR 331; H Sachs, Freiburg; 10 mm \cdot min⁻¹ speed chart). The frequency of chews during rumination was estimated by recording 10–15 rumination cycles (100 mm \cdot min⁻¹ speed chart) during both daytime and night on 3 days. The frequency (min⁻¹) was calculated as the mean number of chews divided by the mean duration of each cycle (including the break between two cycles).

The mean retention time (MRT) of fluid and particles was determined for the total gastrointestinal tract (MRT_{GIT}) and the GIT distally to the RR (MRT_{dist}). For these measurements, two sets of plastic particles with a length of 1 mm and one set of plastic particles with a length of 10 mm, each with a different dye, were used according to Kaske and Engelhardt (1990). The density of all the plastic particles was 1.03 g/mL. At 0730 hours of d 10, three gelatine capsules (4 mL; WDT, Hannover) filled with 3 000 plastic particles (1 mm) were introduced manually through the reticulo-omasal orifice (ROO) and located between the omasal leaves for the estimation of MRT_{dist}. After that, a single dose of 15 mL polyethylene glycol (PEG 4000; 25% w/v; Merck, Darmstadt) as fluid marker was administered into the omasal canal via a plastic tube. To estimate MRT_{GIT}, 10 000 plastic particles with a length of 1 mm and 1 000 plastic particles with a length of 10 mm were mixed with 50 g ground commercial sheep concentrate and were fed to each sheep at 0800 hours. Finally, a single injection of chromium-ethylendiaminotetraacetic acid (Cr-EDTA; 30 mL, 1% w/v; Merck, Darmstadt) was introduced as a fluid marker into the RR through the fistula. Samples of rumen fluid were taken 2, 4, 6, 8, 10, 12, 15, 18, 24 and 36 h after the marker administration. Total faecal output was collected on d 10 at intervals of 3 h, on d 11 at intervals of 6 h, and twice daily from d 12–17. For a second determination of fluid MRT_{dist}, PEG was administered at 0800 hours on d 18. Accordingly, faeces were collected on d 18 and d 19 at intervals of 3 and 6 h, respec-

tively. The fluid MRT_{RR} was determined three times on d 10/11, d 14/15 and d 18/19.

Chromium concentration in the rumen fluid samples was determined by atomic absorption spectroscopy (Perkin Elmer 2100; Überlingen) after centrifugation of the sample (10 min; 6 000 g). The total faecal output was dried over 36 h at 100 °C for determination of DM. A subsample of 20% each was taken from all samples of d 10–13 and from one collection period per day of d 14–20. These subsamples were ground in a coffee grinder (K 6; Bosch, Stuttgart) and sieved through a 500 µm wire-mesh sieve (Retsch, Haan). Preliminary studies had indicated that this method did not change the size of plastic particles. A majority of the 10 mm long plastic particles were found to be reduced in size owing to rumination to 0.5–5 mm long pieces in the faeces. Most of the 1 mm particles had also been comminuted. The plastic particles in each subsample were manually separated from the remaining faecal particles, sorted according to their colour, and weighed. The concentration of the plastic particles was calculated for each set as the number of particles per gram of faecal DM by dividing the weight of the plastic particles found in the subsample by the mean weight of an unchanged plastic particle. For the five experimental periods, the faecal recoveries of particle markers varied from 79.0–94.9% (1 mm particles fed to the sheep), 70.4–83.2% (10 mm particles fed) and 94.1–96.4% (1 mm particles introduced into the omasum) during the respective 10 day collection period. PEG in the faeces subsamples was analysed as described by Hyden (1955).

Rumen fluid volume was determined by dividing the amount of Cr-EDTA introduced by its concentration at time zero using regression analysis to determine the MRT_{RR} of fluid (d 10, 14, 18).

Frequency of ruminoreticular motility was estimated on d 1–5 of each experiment during feeding, rumination and rest. Latex balloons filled with steel balls (ca 40 g) and air (5–10 mL) were placed in the reticulum and the ventral rumen. A third air-filled balloon was placed in the dorsal rumen. The frequency of ruminal contractions was recorded using the same recording system as described above (25 mm · min⁻¹ speed chart). A contraction cycle of reticulum–dorsal rumen–ventral rumen was regarded as an A-cycle. A contraction of the dorsal rumen followed by a contraction of the ventral rumen was

considered as a B-cycle. The recordings were carried out almost evenly distributed throughout day and night and lasted on average in each animal 89 min (feeding), 157 min (rumination) and 63 min (rest), respectively.

The amount of DM in the RR and particle size distribution of ruminoreticular contents were determined by emptying the forestomach completely through the fistula on d 6. The total rumen contents was weighed and mixed. Four subsamples (150–250 g) were taken and the remaining contents were put back into the RR within 10 min. Three subsamples were used for DM determination; the fourth one was further subdivided into six samples (10–15 g) which were immediately wet-sieved. Five sieves (100 mm diameter) with a pore size of 4, 2, 1, 0.5 and 0.25 mm were used (water flow 800 mL · min⁻¹). The samples were soaked in 500 mL tap water. The sample was then placed on the top sieve and sieved for 2 min. Then the upper sieve was removed and the material retained on this sieve was transferred into a glass bowl. This same procedure was carried out for each sieve. After drying (95 °C for 24 h) and weighing, the amount of material retained on each sieve was expressed as a percentage of total DM in the subsample. The percentage of total DM retained on the sieves with 4, 2 and 1 mm pore size was considered as the portion of large particles; the respective percentage of DM retained on the sieves with 0.5 and 0.25 mm pore size was considered as the amount of small particles. The DM passing the sieve with 0.25 mm pore size was denoted as the rest.

