Food particle breakdown in herbivores

Influence of food intake level on energy yield

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INAUGURAL-DISSERTATION zur Erlangung des Grades eines **Dr. med. vet.**
beim Fachbereich Veterinärmedizin der Justus-Liebig-Universität Gießen

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List of abbreviations

AAS	atomic absorption spectroscopy
ADFom	acid detergent fibre; expressed without residual ash
ADL	acid detergent lignin
BR	browser
BW	body weight
CE	chewing effectiveness
cMEAN	continuous mean
CP	crude protein
DM	dry matter
dMEAN	discrete mean
DOMI	digestible organic matter intake
EE	ether extracts
FMR	field metabolic rate
FT	feeding type
GIT	gastro-intestinal tract
GR	grazer
HGT	hohenheim gas test
IM	intermediate feeder
ME	metabolizable energy
ME_{rum}	ME for ruminants
MOF	modulus of fineness
MPS	mean particle size
MRT	mean retention time
NDFom	neutral detergent fibre; not assayed with a heat stable amylase and expressed exclusive of residual ash
OM	organic matter
ROO	reticulo-omasal orifice
RR	reticulorumen
SF	selectivity factor
UIAM	units of intake above maintenance
WAPS	weighted average particle size

General Introduction

Basics of digestion

A balanced energy supply, such that energy consumption is matched by the intake of food energy, is most important for survival and success of an animal. An imbalance leads to excessive weight loss or gain. The total energy assimilated with food is called the gross energy. After subtraction of energy that gets lost via faeces, gas, urine and heat loss remains the net energy that can be used by the animal for, e. g. growth, lactation or reproduction. Net energy can be partitioned into maintenance energy and performance for activity and products. For domestic animals the energy supply is usually balanced by the human via defined diets. Wild animals have to handle oversupply and shortage of energy and nutrients in the course of a year, which is particularly true for herbivores. They entirely rely on the amount and quality of plants available, both changing considerably with seasons. To make use of their high-fibre plant food, herbivores comminute and squash food mechanically during chewing in preparation for the chemical degradation of plant cell walls by microorganisms living in fermentation chambers of herbivores.
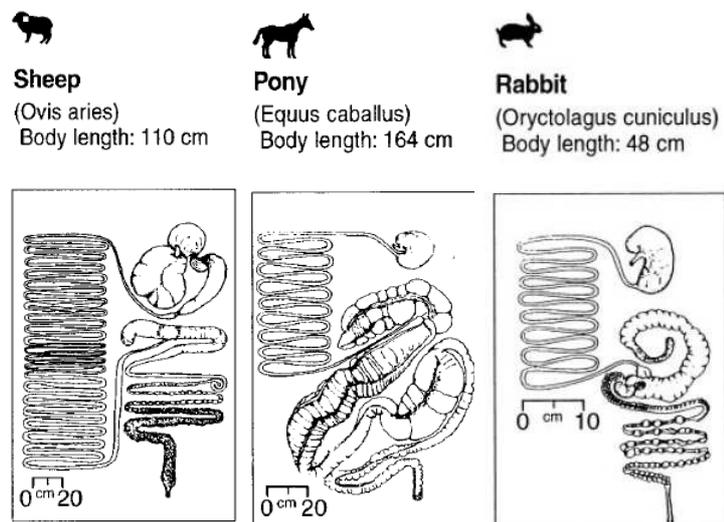
Fig. 1: Schematic view of the digestive tract of a foregut fermenter (sheep), hindgut (colon) fermenter (pony) and caecum fermenter (rabbit) from Stevens and Hume (1998)

Retention of food in ruminants and hindgut fermenters

Hosting the symbiotic microorganisms is not the only use of a voluminous rumen or hindgut. Total gut fill as well as retention time is increased due to fermentation chambers. Large fibre particles are separated from smaller ones and liquid contents by peristalsis of fermentation chambers, like in the reticulorumen (RR) for ruminants that retains large particles with low density until particle size is sufficiently reduced to flow out of the rumen by rumination (Blaxter et al., 1956). Freshly ingested particles are mostly large, while rechewing and microbial degradation decrease size and increase density of particles (Lechner-Doll et al., 1991). Depending on their size and density, there are two particle pools in the RR: Those that can leave and those that can not leave the RR. The chance to leave the rumen via the reticulo-omasal orifice (ROO) is highest for particles in ventral reticulum where it is easier to stay for small particles with high density (Reid, 1986) because of the separation mechanism of forestomach (see figure 2a). During contraction of the reticulum, large particles with low density are shoved caudodorsal, away from the ROO. Considering the outflow rate of digesta markers there is a clear difference between fluid and particulate phase (see figure 3a); particles were retained 1.6 (sheep and goats) to 3 times (cattle and camels) longer than fluid (Lechner-Doll et al., 1991).

The hindgut fermenters can be divided into two groups by the function of their fermentation chamber. At large hindgut fermenters, caecum and proximal colon form a unit. The separation mechanism is clearly inferior to that of ruminants (see figure 2b) and digesta markers of both phases appear almost at the same time in faeces (see figure 3b) (Sakaguchi, 2003; Steuer et al., 2011). A special group among the hindgut fermenters are the caecum fermenters, which are smaller animals (mostly under 5 kg body weight (BW)), with a caecum that is large compared to the rest of the intestine. Special is here the selective retention of fluid and small particles by the

proximal colon via antiperistaltic movements (see figure 2c). These are segmental activities that separate digesta into faecal pellets, and haustral activity, that carries liquids and very small particles back into the caecum (Ehrlein et al., 1983). The content of caecum is referred to as soft faeces which are reingested by the animal to utilize microbial protein (Sakaguchi, 2003). This strategy is reflected in the outflow of fluid and particle phase markers (see figure 3c), where the fluid phase shows several peaks attributable to reingestion and leaves the intestine slower than the particle phase. It is apparent that intense breakdown of food to small particles is of importance for all three digestion strategies.

a)

b)

c)
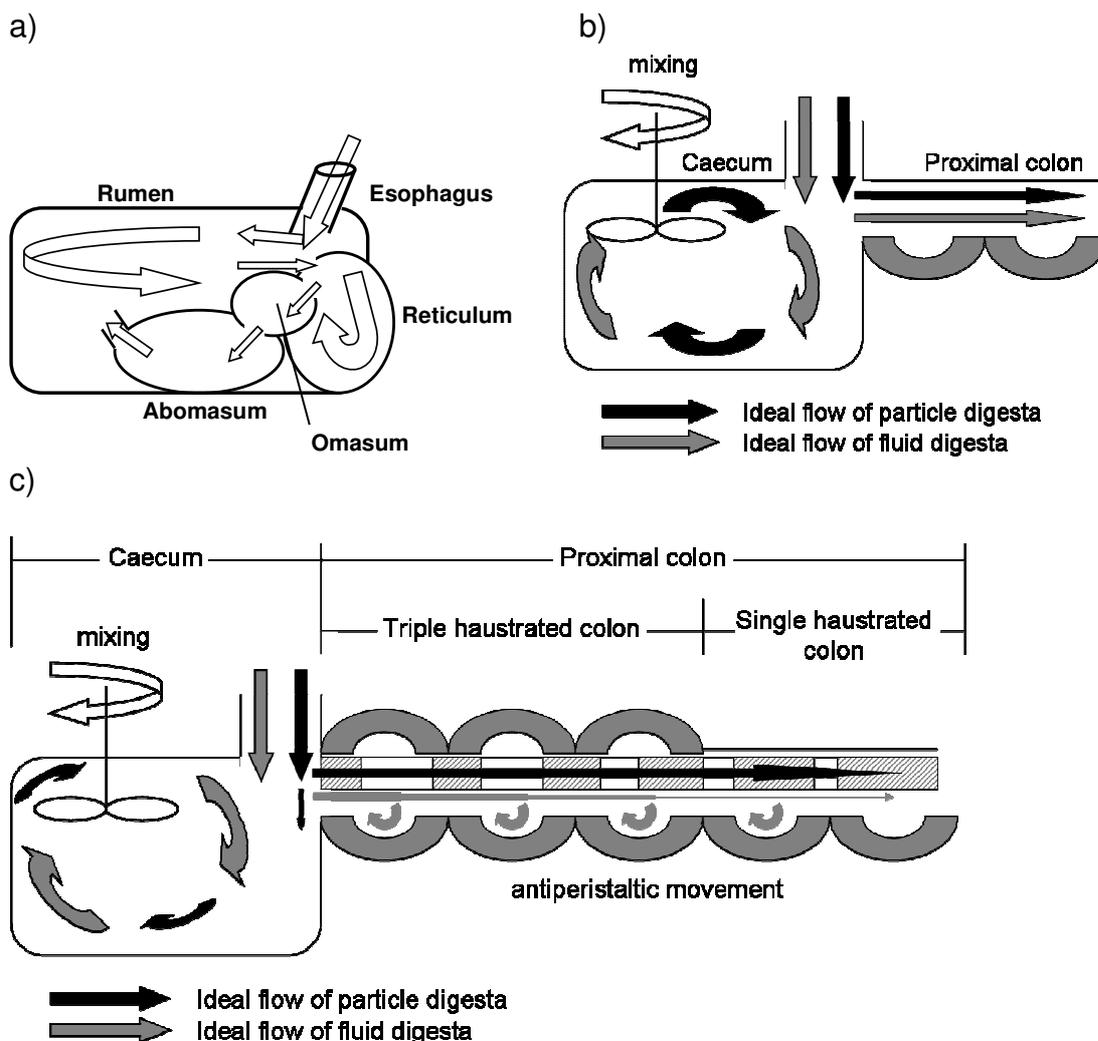
Fig. 2 a-c: Schematic view of digesta flow in fermentation chambers of herbivores.
a) separation mechanism in a reticulorumen
b) no selective retention at hindgut fermenters (Sakaguchi, 2003)
c) separation mechanism of a caecum fermenter (Sakaguchi, 2003)