Faecal particle size distribution was estimated by wet-sieving on d 1, 3, 5 and 7. Faeces samples were taken from the Ampulla recti between 1600 and 1800 hours. Three subsamples (8–10 g) were used for determination of faecal DM. Another three subsamples (2–3 g) were soaked in 500 mL tap water for 12 h and wet-sieved as described above, except that a sieve with 4 mm pore size was not used.

To control the health status of the ewes, two to four heparinized blood samples were taken from the V jugularis during each experimental period at 1000 h. The glucose concentrations were analyzed enzymatically (hexokinase-method) and those of beta-hydroxybutyrate (BHB) were determined with BHB-dehydrogenase (both analyses were carried out in the Clinic for Pigs and Small Ruminants, School of Veterinary Medicine, Hannover). Insulin was ana-

lyzed by radioimmunoassay (Amersham Buchler; analyses were carried out in the Department of Biochemistry, School of Veterinary Medicine, Hannover).

outflow per day divided by the number of A-cycles per day.

Calculations

The MRT_{GIT} of the plastic particles and the MRT_{dist} of the fluid and particles were calculated according to Thielemans et al (1978): $MRT = (\sum c_i \cdot t \cdot dt) / (\sum c_i \cdot dt)^{-1}$, where c_i is the marker concentration in the sample, t is the time-interval after marker administration at which the sample was taken, and dt is the faecal collection interval.

The MRT of the plastic particles in the RR (MRT_{RR}) was calculated as $MRT_{GIT} - MRT_{dist}$. The MRT_{RR} of the fluid was calculated as $MRT_{RR} = k^{-1}$ from the equation $k = (\ln c_0 - \ln c_t) \cdot t^{-1}$, where c_0 is the marker concentration at zero time calculated by regression analysis and c_t is the marker concentration at sampling time t .

Fluid outflow from the RR ($L \cdot h^{-1}$) was calculated as rumen fluid volume divided by the fluid MRT_{RR} . The number of motility cycles per day was estimated as $(F \cdot D_{Feeding}) + (F \cdot D_{Rumination}) + (F \cdot D_{Rest})$ where F is the mean frequency (min^{-1}) of A-cycles and B-cycles, respectively, and D is the mean daily duration ($\text{min} \cdot \text{d}^{-1}$) of the respective activities. Fluid outflow from the RR per opening of the ROO was calculated as rumen

Statistical analysis

SIGMASTAT (Version 1.01; Jandel Corporation) was used for the statistical analysis of the results, which are presented as means and standard errors ($\bar{x} \pm \text{SEM}$). Significant differences at a level of $P < 0.05$ was tested by a one-way repeated measure Anova followed by the Student–Newman–Keuls test for multiple comparisons after checking the uniformity of variances and normality. A one-way repeated measure Anova on ranks was performed for those few results where the equal variance test failed or a significant difference from a normal distribution was found. Correlations between parameters were calculated applying the Pearson Product test.

RESULTS

All five ewes remained clinically healthy throughout pregnancy and lactation irrespective of their marked losses of body weight after parturition as compared with mid pregnancy (EP I). Mean plasma glucose levels tended to be lower during late

Table I. Energy requirement, energy intake and blood parameters during pregnancy and lactation.

	EP I (60–80 d p conc)	EP II (105–125 d p conc)	EP III (128–148 d p conc)	EP IV (10–30 d pp)	EP V (35–55 d pp)
Energy requirement^A (MJ ME · d ⁻¹)	10.8 ^a ± 0.4	16.5 ^b ± 1.2	20.1 ^c ± 2.0	21.2 ^c ± 0.3	16.6 ^b ± 0.4
Energy intake^B (MJ ME · d ⁻¹)	11.3 ^a ± 0.7	14.4 ^b ± 0.3	14.3 ^b ± 0.5	14.7 ^b ± 0.5	16.2 ^c ± 0.5
Blood parameters					
Plasma glucose (mmol/L)	2.87 ^a ± 0.11	2.64 ^a ± 0.12	2.90 ^a ± 0.12	3.04 ^a ± 0.05	3.25 ^b ± 0.05
β-hydroxybutyrate (mmol/L)	0.35 ^a ± 0.02	0.34 ^a ± 0.04	0.42 ^a ± 0.06	0.38 ^a ± 0.03	0.33 ^a ± 0.02
Insulin (μU/mL)	10.5 ^a ± 2.2	7.2 ^a ± 1.0	6.9 ^a ± 0.8	6.0 ^a ± 0.4	6.7 ^a ± 0.7

^A Estimated according to ARC (1980); ^B calculated from feed intake and feed analysis; p conc: post conception; pp: post partum. Mean values and standard errors for five sheep; values with different superscript letters within each row were significantly different ($P < 0.05$).

pregnancy than during lactation (table I). The levels of BHB remained low; a BHB level of 0.9 mmol/L was never exceeded in any animal. No significant differences between the levels of insulin were found between the experimental periods; generally, insulin levels were low (table I).

The birth weight of the lambs met breed standards (single lambs: $6\,070 \pm 545$ g, twins / triplets $4\,340 \pm 865$ g). Milk yields of uni- and multiparous ewes were comparable averaging 1550 ± 113 g/d between d 7 and d 28 pp and $1\,012 \pm 128$ g/d from d 29–60 pp. The weight gains of the lambs were 271 ± 10 g/d for the single lambs and 175 ± 6 g/d for twins from birth to d 60.

Feed intake

Feed intake increased in both experimental periods during late pregnancy (EP II and

III) by about 27% as compared to mid pregnancy (EP I) (table II). No differences in feed intake were found between uni- and multiparous ewes. During early lactation (EP IV), feed intake remained on the same level as during late pregnancy. A further increase of 10% was found during the second month of lactation (EP V). These changes in feed intake between the experimental periods were more pronounced when expressed as intake per kg metabolic BW. On the basis of intake per $\text{kg}^{0.75}$ BW, feed intake had already begun to increase during early lactation (EP IV) compared with late pregnancy (EP II/III); however, the change between EP III and IV was mainly due to the weight loss of the ewes caused by lambing. Feed intake covered the estimated energy requirements of the ewes only during EP I, II and V; EP III and IV were characterized by a considerable energy deficit of the sheep (table I).

Table II. Body weight, feed and water intake levels and rumination characteristics during pregnancy and lactation.

	EP I (60–80 d p conc)	EP II (105–125 d p conc)	EP III (128–148 d p conc)	EP IV (10–30 d pp)	EP V (35–55 d pp)
Body weight (kg)	$75.9^a \pm 2.1$	$78.3^a \pm 2.2$	$83.3^b \pm 2.3$	$64.0^c \pm 2.2$	$63.0^c \pm 1.8$
Intake					
(g DM · d ⁻¹)	$1303^a \pm 76$	$1663^b \pm 40$	$1654^b \pm 55$	$1696^b \pm 53$	$1867^c \pm 58$
g DM · (kg ^{0.75} · d) ⁻¹	$50.7^a \pm 2.8$	$63.3^b \pm 1.6$	$60.0^b \pm 1.2$	$75.3^c \pm 3.9$	$83.7^d \pm 3.4$
(min · d ⁻¹)	$368^a \pm 20$	$452^b \pm 29$	$446^b \pm 35$	$491^b \pm 17$	$472^b \pm 23$
(s · g DM ⁻¹)	$17.1^a \pm 1.2$	$16.4^a \pm 1.4$	$16.3^a \pm 1.7$	$17.4^a \pm 0.8$	$15.3^a \pm 1.1$
Water intake (L · d ⁻¹)	$4.1^a \pm 0.4$	$5.8^{bc} \pm 0.4$	$6.3^{bc} \pm 0.3$	$7.5^c \pm 0.5$	$7.6^c \pm 0.3$
Rumination					
(min · d ⁻¹)	$577^a \pm 17$	$679^b \pm 5$	$667^b \pm 23$	$582^a \pm 16$	$592^a \pm 10$
Frequency ^A (min ⁻¹)	$62.4^a \pm 5.4$	$72.6^b \pm 5.4$	$73.8^b \pm 4.2$	$75.0^b \pm 4.2$	$76.2^b \pm 3.6$
Chews ^B per day (· 10 ³)	$35.8^a \pm 2.6$	$49.2^b \pm 3.7$	$49.6^b \pm 4.3$	$43.7^c \pm 3.2$	$45.4^c \pm 2.8$
(Chews · g DM ⁻¹)	$27.7^a \pm 2.1$	$29.5^a \pm 1.7$	$29.8^a \pm 2.0$	$25.7^b \pm 1.4$	$24.2^b \pm 1.0$

^A Frequency of chews during the rumination cycle (including the break); ^B daily duration of rumination multiplied with the frequency of chews during rumination; ^C $N = 4$; one sheep drank during this period 12–15 L / d; p conc: post conception; pp: post partum. Mean values and standard errors for five sheep; values with different superscript letters within each row were significantly different ($P < 0.05$).

The duration of feed intake increased uniformly during all experimental periods by 26% on average compared to EP I; no variation in the distribution of feed intake between day and night was caused by the different number of daily meals in EP I–III as compared with EP IV and V. The feeding time expended for each g DM did not differ between the experimental periods (table II).

Rumination behaviour

Compared to mid pregnancy (EP I), increased feed intake was accompanied during late pregnancy (EP II and III) by an extended duration of rumination (+ 17%; table II). In contrast, sheep ruminated during lactation (EP IV and V) for a similar length of time to that observed in EP I. The frequency of chews during rumination increased by 19% on average in all periods (II–V) as compared to mid pregnancy (EP I). The number of chews per day was significantly higher during both periods in late pregnancy (+ 38% versus EP I) than during the periods in lactation (+ 25% versus EP I). Thus, the feed was ruminated less intensively during lactation (EP IV and V) than during pregnancy (EP I–III) as indicated by a reduced number of chews per g DM intake (table II).