a) goat
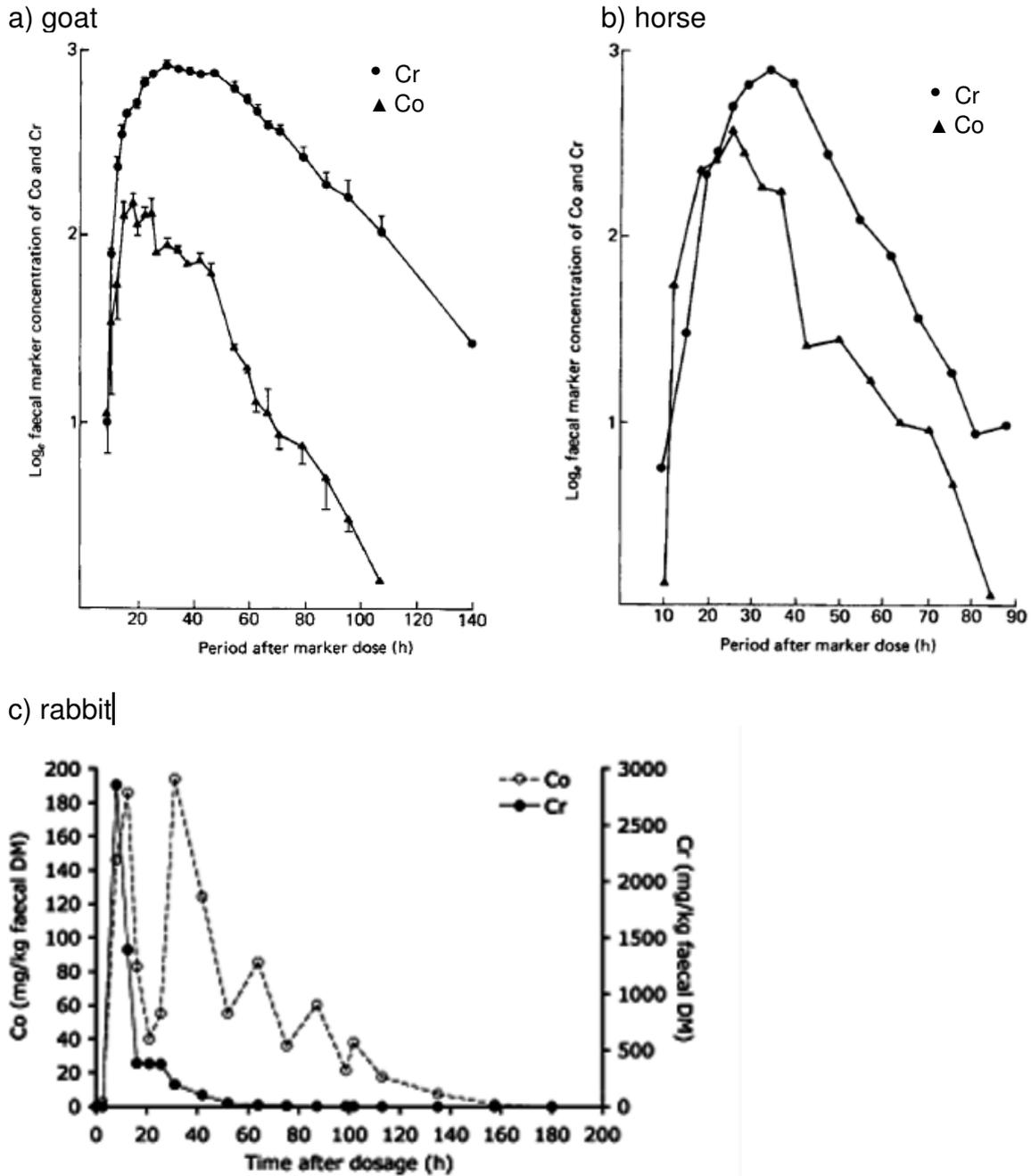
b) horse

c) rabbit

Fig. 3 a-c):   Typical excretion curves of Co-EDTA and chromium-mordanted fibre
from the digestive tract of
a) ruminant (goat) (Udén et al., 1982)
b) large hindgut fermenter (horse) (Udén et al., 1982)
c) caecum fermenter (rabbit) (Franz et al., 2011)

Importance of chewing and nature of teeth

While herbivore diets are typically relatively nutrient-poor and hardly digestible, animals had to evolve a strategy to break down plant structure, which speeds up digestion of plant nutrients as well as it minimizes the volume of food in the gut. Chewing during eating and rumination is the most efficient and major way to enlarge surface for microbial degradation and to reduce the size of food particles and therefore, the volume of material in the gastro-intestinal tract (McLeod and Minson, 1988). Factors affecting the efficiency of chewing are on one the hand the type of teeth and the chewing surface, and on the other hand the amount of ingested food. The dentition of mammals consists of the incisors to harvest food, the canines mainly for inter- or intraspecific fighting, and the premolars/molars mainly for grinding action. According to the main source of food the dentitions show specializations like distinct canines for carnivores to prey and well-marked molars and premolars for herbivores to grind, squish and comminute plant material. The jaw joint, the directions of the upper and lower jaw, and the adductor muscles produce together the tribosphenic chewing stroke that breaks down food to fine particles (Reilly et al., 2001).
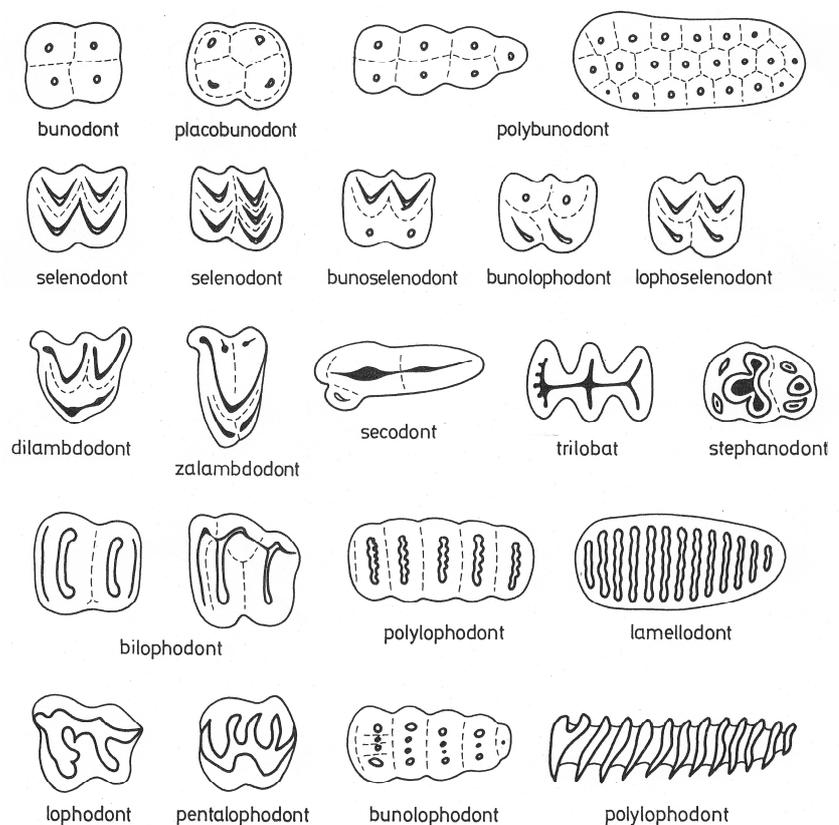
Fig. 4: Overview on molar surfaces in mammals (Thenius, 1989)