Ruminoreticular contents

The fluid volume remained constant during pregnancy (EP I–III) and increased after lambing (EP IV and V) varying by about 15 or 44%, respectively, as a percentage of BW (table III). The percentage of DM did not change during pregnancy but increased during early lactation (EP IV). The amount of DM in the RR also did not differ from EP I to III. It did increase after parturition by 41% on average (table III).

The sieve analysis of ruminoreticular contents revealed a higher portion of large

particles in late lactation (EP V) compared to the other four periods, and a decreased portion of DM passing the smallest sieve (0.25 mm pore size) in EP II, III and V as compared to mid pregnancy (EP I; table III).

Ruminoreticular motility

The frequency of A- as well as B-cycles during feeding, rumination and resting did not vary significantly between the experimental periods (table IV). Averaged mean frequencies for EP I–V during feeding, rumination and resting were 1.74 ± 0.03 , 1.09 ± 0.02 and 1.01 ± 0.04 A-cycles (min^{-1}) and 1.01 ± 0.03 , 0.84 ± 0.03 and 0.46 ± 0.03 B-cycles (min^{-1}). The total number of A-cycles per day did not differ significantly between the experimental periods while the number of B-cycles per day was somewhat higher during lactation (EP IV/V) than in EP I (table IV).

Marker kinetics

In all the experimental periods, the fluid left the RR approximately three times faster than the small particles (1 mm), and the MRT_{RR} of the small particles was about 24 h shorter than the MRT_{RR} of particles fed with a length of 10 mm (table IV). Although the MRT_{RR} of both the fluid and particles changed markedly during pregnancy and lactation, the ratios MRT_{RR} of fluid/ MRT_{RR} of 1 mm particles and MRT_{RR} of fluid/ MRT_{RR} of 10 mm particles did not differ significantly between the experimental periods.

The MRT_{RR} of the fluid and small particles (1 mm) decreased during late pregnancy (EP II and III) by about 20–30% as compared to EP I and remained at this level throughout lactation (EP IV and V; table IV). Also the MRT_{RR} of particles fed with a length of 10 mm decreased by 15–27% during late pregnancy and early lactation (EP

Table III. Rumen fluid volume, dry matter (DM) in the reticulorumen and particle size distribution in the reticulorumen and faeces during pregnancy and lactation.

	<i>EP I</i> (60–80 d <i>p conc</i>)	<i>EP II</i> (105–125 d <i>p conc</i>)	<i>EP III</i> (128–148 d <i>p conc</i>)	<i>EP IV</i> (10–30 d <i>pp</i>)	<i>EP V</i> (35–55 d <i>pp</i>)
Contents of RR					
Fluid volume ^A (L)	12.7 ^a ± 0.5	12.6 ^a ± 0.7	11.8 ^a ± 0.6	13.9 ^b ± 0.7	14.6 ^b ± 0.8
Fluid volume (% of BW)	16.7 ^a ± 0.5	16.1 ^a ± 0.5	14.1 ^a ± 0.5	21.8 ^b ± 1.3	23.2 ^b ± 1.1
Dry matter (%)	8.7 ^a ± 0.3	9.5 ^a ± 0.5	9.3 ^a ± 0.6	11.6 ^b ± 0.7	10.3 ^{ab} ± 0.6
Dry matter ^B (g)	946 ^a ± 81	1023 ^a ± 60	1078 ^a ± 99	1420 ^b ± 116	1444 ^b ± 125
LP ^C (% of total DM)	26.4 ^a ± 2.5	27.2 ^a ± 1.8	31.7 ^a ± 1.7	30.2 ^a ± 2.1	38.3 ^b ± 0.9
SP ^D (% of total DM)	20.9 ^a ± 1.1	27.0 ^b ± 1.2	22.7 ^a ± 0.5	20.3 ^a ± 0.6	21.9 ^a ± 1.0
Rest ^E (% of total DM)	52.7 ^a ± 2.1	45.8 ^b ± 0.9	45.6 ^b ± 1.3	49.5 ^{ab} ± 1.6	39.8 ^c ± 0.3
Faeces					
LP ^F (% of total DM)	5.3 ^a ± 1.0	6.2 ^{ab} ± 2.5	7.6 ^c ± 1.3	7.5 ^c ± 0.8	9.2 ^d ± 0.7
SP ^D (% of total DM)	49.6 ^a ± 1.6	50.8 ^a ± 0.9	50.5 ^a ± 0.8	47.8 ^a ± 1.1	49.0 ^a ± 0.7
Rest ^E (% of total DM)	45.2 ^a ± 1.8	43.1 ^{ab} ± 0.9	41.9 ^b ± 0.7	44.6 ^{ab} ± 1.4	41.8 ^b ± 0.6

^A As determined by Cr-EDTA introduced into the rumen (three estimations per animal per period); ^B as determined by emptying the reticulorumen per fistulam; ^C DM retained on sieves with 4, 2 and 1 mm pore size; ^D DM retained on sieves with 0.5 and 0.25 mm pore size; ^E DM passing the sieve with 0.25 mm pore size (calculated values); ^F DM retained on the sieves with 2 and 1 mm pore size; *p conc*: post conception; *pp*: post partum; LP: large particles; SP: small particles. Mean values and standard errors for five sheep; values with different superscript letters within each row were significantly different ($P < 0.05$).

II–IV) compared with mid pregnancy (EP I). During late lactation (EP V), these particles were retained longer in the RR than in the previous periods; however, the MRT_{RR} was still shorter than during mid pregnancy (EP I).

The calculated flow of fluid through the reticulo-omasal orifice during each opening increased by 20–36 % during late pregnancy (EP II and III) and lactation (EP IV and V) as compared to mid pregnancy (EP I) (table IV).

The fluid passed through the distal GIT in all experiments faster than particles, but the absolute differences between the MRT_{dist} of the markers were small (1.5–2 h). A significantly reduced MRT_{dist} for the fluid and particulate markers (14–21 %) was observed during EP II–V as compared with mid pregnancy (EP I); however, the absolute changes were only 1.5–2.3 h (table IV).

The apparent digestibility of the OM remained unchanged in EP II as compared with EP I while a significant decrease was found in EP III and EP IV. Significantly higher values were determined in EP V compared to EP I–IV (table IV).

Sieve analysis of faeces

The portion of large particles in faeces increased in EP III and IV by about 40% as compared to EP I and II. During late lactation (EP V), a further increase was observed indicating an almost redoubling of this portion as compared to mid pregnancy (EP I; table III). The portion of material passing through the smallest sieve with the 0.25 mm pore size was reduced correspondingly by the respective amounts approximately. No differences were observed for the amount of small particles; their portion of DM

Table IV. Ruminoreticular motility and characteristics of digesta passage during pregnancy and lactation.

	<i>EP I</i> (60–80 d <i>p conc</i>)	<i>EP II</i> (105–125 d <i>p conc</i>)	<i>EP III</i> (128–148 d <i>p conc</i>)	<i>EP IV</i> (10–30 d <i>pp</i>)	<i>EP V</i> (35–55 d <i>pp</i>)
Ruminoreticular motility					
A-cycles (d ⁻¹)	1647 ^a ± 42	1847 ^a ± 118	1882 ^a ± 84	1824 ^a ± 46	1920 ^a ± 48
B-cycles (d ⁻¹)	920 ^a ± 50	990 ^a ± 22	977 ^a ± 85	1092 ^b ± 58	1130 ^b ± 66
Digesta passage					
MRT _{RR}					
– of fluid ^A (h)	15.1 ^a ± 0.9	11.0 ^b ± 0.7	10.1 ^b ± 0.5	10.9 ^b ± 0.4	10.9 ^b ± 0.7
– of 1 mm particles ^B (h)	47.1 ^a ± 2.1	37.7 ^b ± 0.9	32.2 ^b ± 1.5	34.3 ^b ± 1.4	39.6 ^b ± 4.1
– of 10 mm particles ^C (h)	65.1 ^a ± 1.3	55.2 ^{bc} ± 2.0	47.6 ^b ± 2.2	54.0 ^{bc} ± 2.5	57.9 ^c ± 4.8
MRT _{dist}					
– of fluid ^D (h)	14.5 ^a ± 0.8	12.5 ^b ± 0.2	12.9 ^b ± 0.3	11.4 ^b ± 0.2	12.1 ^b ± 0.3
– of 1 mm particles ^E (h)	16.8 ^a ± 1.5	14.0 ^b ± 0.3	15.3 ^b ± 0.9	13.0 ^b ± 0.3	13.9 ^b ± 0.7
Fluid flow through ROO ^F (mL per opening)	12.5 ^a ± 1.0	15.1 ^b ± 0.8	15.0 ^b ± 0.7	17.0 ^b ± 1.3	16.9 ^b ± 0.9
OM digestibility					
(%)	57.6 ^a ± 0.8	58.5 ^a ± 0.8	55.9 ^b ± 0.7	55.9 ^b ± 1.2	59.8 ^c ± 0.6

^A As determined by Cr-EDTA introduced into the rumen (three estimations per animal per period); ^B plastic particles (1 mm - 1.03 g/mL) were fed; ^C plastic particles (10 mm - 1.03 g/mL) were fed; ^D as determined by introducing polyethyleneglycole through the reticulo-omasal orifice (ROO) into the omasal canal; ^E gelatine capsules filled with plastic particles (1 mm - 1.03 g/mL) were introduced through the ROO into the omasum; ^F calculated as rumen outflow per day divided by the number of ROO-openings per day; *p conc*: post conception; *pp*: post partum; MRT_{RR}: mean retention time of fluid and plastic particles (1.03 g/mL) in the reticulorumen; MRT_{dist}: mean retention time distally to the reticulorumen. Mean values and standard errors for five sheep; values with different superscript letters within each row were significantly different ($P < 0.05$).

remained constant throughout all experimental periods.

The most important changes of parameters determined during EP I–V are summarized schematically in table V.