A classification of the molars is made by reference to the pattern of the tooth crown into bunodont (omnivores), dilambdo- and zalambdodont (insectivores), selenodont and lophodont types (herbivores) (figure 4) (Thenius, 1989). The grinding of the herbivore molars is achieved by enamel folds that function as a grater. Plants are pulled off or cut by the incisors and in the following triturated between the molars. In all of the several species of the order of lagomorphs (like rabbits), the incisors are constantly growing and used as cutting pliers. The molars are lophodont and anisognath, which means that the upper jaw is wider than the lower. By chewing movements enamel edges develop at the lingual lower and the buccal upper jaw (figure 5a). The molars of perissodactyls are also lophodont. The highly increased number of enamel folds results in prismatic teeth and finally in rootlessness and hypsodonty (figure 5b). The molars of artiodactyls can be bunodont (e.g. suids) or selenodont (e.g. ruminants). The crown height of ruminants can vary from brachydont over subhypsodont to hypsodont in relation to abrasiveness of diet (figure 5c).
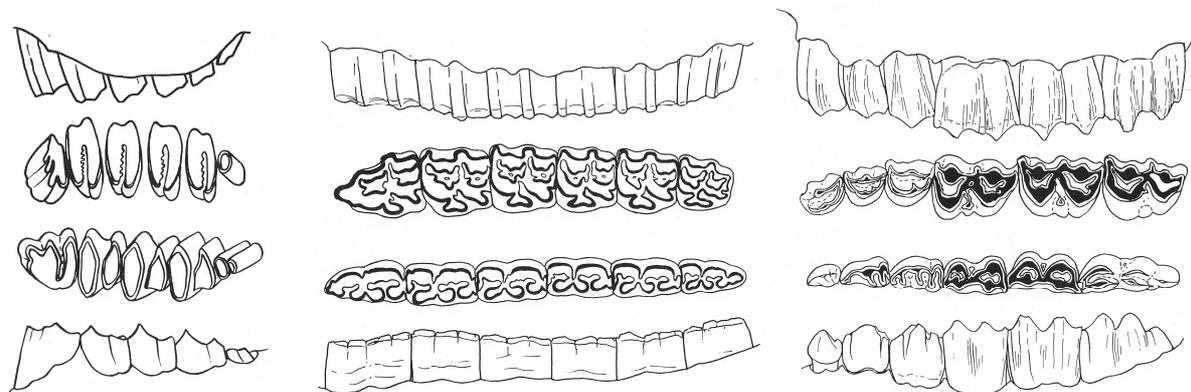
Fig. 5: Schematic illustration of molars of a) rabbit (*Oryctolagus cuniculus*), b) hindgut fermenter (*Equus grevyi*), and c) ruminant (*Bos primigenius taurus*) (Thenius, 1989)

The chewing efficiency of selenodont molars is increased by angled edges at the dental cusps that require primarily lateral movements of the jaw. During evolution herbivores of all species developed specialized molars; their surface complexity

reflects the consumed diet and comminutes plant material efficiently (Evans et al., 2007). A clear relationship between the complexity of molar design and the size of faecal particles of several herbivore mammals underline the importance of chewing efficiency (Fritz et al., 2009). The total amount of food (and energy) intake is therefore limited by comminution of food via chewing. This is an evident challenge e.g. for feeding of dairy cows, which are not able to consume sufficient amounts of energy during lactation because of limited reticuloruminal capacity. Dado and Allen (1995) compared milk production (kg/d), dry matter intake (kg/d) and total chewing time (min/kg DM) at early lactating Holstein cows fed a high fibre diet with and without additional inert fibre bulks. While milk production (31.4 to 29.2 kg/d) and dry matter intake (18.7 to 16.6 kg/d) decreased with adding the inert fibre, total chewing time increased (45.9 to 52.7 min/kg DM), both due to an increase of eating time (19.0 to 21.9 min/kg DM) and of ruminating time (27.0 to 30.8 min/kg DM). Therefore knowledge of the influence of diet and digesta particle size for digestive processes of herbivores is important in animal nutrition and for a thorough understanding of digestive physiology.

Consequences of increased food intake

While data is available in literature that describes digestive variables like mean retention time (MRT) or digestibility of the diet at different intake levels, there is few (ruminants) or no (hindgut fermenters) data available for faecal particle size when intake level changes. Increasing food intake, above level of maintenance, is found during periods of increased energy needs, e.g. while growing or during lactation. It can be said that in all mammals, lactation typically is the moment in lifetime with highest energy needs. Via the concomitant increase in intake, these higher energy

requirements also put extra demands on the processing capacity of the digestive tract of the animal. Since the amount of food that can be utilized is limited by its volume in the gut, any increase of digesta particle size puts additional constraints on any further increase of food intake.

The aim of this study was to determine the influence of food intake level on digestive variables in herbivores. Particularly the effect of lactation on these was studied, as moment in lifetime with highest physiological energy requirements and therefore highest voluntary intake level (chapter 1). Following the conclusions of the literature review, more detailed investigations were done with a small ruminant (goat; chapter 2) and a hindgut fermenter (rabbit; chapter 3).

Chapter 1

Lactation and food particle breakdown in wild herbivores: Estimation of faecal particle size as a function of food intake level

Abstract

Numerous studies have found a connection between risen energy needs in lactation and food intake level as well as chewing movements per minute. Both increase during lactation to compensate for higher energy requirements. At the same time, retention time and thus digestibility of food decrease. In this context the question arises, to what extent digesta particle breakdown changes. In this study, changes of faecal mean particle size (MPS) related to food intake were estimated as an indicator for chewing efficiency of wild herbivores. Based on milk yield and milk components of wild herbivores (from literature), a factor was calculated to show how the energy requirements of lactating animals differ from maintenance requirements of the same species. Faecal MPS data from a variety of wild herbivores at maintenance energy requirements could be compared with literature-based percentage changes in faecal MPS of herbivores at increasing levels of food intake. The factor describing the increase in intake due to lactation was also used to estimate the increase of faecal MPS during lactation of wild herbivores which was between 8.5 to 15.5%, associated with the body weight (BW) of the animal. Generally, animals with larger BW had a lower increase of total energy requirements due to lactation compared to animals with low BW.

1. Introduction

1.1 General relations

As a consequence of their physical and chemical characteristics, plants as food set some particular requirements on the digestive system of herbivores. Plant cell wall can not be digested autoenzymatically (Collinder et al., 2003) but only by microorganisms harboured in a fermentation chamber before or behind the small intestine. However, some of the constituents of plant material are notoriously slow (cellulose) or non-digestible (lignin, cutin) even for microbes. They also have a limited capacity to penetrate the cutin surface of leaves (fungi being an exception), and mainly attack the plant cell wall from its outer surface. Therefore, the surface to volume ratio of a particle is particularly important for microbial colonisation and digestion of plant material; this ratio is significantly increased by comminution, which means that more microorganisms per unit of volume can colonize and degrade the food (Poppi et al., 1980b; 1981; Pond et al., 1984; Pérez-Barbería and Gordon, 1998; Wilman et al., 1999), accelerating the digestive process considerably. Besides this influence on chemical digestion, thorough comminution will also allow a higher intake due to the corresponding reduction of the volume of digesta contents.

1.2 Lactation, intake, chewing behaviour and particle size

In front of this background it is getting clear why comprehensive comminution of food particles plays a central role in the digestive process of mammalian herbivores, and why the development of effective chewing batteries occurred repeatedly among them. However, with an increasing amount of material that needs to be processed, even the most sophisticated comminution capacity becomes increasingly challenged. Within the range of physiological events occurring regularly during a mammal's

lifespan, lactation must be considered the period of highest energy requirements, and in consequence highest food intake levels: E.g., the dry matter intake (g/kg$^{0.75}$ body weight (BW)) of lactating black-tailed deer with twins was 70%, and with one calf still 35% higher than that of non-lactating animals (Sadleir, 1980). A connection between increased energy needs in lactation and food intake level as well as chewing movements per minute can be demonstrated (Clutton-Brock et al., 1983; Penning et al., 1995; Gibb et al., 1999). Trials with Bighorn sheep *(Ovis canadensis)* (Blanchard, 2005) showed that lactating ewes ruminated 1.21 times faster (chews/s), which can be interpreted as a strategy to keep food comminution in pace with increased intake. However, despite such efforts, chewing time spent per kg of ingested material decreases with increasing intake (Coulon et al., 1987).

In consequence, the size of food particles in the gastro-intestinal tract appears to increase with increasing food intake level, as indicated by trials with rumen fistulated steers (Kovács et al., 1997a; 1997b; 1998) and nonlactating dairy cows (Okine and Mathison, 1991b). Further quantification of changes of faecal particle size (as the result of chewing behaviour relevant for digestion) in relation to increased food intake level becomes desirable as a final test and quantification of the constraints induced by higher feed intakes.

1.3 Description of the model

Based on available literature data, it was the intention of this study to give estimates for changes in food particle comminution occurring due to the increased food intake during lactation. This approach involved a stepwise estimation of the relevant factors: First of all, estimations of milk output [kg/d] and average energy content [MJ/kg] were needed to calculate the average energy output [MJ/d] via milk during a lactation period for a range of wild herbivores. In a second step, this was related to the

maintenance energy requirements and this value (the percentage of the increase of energy requirements) was taken as a measure for the increase of food intake level due to increased energy requirements. Finally, by using data on faecal particle size in a variety of wild ruminants (at maintenance intake level) in combination with available data from domestic ruminants on the change of particle size with intake level, the increase of mean particle size (MPS) during lactation was estimated for different size classes of ruminants.

2. Materials and Methods

2.1 Energy output via milk

Table 1 gives an overview of milk components of several wild and domesticated species. The energy content of the milk (MJ/kg) was calculated by a regression equation following Tyrrell and Reid (1965), as modified by Nostitz and Mielke (1995):

$$E = 0.384 * F + 0.223 * P + 0.199 * L - 0.108$$

where E is the energy content of the milk (MJ/kg), F is the fat content (%), P is the protein content (%) and L is the lactose content (%) in milk. By integration of the three major components, milk energy content of different species with strongly diverse compositions can be described with good precision. In addition Table 1 provides information on the average milk yield over a lactation period. These data comes partly from literature and partly from calculations following Hanwell and Peaker (1977). The latter authors describe the correlation of body weight and milk yield by the following allometric equation:

$$\text{Milk yield (kg/day)} = 0.084 * BW^{0.77}$$

Table 1: Milk contents and milk yield of 51 species of herbivores

Species	Fat (%)	Protein (%)	Lactose (%)	Energy (MJ/kg)	N	Source of data	Average milk yield (kg/day)	Source of data
Proboscidea								
Elephantidae								
Asian elephant	7.95	4.60	5.24	5.01	4	Simon (1959); Reuther (1969)	34.7[b]	Hanwell & Peaker (1977)
African elephant	9.30	5.10	3.70	5.34	30	McCullagh and Widdowson (1970) Osthoff et al. (2007a)	37.9[b]	Hanwell & Peaker (1977)
Perissodactyla								
Equidae								
Ass	1.82	1.74	5.87	2.15	9	Oftedal and Jenness (1988)	1.3[a]	Guo et al. (2007)[4]
Plains zebra	2.20	1.63	7.00	2.49	5	Oftedal and Jenness (1988)	6.2[b]	Hanwell & Peaker (1977)
Domestic horse								Bouwman & van der Schee (1978)[1];Smolders (1990)[4];
	1.46	1.82	6.74	2.20	8	Oftedal and Jenness (1988)	15.9[a]	Oftedal (1983)[3]
Przewalski horse	1.50	1.55	6.72	2.15	14	Oftedal and Jenness (1988)	5.9[b]	Hanwell & Peaker (1977)
Mountain zebra	2.20	1.63	7.00	2.49	7	Oftedal and Jenness (1988)	6[b]	Hanwell & Peaker (1977)

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Table 1 (continued): Milk contents and milk yield of 51 species of herbivores

Species	Fat (%)	Protein (%)	Lactose (%)	Energy (MJ/kg)	N	Source of data	Average milk yield (kg/day)	Source of data
Tapiridae								
Baird's tapir	1.90	4.60	5.30	2.70	4	Oftedal and Iverson (1995)	5.4[b]	Hanwell & Peaker (1977)
Malayan tapir	3.40	5.70	5.30[x]	3.52		Langer (2008)	4.2[b]	Hanwell & Peaker (1977)
Lowland tapir	3.90	4.40	5.30	3.43	3	Oftedal and Iverson (1995)	3.7[b]	Hanwell & Peaker (1977)
Rhinocerotidae								
White rhinoceros	0.30	1.40	6.70	1.65	1	Wallach (1969); Langer (2008)	24.6[b]	Hanwell & Peaker (1977)
Black rhinoceros	0.20	1.40	6.60	1.59	11	Oftedal and Iverson (1995)	13.0[a]	Váhala et al. (1995)[5]
Indian rhinoceros	1.40	1.39	7.60	2.25	1	Nath et al. (1993)	17.7[a]	Hagenbeck (1969)[5]
Artiodactyla								
Antilocapridae								
Pronghorn	13.00	6.90	4.00	7.22		Langer (2008)	0.9[a]	Wild et al. (1994)[b]
Bovidae								
Impala	20.40	10.80	2.40	10.61		Langer (2008)	1.6[b]	Hanwell & Peaker (1977)
Springbok	14.50	7.40	4.20	7.95	3	Osthoff et al. (2007b)	1.2[b]	Hanwell & Peaker (1977)
Blackbuck	9.26	6.90	4.35	5.85	3	Dill et al. (1972)	1.3[b]	Hanwell & Peaker (1977)

Table 1 (continued): Milk contents and milk yield of 51 species of herbivores

Species	Fat (%)	Protein (%)	Lactose (%)	Energy (MJ/kg)	N	Source of data	Average milk yield (kg/day)	Source of data
Bison	1.70	4.80	5.70	2.75	4	Langer (2008)	10[b]	Hanwell & Peaker (1977)
Gayal	7.00	6.30	5.20	5.02	4	Oftedal and Iverson (1995)	2.9[a]	Islam et al. (1993)[4]
Zebu	4.70	3.20	4.70	3.35		Jenness (1986)	2.0[a]	Coulibaly & Nialibouly (1998)[4]; Bonfoh et al. (2005)[4]
Domestic cattle	3.70	3.20	4.60	2.94		Oftedal (1984)	13.7[a]	Yates et al. (1971)[3]; Robison et al. (1978)[1]; Le Du et al. (1979)[2]; Auchtung et al. (2002)[3]
Water buffalo	7.40	3.80	4.80	4.54		Jenness (1986)	10.6[a]	Devendra (1980)[1&4]; Ludri et al. (1989)[4]
Domestic goat	3.80	2.90	4.70	2.93		Oftedal (1984)	1.8[a]	Devendra (1980)[1&4]; Ludri et al. (1989)[4]
Ibex	12.40	5.70	4.40	6.80	24	Jenness (1986)	0.9[a]	Maltz & Shkolnik (1984)[3]
Blue duiker	12.2	9.8	3.8	7.52	10	Taylor et al. (1990)	0.06[a]	Taylor et al. (1990)[1]
Dorcas gazelle	8.80	8.80	5.70	6.37	16	Jenness (1986)	0.6[a]	Maltz & Shkolnik (1984)[3]
Thomsons gazelle	19.60	10.50	2.70	10.30		Langer (2008)	0.8[b]	Hanwell & Peaker (1977)
Sable antelope	5.00	6.20	5.30	4.25	6	Oftedal and Iverson (1995)	5.3[b]	Hanwell & Peaker (1977)

Table 1 (continued): Milk contents and milk yield of 51 species of herbivores

Species	Fat (%)	Protein (%)	Lactose (%)	Energy (MJ/kg)	N	Source of data	Average milk yield (kg/day)	Source of data
Mountain goat	8.10	6.40	4.3	5.29	28	Oftedal (1984)	0.7[a]	Carl & Robbins (1988)[3]
Musk ox	10.90	11.90	2.10	7.15	5	Baker et al. (1970)	2.4[a]	Parker et al. (1990)[3]
Domestic sheep	7.30	4.10	5.00	4.60		Oftedal (1984)	2.1[a]	Doney et al. (1979)[1 & 2], Dove & Freer (1979)[3] ; Snowder & Glimp (1991)[1]
Bighorn sheep	5.30	5.50	4.60	4.07		Langer (2008)	0.9[a]	Wild et al. (1994)[5]
Dall sheep	11.20	9.40	4.60	7.20	8	Cook et al. (1970a)	1.7[b]	Hanwell & Peaker (1977)
Eland	9.90	6.30	4.40	5.97	11	Treus and Kravchenko (1968)	1.5[a]	Treus & Lobanov (1971)[4]
Cervidae								
Moose	10.05	12.30	0.56	6.61	3	Cook et al. (1970b)	2.9[a]	Shochat & Robbins (1997)[5]; Reese & Robbins (1994)[3]
Roe deer	6.70	8.80	3.8	5.18	1	Pinter (1963)	0.97[a]	Pinter (1963)[5], Wayre (1967)[5]
Iberian red deer	11.50	7.60	5.90	7.18	14	Landete-Castillejos et al. (2000)	1.2[a]	Arman et al. (1974)[1&4] Landete-Castillejos et al. (2000)[1&4] ; Garcia et al. (1999)[1]

Table 1 (continued): Milk contents and milk yield of 51 species of herbivores

Species	Fat (%)	Protein (%)	Lactose (%)	Energy (MJ/kg)	N	Source of data	Average milk yield (kg/day)	Source of data
Mule deer	14.50	8.00	4.00	8.04	24	Mueller and Sadleir (1977)	1.1[a]	Sadleir (1980)[1]; Carl & Robbins (1988)[3]
White-tailed deer	5.83	10.14	7.14	5.81	9	Robbins, Moen (1975)	1.8[b]	Hanwell & Peaker (1977)
Reindeer	15.50	9.90	2.50	8.55	5	Gjøstein et al. (2004)	0.6[a]	Gjøstein (2004)[4]; McEwan & Whitehead (1971)[3]
Giraffidae								
Giraffe	4.80	4.00	4.90	3.60	3	Oftedal and Iverson (1995)	6.3[a]	Dagg & Foster (1976)[1]
Okapi	4.4	16.6	4.2	6.12	2	Gregory et al. (1965)	5.5[b]	Hanwell & Peaker (1977)
Nonruminantia								
Camelidae								
Bactrian camel	5.65	3.55	4.24	3.70	10	Zhang et al. (2005)	10.0[a]	Sawaya et al. (1984)[4]
Dromedary	3.60	3.00	4.40	2.82	11	Sawaya et al. (1984)	5.5[a]	Yagil & Etzion (1980)[3]
Llama	4.70	4.23	5.93	3.82	10	Riek and Gerken (2006)	2.3[a]	Riek, Gerken & Moors (2007)[3]
Alpaca	3.20	3.90	5.60	3.10	24	Clave (2003); Riek and Gerken (2006)	0.5[a]	Leyva & Markas (1991)[4]