DISCUSSION

Changes of roughage intake during pregnancy and lactation

In EP I, the intake of the five ewes was in the same range as cited in literature for non-pregnant sheep fed on coarse roughage

(55–60 g DM /kg BW^{0.75} per day; ARC, 1980). An increase in feed intake during pregnancy has also been observed by other authors (Reid and Hinks, 1962; Forbes, 1968, 1970; Tissier et al, 1975; Newton and Orr, 1981). However, in contrast to the generally accepted conviction that intake declines during the last weeks of pregnancy (Forbes, 1986), the feed intake level remained elevated during late pregnancy (EP II, III) compared to mid pregnancy (EP I) in agreement with observations of Arnold (1975) and Bermudez et al (1989). The high level of feed intake during late pregnancy

Table V. Summarized changes of digestive and ingestive parameters during pregnancy and lactation as compared with mid pregnancy (EP I).

	<i>Pregnancy</i>	<i>Lactation</i>
Feed intake (g DM· d ⁻¹)	↑↑	↑↑ → ↑↑↑
Fluid volume in RR (L)	=	↑
Dry matter in RR (g)	=	↑↑↑
Rumination chews (d ⁻¹)	↑↑↑	↑↑
chews/g DM intake	=	↓
Large particles ^A (% of DM) in contents of RR in faeces	= = → ↑↑↑	= → ↑↑↑ ↑↑↑
MRT _{RR} fluid (h)	↓↓	↓↓
particles (h)	↓↓	↓↓ → ↓
MRT _{dist} fluid and particles (h)	↓	↓
A-cycles (day ⁻¹)	=	=
Fluid flow through ROO (mL per opening)	↑↑	↑↑

^A DM retained on sieves with 4, 2 and 1 mm pore size; =: no significant change; ↑/↓: increase/decrease of 10–20%; ↑↑/↓↓: increase/decrease of 20–30%; ↑↑↑: increase of > 30%; →: development during pregnancy (EP II versus III) or lactation (EP IV versus EP V).

(EP III) may have been caused by the high feeding frequency, which provided a strong stimulus to maximize the intake; ad libitum intake of late-pregnant ewes fed only 2 × 180 min per day was markedly lower than that of ewes having access to feed throughout the day (Dittrich et al, 1984). Elevated levels of plasma estrogens during late pregnancy have been suggested to cause a depression in feed intake (Forbes, 1971). However, the level of unconjugated estrogens increases in ewes at less than about 2 days ante partum (Edqvist and Stabenfeldt, 1980; Hoffmann, 1994). This late increase

may be another explanation for the high intakes observed in EP III.

The size of the uterus of ewes bearing singles and twins, respectively, differs by about 100%. However, feed intake and rumen fluid volumes were the same for uni- and multiparous ewes, similar to the findings of other authors (Tissier et al, 1975; Foot and Russel, 1979; Newton and Orr, 1981; Weston, 1988). Thus, the size of the uterus was not the main determining factor in feed intake as claimed by Mäkelä (1956) and Forbes (1968). The observation that during pregnancy, the limited space in the abdominal cavity is compatible with high

roughage intake, may reflect the additivity of peripheral and metabolic signals (Forbes, 1995). As reported by other authors (eg, Foot and Russel, 1979; Dittrich et al, 1984), the feed intake of the ewes did not peak until the second month of lactation (EP V). However, rumen fluid volume, digesta passage characteristics, ruminoreticular motility and rumination behaviour were comparable in the first month (EP IV) and second month (EP V) after parturition. Accordingly, we may speculate that the delayed increase in feed intake was caused primarily by metabolic signals.

The milk yield was already reduced by about 35% as compared to EP IV when the feed intake peaked. Thus, milk production during early lactation developed independently of feed intake although, in general, milk yield is influenced by dry matter intake considerably when different diets had been compared (eg, Broster, 1972).

Body condition is known to influence feed intake markedly (Bines and Morant, 1983). Thus, the relation between feed intake and the loss of body weight during pregnancy and lactation was investigated. To get a rough impression about the loss of body reserves, we calculated the 'body weight_{empty}' defined as body weight minus the weight of rumen contents (fluid and dry matter) minus the weight of the pregnant uterus (estimated according to ARC, 1980) for each experimental period. In fact, a significant correlation could be proved when the BW_{empty} losses were related to feed intake per kg^{0.75} (fig 1) or directly to the absolute feed intake ($r = 0.63$; $P < 0.001$), as compared with mid pregnancy (EP I). The relation between the current energy requirement (table I) and feed intake per kg^{0.75}, on the other hand, was rather poor ($r = 0.44$; $P < 0.05$). It may be speculated that the long-term regulation of body weight is vigorously involved in the changes of feed intake observed during lactation.

Factors enabling increased roughage intake during pregnancy and lactation

Role of rumen fluid volume

Probably due to the rather high feed intake during late pregnancy (EP II, III), the rumen fluid volume remained unchanged compared with mid pregnancy. These results are in agreement with Gunter et al (1990) and Faichney and White (1988) while Forbes (1970) and Weston (1988) reported that rumen volume decreased in late pregnancy ewes by 14–22%. The increase in rumen fluid volume and rumen fill during lactation as compared to mid pregnancy (EP I) may explain why the particle MRT_{RR} tended to be longer during the second month of lactation than during late pregnancy. Although the volume of the pregnant uterus may account for 8 (single lamb) up to 15 L (triplets) towards the end of pregnancy, the increase in rumen fluid volume was only about 2 L during the weeks after parturition. However, the increase in dry matter content of the RR during lactation was more pronounced than that of rumen fluid volume. Accordingly, the packing density of the digesta was increased, which could be explained by a reduced sensitivity of tension receptors in the forestomach during lactation (Baile and Forbes, 1974). These results demonstrate that the volume of the reticulorumen is not simply dependent on the space available in the abdominal cavity but that it is regulated in a much more complex way; considerable variation of rumen fill have been shown also depending on the type and the availability of the diet (eg, Weyreter and Engelhardt, 1986; Lechner-Doll et al, 1991; Bosch et al, 1991) and the palatability of the feed (Faverdin et al, 1995).