Table 1 (continued): Milk contents and milk yield of 51 species of herbivores

Species	Fat (%)	Protein (%)	Lactose (%)	Energy (MJ/kg)	N	Source of data	Average milk yield (kg/day)	Source of data
Suidae								
Domestic pig	6.26	5.64	5.52	4.65	350	Klobasa et al. (1987)	6.5[a]	Linzell et al. (1969)[2]; Lewis et al. (1978)[1]; Yang et al. (1980)[3]
Rodentia								
Caviidae								
Guinea pig	5.70	6.30	4.80	4.44	10	Oftedal and Iverson (1995)	0.02	Mepham and Beck (1973)[1]; Oftedal (1981)[3], Anderson et al. (1984)[4]
Lagomorpha								
Leporidae								
European hare	15.60	10.00	1.50	8.41	30	Lhuillery et al. (1984)	0.06[a]	Hackländer et al. (2002)[4]
Rabbit	15.20	10.30	1.80	8.38	56	Coates et al. (1964)	0.12[a]	Cowie (1969)[1]; Peaker & Taylor (1975)[1]
Eastern cottontail rabbit	14.40	15.8	2.7	9.48	4	Anderson (1975)	0.02[a]	Pascual et al. (1999b)[4]

[a] = from literature
[b] = calculated
[1] = Weigh-suckle-weigh procedure
[2] = Timed-milking procedure
[3] = Isotope dilution procedure
[4] = Hand milking
[5] = Daily feed intake of artificial reared young
[x] = estimated value

Average daily milk production rather than peak milk production was considered as the most adequate measure for comparison for this study. While energy requirements during maximal lactation are easier to define (and therefore often build the data background in comparative studies on lactation, e.g. (Oftedal, 1984; Riek, 2011)), in addition to increased food intake they are typically covered by body reserves, which will lessen the influence of energy requirements on chewing efforts in the short term. However, in the long run these body reserves will still have to be replaced, and when considering the overall burden on food comminution from additional energy requirements during lactation, it appears most logical to use average milk production during a whole lactation cycle as the measure for additional food intake due to lactation. On average, peak lactation milk yield is on the size of 120-150% of average daily milk yield (as estimated from lactation curves for dairy cattle, sheep, pigs and horses as given in Kirchgeßner (2011)). Metabolizable energy (ME) requirement for milk production was calculated according to the following equation:

$$ME \text{ (MJ/d)} = C \text{ (MJ/kg)} * Y \text{ (kg/d)} * 100 / 60$$

where ME is the energy demand for milk production, C is the energy concentration of the milk and Y is the average daily milk yield over the whole lactation; the efficiency factor k for milk production (k = 60%) (GfE, 2001) is included in the calculation.

2.2 Increase of energy requirements during lactation

For the field metabolic rate (FMR) of wildlife, 580 kJ ME/kg$^{0.75}$ BW was assumed. Due to the higher physical activity, the FMR is ca. 29% higher than maintenance requirements for domestic animals, as assumed by Robbins (1993). It should be stated that this value (580 kJ ME/kg$^{0.75}$ BW) represents rather the lower end of realistic estimations, and especially animals under harsher environments like

mountains can have considerably higher maintenance requirements. For example, for lactating cows under alpine conditions, a 1.35 - 2.55 fold increase in energy requirement compared to cows in the lowland was estimated (Christen et al., 1996; Berry et al., 2001) The percentage increase of energy requirement during lactation was calculated by division of energy demand during lactation by maintenance energy requirements.

$$I (\%) = E (MJ/d) / FMR (MJ/d) *100$$

Where I is the percentage increase of energy requirements during lactation, E is the energy requirement for milk production and FMR is the field metabolic rate. Therefore, the factor I describes how energy requirements of lactating animals differ from nonlactating, giving an estimation of the size of the increase of intake during lactation. The average value over all species was 210%, so the maintenance energy requirement has to be multiplied by the factor 2.1.

The data on body weight of the animals were obtained from the comprehensive literature collection of Owen-Smith (1988), the Mammalian Species Systematic List (http://www.science.smith.edu/msi/msiaccounts.html, 2010) and the Animal Diversity Web of the university of Michigan (http://animaldiversity.ummz.umich.edu, 2010).

2.3 Particle size and food intake

Chewing is generally regarded as the major event reducing length of food particles (Ulyatt et al., 1986). Following McLeod and Minson (1988), in ruminants 75% of the breakdown of food particles are accomplished by teeth. While 25% is related to chewing during eating and 50% to chewing during rumination, the remaining 25% can be attributed to physical attrition and bacterial degradation (17%) plus large particles remaining in faeces (8%) (excluding these remaining faecal particles from

calculation results in a contribution of chewing of 82% and of digestion/ detrition of 18% of total particle breakdown). In consequence, faecal particle size represents a reliable measure of food comminution.

To determine the effects of an increase in food intake level on MPS in faeces, several studies were used that worked with ruminants under defined conditions (Okine and Mathison, 1991b; Kovács et al., 1997a; 1997b; 1998). In all studies faecal particle size was increased at higher food intake. Data on non-ruminants were found to represent a serious data bottleneck (literarily no data available), and so all major conclusions on changes of faecal particle size with intake level necessarily needed to be restricted to ruminants. A trial with rumen fistulated steers at three intake levels of a diet consisting of 68% forage (silages) and 32% concentrate on a dry matter basis (1997a; Kovács et al., 1997b; 1998) showed an increase of MPS of 6% when doubling intake level from maintenance. Thus the surface-volume proportion of the particles for microbial degradation and fermentation is decreased, although this negative influence for total energy balance is obviously overcompensated by the higher amount of food intake.

2.4 Particle size at maintenance energy requirements

Due to the lack of data on faecal particle size at different intake levels in non-ruminants, data collection was restricted to ruminants. Faecal MPS of 83 wild ruminants with maintenance energy requirements/food intake level (Clauss et al., 2002; Fritz, 2007) was calculated. All animals were adult, obviously healthy and without dental problems. They were divided in three groups according to body size following Clauss et al. (2002), animals under 100 kg (n = 37), from 100 to 250 kg (n = 23) and over 250 kg (n = 23), to simplify the classification of species into the model.

To have a data source as comparable as possible, the MPS from the data set was recalculated by an exponential model developed by Fisher et al. (1988) using the non-linear model procedure of SAS (2007).

$$R = 100 * e^{-(s^a - bs)}$$

R = particle size data expressed as cumulative percent weight oversize

R' = first derivative of cumulative percent weight oversize

s = screen size in millimetres

a and b = estimated parameters

Then an adaptation of the model followed (Kovács et al., 1997b), to enhance the number of steps between the sieve with the largest and the smallest pore size.

$$\text{Step} = (L - 0.063) / 1000$$

$$R' = 100 * e^{(bs - s^a)} * (b - as^{(a-1)})$$

The first derivative (R') of the equation above was used to calculate the MPS according to the equation below:

$$\text{Mean size} = \frac{\sum_{i=1}^{1000} step * R' * (0.063 + i * step)}{\sum_{i=1}^{1000} step * R'}$$

L = double the aperture of the largest sieve [mm]

The average MPS of the three groups was calculated from the computed MPS in faeces of every species of wild herbivores in maintenance. Then the average increase of energy requirements was calculated for all species, arranged in the same groups depending on body weight. The percentage increase of MPS during lactation was estimated by the calculated regression. In this way the increase of MPS at increasing food intake levels during lactation of wild herbivores could be estimated.

2.5 Statistics

Statistical evaluation of differences between the BW classes was done via a one-way ANOVA (GLM procedure of SAS (2007)), The unbalanced design of dataset was considered. Means comparison between body weight classes were done with the Tukey-Kramer method.

3. Results

Data on the major components of milk and the milk yield are shown in Table 1. Considerable species differences in milk composition are present (figure 6). Horses and rhinoceroses show a far higher lactose and lower protein and fat content in their milk than other species. In contrast to horses and rhinoceroses, artiodactyls produce milk with much higher fat and protein contents, and in return
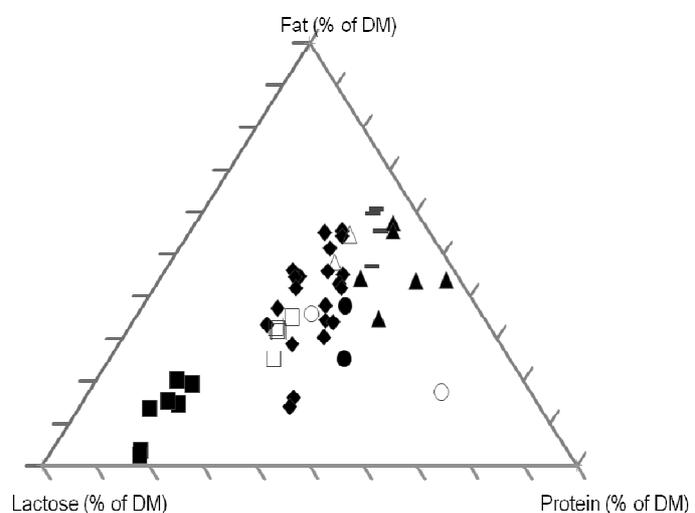
Fig. 6: Ternary diagram of percentage milk composition in dry matter (DM) of 53 species of herbivores.

■ Equidae & Rhinocerotidae ♦ Bovidae
▲ Cervidae ○ Giraffidae ▬ Lagomorpha
● Tapiridae □ Camelidae △ Elephantidae

lower lactose content, just as elephants, lagomorphs and rodents. Despite being perissodactyls, tapirs are in the same scatter plot as bovids and cervids. The relation between the calculated energy content of milk and the average daily milk yield is shown in figure 7. Species with high milk energy content, like reindeer, Thomson gazelle, mule deer or impala, produce smaller amounts than species having a low energy content like horses or rhinoceroses. Table 2 shows data on BW and the FMR,

the energy output in MJ/day based on the metabolic body size and the calculated percentage increase of energy requirements during lactation for milk production. The average increase is 110% (equivalent to 2.1 fold maintenance energy requirements). Highest values for the increase in energy requirements were seen in antelopes and gazelles (~200%) while camels have values below the average (approximately 54%), as
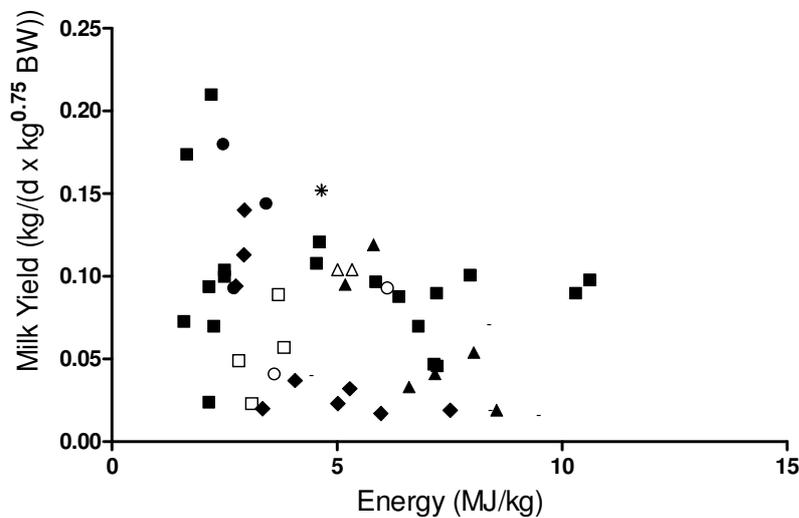
Fig. 7: Daily milk yield (kg/(d x kg$^{0.75}$ BW)) and energy content of the milk (MJ/kg) in 53 species of herbivores.

■ Equidae & Rhinocerotidae ◆ Bovidae ▲ Cervidae
○ Giraffidae – Lagomorpha ● Tapiridae □ Camelidae
△ Elephantidae * Suidae

a result of small yield and low energy content of milk. The MPS of different ruminants as recalculated with an exponential model (Fisher et al., 1988; Kovács et al., 1997b) is shown in Table 3. The differences in the increase of energy requirements during lactation and the differences in MPS during maintenance between species, as well as the estimated MPS in faeces at lactation can be seen in Table 4. The trend of the increase in MPS was estimated via the regression: Differences in MPS [%] = 9.00 x intake factor − 6.28 (R^2 = 0.32; p = 0.24); the intake factor represents the multiplier of intake for maintenance (e.g. 1.5 if the intake of the animal is 1.5 times its maintenance requirements). Based on this estimation, at 1.64-fold intake level (maintenance plus 64%) the trend of MPS is by 8.5% to bigger particles, at maintenance plus 102% by 12.2%, and at maintenance plus 142% by 15.5%.

Table 2: **List of 51 herbivores used in calculation of increase of energy requirements during lactation**

Species	BW (kg)	Energy requirement for milk production (MJ/d)	Average total energy requirement during lactation (MJ/d)	Increase of energy requirements due to lactation
Proboscidea				
Elephantidae				
Asian elephant	2500[a]	289.8	495.4	141 %
African elephant	2800[a]	337.3	561.2	151 %
Perissodactyla				
Equidae				
Ass	200[a]	4.7	35.6	15 %
Plains zebra	265[a]	25.6	63.8	67 %
Domestic horse	320[a]	58.3	102.3	132 %
Przewalski horse	250[b]	21.1	57.7	58 %
Mountain zebra	256[a]	26.6	63.8	71 %
Tapiridae				
Baird's tapir	225[b]	29	62.8	86 %
Malayan tapir	160[a]	24.5	50.7	94 %
Lowland tapir	135[a]	21	44	91 %
Rhinocerotidae				
White rhinoceros	1600[a]	67.7	214.9	46 %
Black rhinoceros	1006[a]	34.5	138.3	33 %
Indian rhinoceros	1600[a]	66.4	213.5	45 %
Artiodactyla				
Ruminantia				
Antilocapridae				
Pronghorn	52[c]	10.8	22.1	96 %
Bovidae				
Impala	45[a]	27.8	37.9	275 %
Springbok	31,5[a]	15.2	23	197 %
Blackbuck	35[a]	12.7	21	151 %

Table 2 (continued): List of 51 herbivores used in calculation of increase of energy requirements during lactation

Species	BW (kg)	Energy requirement for milk production (MJ/d)	Average total energy requirement during lactation (MJ/d)	Increase of energy requirements due to lactation
Bison	495[a]	41	102.1	67 %
Gayal	620[b]	24.3	96.5	34 %
Zebu	450[a]	11.2	68	20 %
Domestic cattle	450[a]	67.1	124	118 %
Water buffalo	450[b]	80.2	137	141 %
Domestic goat	40[a]	8.8	18	95 %
Ibex	40[b]	10.2	19.5	110 %
Blue duiker	4.7[a]	0.8	2.6	41 %
Dorcas gazelle	13[c]	6.4	10.4	160 %
Thomsons gazelle	18.5[a]	13.6	18.8	261 %
Sable antelope	220[a]	37.8	71.1	114 %
Mountain goat	73[c]	6.2	20.7	42 %
Musk ox	228[c]	28.6	62.7	84 %
Domestic sheep	45[a]	16.1	26.2	159 %
Bighorn sheep	71[c]	6.1	20.3	43 %
Dall sheep	50[c]	20.5	31.5	188 %
Eland	383[a]	15	65.3	30 %
Cervidae				
Moose	396[a]	32	83.6	62 %
Roe deer	22[a]	8.4	14.3	142 %
Iberian red deer	90[a]	14.4	31.4	84 %
Mule deer	55[a]	14.7	26.5	125 %
White-tailed deer	52[a]	17	28.3	151 %
Reindeer	100[a]	8.6	26.9	46 %
Giraffidae				
Giraffe	825[a]	37.8	127.3	42 %
Okapi	230[c]	56.4	90.8	164 %

Table 2 (continued): List of 51 herbivores used in calculation of increase of energy requirements during lactation

Species	BW (kg)	Energy requirement for milk production (MJ/d)	Average total energy requirement during lactation (MJ/d)	Increase of energy requirements due to lactation
Nonruminantia				
Camelidae				
Bactrian camel	545[a]	61.7	127.3	94 %
Dromedary	545[a]	25.9	91.5	39 %
Llama	140[b]	14.6	38.3	62 %
Alpaca	60[b]	2.6	15.1	21 %
Suidae				
Domestic pig	150[b]	50.4	75.3	202 %
Rodentia				
Caviidae				
Guinea pig	0.30[b]	0.15	0.4	63 %
Lagomorpha				
Leporidae				
European hare	4.5[b]	0.8	2.6	47 %
Rabbit	2.0[b]	1.7	2.7	171 %
Eastern cottontail rabbit	1.3[c]	3.2	3.9	446 %

BW body weight
[a] Owen-Smith (1988)
[b] Animal Diversity Web; University of Michigan [http://animaldiversity.ummz.umich.edu (2010)]
[c] Mammalian Species Systematic list [http://www.science.smith.edu/msi/msiaccounts.html (2010)]

Table 3: **Faecal mean particle size (MPS, mm) and feeding type (FT) of 83 species of ruminants at maintenance requirements (Clauss et al., 2002; Fritz, 2007)**

under 100 kg Species	FT	MPS (mm)	from 100 to 250 kg Species	FT	MPS (mm)	over 250 kg Species	FT	MPS (mm)
Klipspringer	BR	0.61	Nyala	BR	0.67	Moose	BR	0.91
Indian muntjac	BR	0.56	Greater kudu	BR	0.88	Giraffe	BR	1.14
Roe deer	BR	0.53	Okapi	BR	1.05	Takin	IM	0.63
Tufted deer	BR	0.62	Bongo	BR	0.72	Wapiti	IM	0.70
Gerenuk	BR	0.52	Buchara deer	IM	0.57	Eland	IM	0.76
White-tailed deer	BR	0.52	Eld's deer	IM	0.58	Roan antelope	GR	0.65
Mule deer	BR	0.59	White-lipped deer	IM	0.63	Forest buffalo	GR	0.73
Swamp deer	BR	0.71	Rusa deer	IM	0.59	Yak	GR	0.66
Lesser kudu	BR	0.77	Lowland anoa	IM	0.56	Banteng	GR	0.66
Sitatunga	IM	0.69	Red deer	IM	0.68	African buffalo	GR	0.67
Dorcas gazelle	IM	0.55	Reindeer	IM	0.53	European bison	GR	0.61
Goitered gazelle	IM	0.57	Sambar deer	IM	0.66	American bison	GR	0.66
Blue sheep	IM	0.53	Barasingha	IM	0.52	Gaur	GR	0.68
Kameroun sheep	IM	0.53	Père David's deer	GR	0.56	Water buffalo	GR	0.79
Springbok	IM	0.61	Beisa oryx	GR	0.64			
Pampas deer	IM	0.68	Black wildebeest	GR	0.58			
Wild goat	IM	0.48	Hartebeest	GR	0.63			
Saiga antelope	IM	0.53	Scimitar-horned oryx	GR	0.77			
Goral	IM	0.53	Waterbuck	GR	0.65			
Mhorr gazelle	IM	0.52	Gemsbok	GR	0.57			
Pronghorn	IM	0.58	Musk ox	GR	0.58			
Chamois	IM	0.68	Zebu	GR	0.64			
Markhor	IM	0.61	Sable antelope	GR	0.65			