Changes in the MRT_{RR} and MRT_{dist} of fluid and particles

Our results agreed with those of Coffey et al (1989) who observed a marked increase in

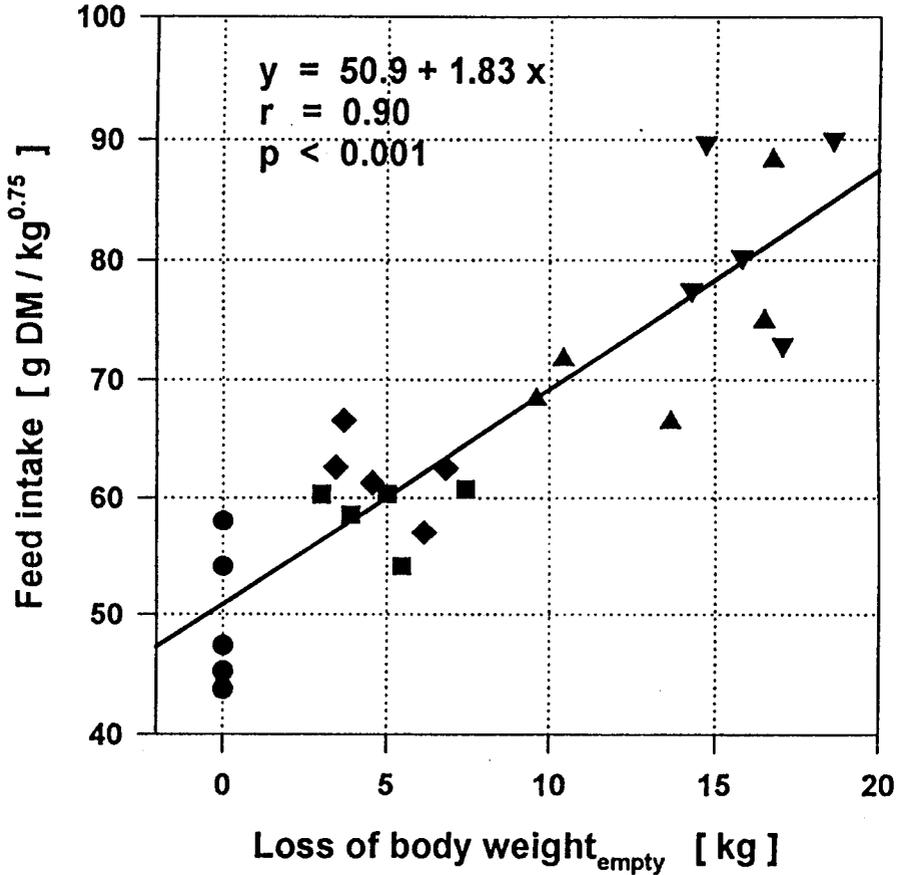


Fig 1. Relationship between daily feed intake (g DM / kg^{0.75}) and loss of body weight during late pregnancy and lactation as compared to mid pregnancy (EP I); BW_{empty}: body weight minus weight of rumen contents minus estimated weight of the pregnant uterus; ●: d 70 – d 80 post conception (EP I); ◆: d 115 – d 125 p conc (EP II); ■: d 138 – d 148 p conc (EP III); ▲: d 20 – d 30 post partum (EP IV); ▼: d 45 – d 55 pp (EP V).

digesta passage from the RR in pregnant ewes fed ad libitum as compared to non-mated ewes. An increased passage rate of digesta from the RR has also been demonstrated for late pregnancy ewes fed at a constant level throughout pregnancy (Faichney and White, 1988; Weston, 1988; Gunter et al, 1990) indicating that feed intake seems to

be not the only causative factor for changes in MRT_{RR}.

In our experiments, increased digesta passage during pregnancy and lactation was achieved by a uniform increase in the passage rate of all markers. This was documented by constant ratios of MRT_{RR} of fluid/MRT_{RR} of 1 mm particles, MRT_{RR} of

fluid/ MRT_{RR} of 10 mm particles and MRT_{RR} of fluid/ MRT_{dist} for both fluid and plastic particles. In addition, the relation between the portion of large particle in the RR and the portion of large particles in the faeces ($r = 0.77$; $P < 0.001$) remained constant even when more large particles were present in the RR (EP IV and V). These results reveal further evidence that the sorting process of particulate matter in the reticulum is based primarily on the separation of particles according to their density during the biphasic reticular contraction (Kaske et al, 1992). The ROO itself, on the other hand, appears not to discriminate strictly the passage of larger feed particles as an experimentally induced impairment of reticular contractions is accompanied by a drastically increased amount of large feed particles leaving the RR (Kaske and Midasch, 1997).

Increased water intake during late pregnancy has been suggested to affect the MRT_{RR} of rumen solutes as well as rumen osmolality (Faichney and White, 1988). Higher intakes of water during late pregnancy were also observed in EP II and III compared with mid pregnancy. However, a significant relation between water intake and the fluid MRT_{RR} was only found when using the data from four ewes ($r = -0.78$; $P < 0.01$). The fifth ewe (who bore the triplets) drank 12–15 L per day in EP III without any extraordinary deviations in digesta passage or motility parameters. Thus, the specific importance of polydipsia during pregnancy remains unclear.

In agreement with Weston (1988), not only the MRT_{RR} but also the MRT_{dist} of the fluid and particles decreased significantly during late pregnancy and lactation. The clearly negative relationship between the MRT_{dist} of the fluid and feed intake ($r = -0.76$; $P < 0.001$) may have indicated that reticular outflow was strongly influenced by factors occurring distal to the RR. In pylorotomized sheep, the passage rate of fluid and particulate matter from the RR

increased drastically together with a persisting increase in feed intake by 48% (Malbert and Ruckebusch, 1989). These observations supported the hypothesis that the primary control of digesta outflow from the RR may occur distally to the ROO (Dardilat, 1987; Mathison et al, 1995).

As MRT_{RR} as well as MRT_{dist} decreased markedly during both late pregnancy and lactation as compared with mid pregnancy, the accompanying changes in OM digestibility were surprisingly low. A reduction in DM digestibility of the same magnitude, however, has been reported by Coffey et al (1989). Gunter et al (1990) did not find any effect on DM digestibility irrespective of their observation of an increased passage rate in the GIT. Although the apparent OM digestibility represents only a very rough measure of digestive processes, these results may reflect an improved digestive efficiency in pregnant sheep.

Particle breakdown during rumination

The duration of the eating period per g DM remained constant throughout all the experimental periods. Thus, the differences in the particle size distribution in the rumen contents can only be explained by different particle breakdown rates due to rumination. The number of chews per day during rumination increased during late pregnancy by nearly the same percentage as feed intake. As a result, the breakdown of large particles due to rumination (chews per g DM) remained unchanged during pregnancy, and this corresponded to the similar particle size distributions in the forestomach contents throughout pregnancy. During lactation, particle breakdown during rumination was reduced and, in turn, more large particles were found in the rumen contents. Nevertheless, the MRT_{RR} of fed plastic particles with a length of 10 mm was shorter during late pregnancy and lactation than during mid pregnancy (EP I). As a result, the portion of large feed particles in the faeces increased

considerably (EP III–V). The results provided strong evidence that particle breakdown due to rumination did not limit digesta outflow from the RR under our experimental conditions.

Surprisingly, the daily duration of rumination was not prolonged during lactation compared to mid pregnancy (EP I) although the feed intake was elevated. The rumination reflex is initiated by mechanical stimulation of receptors in the wall of the RR. Our results may have indicated that the activation of these mechanoreceptors was reduced during lactation. This was probably due to the enlarged volume of the RR. The frequency of chews during rumination, on the other hand, remained high. In conclusion, the sheep seemed to be able to regulate the breakdown of large particles during rumination not only by changing the duration of rumination, but also by changing the frequency of their chews. Obviously, both these parameters are not controlled by the same triggering signal.

Ruminoreticular motility and digesta passage

Although the number of A-cycles per day was related to the feed intake ($r = 0.66$; $P < 0.01$), it did not vary significantly between EP I–V. The latter result supported the assumption of Ulyatt et al (1986) that the daily number of A-cycles is more or less constant in ruminants. The frequencies of A- and B-cycles during feeding, rumination and resting represented the only measured parameters that did not change significantly in any of the experimental periods. As a result, the increased digesta passage rate during late pregnancy cannot be explained as being primarily due to an enhanced propulsive activity of the forestomach system. Instead, the shorter MRT_{RR} of the fluid and particles was mainly the result of a larger amount of digesta passing through the ROO during each opening. This phenomenon could be explained by the following: a) an

increased pressure gradient between the reticulum and the omasal canal during the opening of the ROO; b) an enlarged size of the opened ROO; and/or c) a longer duration of the period when the ROO is open. The latter seems to be of major importance as the duration of reticular contraction appears to be more closely related to digesta flow through the ROO than with either the frequency of contractions or the pressure differences created during the contraction (Okine et al, 1989; Croom et al, 1993; Okine et al, 1993; Mathison et al, 1995).

CONCLUSIONS

The MRT_{RR} and MRT_{dist} of fluid and particles, rumination rate and rumen fluid volume are controlled by the animal over a remarkably wide range during pregnancy and lactation independently of the feed characteristics. Consequently, the intake of roughage can be markedly increased during periods of increased energy demand. As the frequency of A-cycles during feeding, rumination and resting remained fairly stable, the increased rate of digesta passage was primarily achieved by an increased amount of digesta passing into the ROO during each opening. Particle breakdown did not play a primary role in the passage of particulate matter through the ROO under our experimental conditions. Obviously, the particle size distribution in the reticular outflow represented the result of the particle distribution in the forestomach and particle separation processes in the reticulum related to the sequence of the reticular contractions.

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