Table 3: **Faecal mean particle size (MPS, mm) and feeding type (FT) of 83 species of ruminants at maintenance requirements (Clauss et al., 2002; Fritz, 2007)**

under 100 kg Species	FT	MPS (mm)	from 100 to 250 kg Species	FT	MPS (mm)	over 250 kg Species	FT	MPS (mm)
Dama gazelle	IM	0.66						
Roundhorn sheep	IM	0.59						
Impala	IM	0.58						
Alpine ibex	IM	0.68						
Mountain goat	IM	0.50						
Fallow deer	IM	0.58						
Sika deer	IM	0.60						
Axis deer	IM	0.62						
Indian blackbuck	GR	0.68						
Mouflon	GR	0.59						
Reedbuck	GR	0.55						
Blesbok	GR	0.48						
Addax	GR	0.56						
Lechwe	GR	0.60						

Table 4: Least squares means of faecal mean particle size (MPS, mm) of 83 species of ruminants at maintenance requirements, and increase of energy output (%) during mean lactation of 28 species of ruminants

Body size	under 100 kg	100 to 250 kg	over 250 kg
Faecal MPS (mm)[1]	0.59[a] (SE 0.014)	0.68[b] (SE 0.017)	0.80[c] (SE 0.024)
Increase of energy requirements due to lactation (%)[2]	142[a] (SE 14.8)	102[ab] (SE 29.6)	64.3[b] (SE 20.90)
Increase of MPS due to lactation (%)	15.5	12.2	8.5
Estimated faecal MPS during lactation (mm)	0.68	0.77	0.87

[1]P-values MPS (mm): under 100 kg vs. 100 to 250 kg = 0.0002; under 100 kg vs. over 250 kg = <0.0001; 100 to 250 kg vs. over 250 kg = 0.0005
[2]P-values increase in energy output (%): under 100 kg vs. 100 to 250 kg = 0.4506; under 100 kg vs. over 250 kg = 0.0141; 100 to 250 kg vs. over 250 kg = 0.5574

4. Discussion

4.1 Energy output via milk

The energy content of milk is determined by its fat, protein and lactose contents. Fat contains more energy (39 kJ/g) than protein (23 kJ/g) and lactose (18 kJ/g). Due to the osmotic characteristic of sugar, a high proportion of lactose relative to fat and protein leads to a low dry matter content of milk. In consequence a high energy content of milk is usually related to a high amount of fat (and to a lesser degree protein) relative to lactose. Species can be ranked along an axis defined by the two extremes of lactation strategies: Producing small amounts of high energy milk or producing high amounts of low or medium energy milk. A broad data set was used in this study; in consequence this meant a somewhat heterogeneous data structure since for some species numerous samples with a variety of variables were available, while for others only data from a few animals or stages of lactation was found. The

variables used were body weight of the animals, the milk components fat, protein and lactose and mean daily milk yield. Especially with milk yield there are some gaps in the data set, which had to be filled by calculated values.

Hardly any data on energy contents estimated via calorimetry exist for the milk of the different species. In the past several groups reflected on the best way to determine energy content of milk by the three major organic components without using bomb calorimetry (Tyrrell and Reid, 1965; Nostitz and Mielke, 1995). Nostitz and Mielke (1995) compared the results of two trials (assay of fat, protein and lactose contents as well as calorimetric determination of milk energy) with strongly varying milk samples of 16 animals of the breed black pied dairy cattle, and the samples of a rather homogenous herd of the same breed with the equations of different authors (Gaines and Davidson, 1923; Tyrrell and Reid, 1965; 1984). The values determined by calorimetry were compared to the calculated values of the regression equations. As most qualified for the purposes of this study an equation was considered that includes the concentration of fat, protein and lactose. The precision of the considered equations increases if protein content is included in addition to fat. In the trials of Nostitz and Mielke (1995) the integration of milk lactose content did not result in an increase of accuracy, because the lactose content in milk is almost constant during lactation within a species. However, to compare different species it is necessary to use all three variables which all differ strongly between species. In a next step, data is needed on daily milk yield (kg/d), for an accurate determination of daily energy requirements during lactation. Not from all species these data have been as precisely ascertained as it is standard for domestic animals, because of the obvious challenge of quantifying milk output in wild animals. The methods to determine milk yield were weigh-suckle-weigh procedure (Devendra, 1980; Taylor et al., 1990; Garcia et al., 1999), timed-milking procedure (Linzell et al., 1969; Doney, 1979), isotope dilution

procedure (Yagil and Etzion, 1980; Oftedal, 1981; Reese and Robbins, 1994), hand milking (Bouwman and van der Schee, 1978; McKenzie and Anderson, 1979; Smolders et al., 1990; Guo et al., 2007) as well as conclusions from the daily feed intake of artificially reared young (Pinter, 1963; Hagenbeck, 1969). Although many different methods of milk yield determination were permitted in this study, there were still gaps in the data set. The equation of Hanwell and Peaker (1977) based on data of 19 species had to be used to fill these by estimating the approximate daily milk yield from BW, assuming a constant allometric relation to daily milk output.

4.2 Increase of energy requirements during lactation

Energy requirements for lactation were put into relation to FMR (Nagy, 1987; Robbins, 1993) for a quantification of the expectable increase in food intake related to the increased energy requirement. The FMR was calculated as basal metabolic rate multiplied by 1.75 plus 15% added for free ranging conditions (Kleiber, 1961; Blaxter, 1989; Robbins, 1993). Following Robbins (1993) it includes the basal metabolic rate, heat increment of feeding and energy requirements due to activity and thermoregulation. Another way was described by Nagy (1987) who calculated the FMR of diverse species by different exponential functions. The outcomes are on average 21.5% higher than Robbins stated. In this study the calculation of FMR was done according to Blaxter (1989) and Robbins (1993), and subsequently requirements for milk production were added. This approach allows a differentiated view over all species in the study, with strongly varying lactational or reproductional strategies, and shows the increase of energy requirements during lactation that has to be balanced by animals via increased food intake.

4.3 Particle size reduction – mechanisms

To approach the question how an increase of food intake, efficiency of masticatory apparatus and energy status of an animal cohere, it has to be clarified to which degree the size of faecal particles is determined by comminution or other processes like bacterial fermentation or gut movement. This issue was discussed by many groups and it was shown that particle size distal of the rumen does not differ much from faecal particle size (Grenet, 1970; Poppi et al., 1980b; Uden and Van Soest, 1982; Martz and Belyea, 1986). Other authors arrived at similar results for the analysis of samples from the oesophagus, ileum and faeces of fistulated horses (Meyer et al., 1986), and for samples from stomach and faeces of kangaroos (Freudenberger, 1992). These results are in agreement with McLeod and Minson (1988), who defined that approximately ~80% of total particle breakdown is a result of chewing, and with Wilson et al. (1989a; 1989b) who ascertained that particle width is influenced by microorganisms and chewing, while particle length is almost exclusively influenced by masticatory movements. It must be mentioned that studies working with *in situ* incubation arrived at much higher values (up to 50%) for microbial degradation and physical abrasion (Nocek and Kohn, 1988; Bowman and Firkins, 1993). Indeed it remains unresolved to what extent the long incubation period of 100 hours and friction between particles and fibre bags artificially increased the results on particle size comminution.

4.4 Faecal particle size at different intake levels

For an estimation of the influence of lactation on food comminution, data on faecal particle size at maintenance and at higher intake levels are necessary. While a broad data source on MPS at maintenance requirements is available mainly from two comprehensive studies (Clauss et al., 2002; Fritz, 2007), only data from few studies

and only on ruminants is available on the influence of intake on particle size. If only studies are considered that give data in a way that allows quantification according to Kovács et al. (1997a; 1997b), data is restricted to large ruminants (cattle). In consequence, this study could deal with ruminating herbivores only, and attention was directed on mean faecal particle size.

4.5 Influence of body weight

In their seminal contribution, Hanwell and Peaker (1977) found a decreasing energy output with body weight (energy output in milk [MJ/d] = 0.72 * $BW^{0.69}$), indicating a decrease of investment in lactation relative to BW. This was confirmed by data of Oftedal (1984), who reported an allometric relation of energy output via milk of 83.2*$BW^{0.73}$ for ungulates. Allometric regressions based on the data gathered for this study (excluding those milk yield which was estimated via the Hanwell and Peaker (1977) equation) arrived at a comparable allometric coefficient for daily milk yield, while for energy output via milk the coefficient was considerably lower in this study.

Table 5: Allometric equations for milk yield and energy output via milk

Milk yield [g/d]	0.084 x $BW^{0.77}$	(Hanwell and Peaker, 1977)
	0.070 x $BW^{0.74}$	this study
Energy output via milk [MJ/d]	0.532 x $BW^{0.69}$	(Hanwell and Peaker, 1977)
	1.257 x $BW^{0.46}$	this study

In general, data of this study also support a trend of lower energy/milk output (relative to BW) at higher BW for ruminants (Table 4), where a lower energy output was confirmed for the group of highest BW (>250 kg) compared to that of lowest BW (<100 kg). In consequence, the increase of particle size due to lactation can be

considered to be less pronounced in large compared to small animals. From the perspective of digesta particle size, this should somewhat attenuate the constraint imposed on the digestive process of ruminants by a comparatively large digesta particle size of species of large BW (Uden and Van Soest, 1982; Clauss et al., 2002; Fritz, 2007), as shown in Table 4.

4.6 Influences of ecology and breed

The energy output via milk is not only connected to the body size of an animal, but also to living and environmental conditions. The mountain goat *(Oreamnus americanus)* for example had a relatively low additional energy output of 46% during lactation (BW group average 142%) due to the very small average milk yield of 0.7 kg/day. The same is true for the reindeer *(Rangifer tarandus)* with an additional energy output of 46% (BW group average 102%) and an average milk yield of 0.6 kg/day. Another example is the eland *(Taurotragus oryx)* with 29% additional energy output (BW group average 64%) and a milk yield of 1.5 kg/day.

On the other hand, animals bred for milk production like dairy cattle *(Bos taurus)* or buffalo *(Bubalus bubalis)* are with a plus of 118% and 141% in excess of the rest of the group (BW group average 64%) because of their high milk yield (13.7 and 10.6 kg/day). Obviously, originally all of the milk produced was used to nurse the young (Isaac, 1962). Domestication caused an increasing shift towards special products like meat or milk. During the last 150 years a massive gain of milk yield per cow was reached by genetic selection and improved feeding conditions (Haenlein, 2007).

4.7 Importance of chewing for digestion

Obviously there is a link between energy requirements/food intake, chewing behaviour, and faecal particle size of an animal. This link can be characterised by taking a closer look on digestion strategy of herbivores. They had to develop a way to

overcome the resistant structure of plant cell wall. The microorganisms in fermentation chambers digest the cell walls and make the plant nutrients available for the animal. Different groups discussed the issue under which circumstances the system in the fermentation chambers works best (Dehority and Johnson, 1961; Dehority et al., 1962; Emanuele and Staples, 1988; Ellis et al., 2005). Pond et al. (1984) revealed that mechanical comminution of plant food plays an important role for overall digestion of such material. In addition to the effect of an increase of surface in relation to total volume, the chewing movement leads to a squashing of cell contents which was considered as important as comminution alone (Pond et al., 1984). Simple comminution of plant food without the typical squashing and grinding of chewing teeth effects lower digestibility of plant material (Akin and Burdick, 1981). Besides that, the reduction of total volume leads to an increased food intake (Ellis, 1978). Together these attributes of chewing movement result in a significant plus of energy available for the animal. The amount of energy that can be extracted from food therefore depends on chewing behaviour and comminution activity, but seemingly also depends on body weight of the animal (Table 4). That is coevally an indicator for the amount of energy needed for maintenance and products (lactation). Body size appears positively correlated to particle size in faeces but negatively related to body weight-related metabolic requirements for lactation. Lower body size accompanies with smaller faecal particles and higher energy output during lactation, whereas the differences between groups at lactation were not statistically significant. Some significant data gaps became overt in the course of the data collection for this study. Besides daily milk yield of groups like elephants or tapirs, this is particularly true for the influence of food intake on digesta (faecal) particle size as realized by the animal: Systematic data on non-ruminants was found to be virtually absent from literature, and even data on ruminants was largely restricted to cattle. From this

background, data of the following chapters filling gaps on small ruminants (goats) and rabbits are of particular relevance.

Major findings:

- The MPS increases due to lactation by between 8.5 to 15.5% and is associated with the body weight of the animal.

- Animals with large body weight have a lower increase of total energy requirements (and therefore a lower estimated increase of MPS) due to lactation compared to animals with small body weight.

- The higher DM intake of food during lactation causes increased MPS in the digestive tract, which has the potential to lower digestibility of food.

Chapter 2

Influence of intake level on faecal particle size and digestive variables in lactating goats

Abstract

Significant increases in food intake as occurring during lactation influence digestive variables like digesta retention time and digesta particle size, both relevant for digestibility of the diet. This study evaluated the effect of an increase in intake (1x, 2x and 3x maintenance level) in dairy goats, measured at the respective stages of their lactation cycle. The animals were fed a diet of 50% concentrate and 50 % chopped grass hay. Digestive variables measured were mean retention time (MRT) of particles and solutes (MRTparticle and MRTsolute), digestibility of organic matter (OM) and cell wall (neutral-detergent fibre not assayed with a heat stable amylase and expressed exclusive of residual ash; NDFom), mean particle size (MPS), dry matter (DM) gut fill (calculated) and digestible organic matter intake (DOMI). An increasing intake lowered MRTparticle (values always in the order low, medium, high intake: 71 ± 8.9; 47 ± 4.8; 39 ± 2.4 h), OM digestibility (68 ± 2.1; 65 ± 1.1; 59 ± 2.1%) and NDFom digestibility (49 ± 3.4; 47 ± 2.7; 40 ± 2.9%) and increased MPS (0.53 ± 0.02; 0.55 ± 0.02; 0.59 ± 0.02), gut fill (1866 ± 107; 2474 ± 71.8; 3178 ± 161 g DM) and DOMI (550 ± 17.1; 1081 ± 17.3; 1487 ± 53.5 g/d). Polynomial contrast analyses indicated a linear effect in all cases. Based on linear regression, the results indicate a decrease of MRTparticle of 16 h/unit of intake above maintenance (UIAM) and an increase of MPS of 0.08 mm/UIAM. The resulting decrease in digestibility of 4.1%/UIAM (OM) and 4.6%/UIAM (NDFom) is in line with estimates of a decrease of digestibility by 4%/UIAM for cattle.

1. Introduction

In many aspects, the digestive process in ruminants represents one of the most elaborate among large herbivores. This is true in key features for herbivores like mean retention time (MRT) of digesta (Pearson, 2006; Clauss et al., 2010; Steuer et al., 2011) , and also digestibility of organic matter (OM) or fibre (Colucci et al., 1982; Foose, 1982; Pearson, 2006).

A microbial community capable of fibre digestion is present in most herbivores. Besides the location of the fermentation chamber (forestomach, allowing digestion of the developing microbial mass), ruminants are characterised by intensive comminution via re-chewing of ruminal contents in combination with the selective retention and sorting mechanism of the forestomach (Clauss et al., 2010). Factors affecting passage from the reticulorumen are size (length and width) (Martz and Belyea, 1986, Poppi et al., 1980, Welch, 1982), and specific gravity and buoyancy of particles (desBordes and Welch, 1984; Ehle, 1984; Ehle and Stern, 1984; 1986; Kaske and Engelhardt, 1990; Schettini et al., 1999), the latter increasing related to changes in hydration, ion-exchange and cell destruction (Hooper and Welch, 1985; Kaske and Engelhardt, 1990). In short, particle size and density are subject to changes during the digestion process attributed to chewing during rumination and microbial degradation. An important consequence of this elaborate system is that the food comminution process results in particularly fine faecal particles in ruminants (Fritz et al., 2009).

While any herbivore works most efficiently (in terms of digestibility) at maintenance intake level, during periods of higher requirements such as growth and lactation, a larger amount of food has to be processed, partly compromising digestive processes. Under such circumstances, particularly "ultimate" chewers as ruminants experience

constraints. While such periods of increased energy requirements can include further limitations (like reduced space availability for digestive organs in the body cavity due to the growth of the foetus during the last month of gestation, resulting in a reduced rumen volume (Forbes, 1970; Weston, 1988), or changes in intake due to hormonal changes (Forbes, 1986)), the increase in intake represents the by far most significant challenge: For a given time period like a day, more material needs to be chewed and pass the guts of the animal. In general, higher food intake means less chewing per unit of food (Welch, 1982), and faster passage of food (Lechner-Doll et al., 1991). In consequence, increased intake can be safely expected to lead to an increase in digesta particle size, potentially contributing to a reduction in digestibility.

Lactation is considered the most significant period in terms of increased energy requirements. They reach highest levels and have to be met by a largely increased intake to avoid excessive weight loss due to the use of body stores for milk production (Sadleir, 1980; Thaker and Bilkei, 2005). A self-evident rule of diet planning for dairy cattle indicates that the food processing machinery is approaching its limits during lactation: Although the feeding of significant amounts of forage to ruminants is necessary to keep their digestive processes within the physiological limits (De Boever et al., 1990), high-yielding animals cannot be fed on a forage diet alone, but need to be given a certain proportion of concentrate (not only high energy content, but also low processing demands) to be able to ingest (and comminute) sufficient energy for high milk yield.

While the direction of changes triggered by a higher intake is clear, the size of the effect comes into focus: How much is retention time decreased and how much is particle size increased by food intake? This also describes the flexibility of the response of the animal to constraints for digestive processing (Clauss et al., 2007b). Some studies have focused on the effect of intake level (1 and 2 fold maintenance)

on a range of digestive variables at a constant diet, like Shaver et al. (1988), Okine and Mathison (1991b), Kovács et al. (1997a) and Kaske and Groth (1997). Most have been performed on large ruminants (exception: sheep in Kaske and Groth (1997)). Animals of smaller body size have been shown to have particularly high investments into lactation as related to their metabolic body size (Linzell, 1972; Hanwell and Peaker, 1977). As outlined in chapter 1, this fact plus the general lack of data in small ruminants (particularly concerning food comminution) make goats a particularly rewarding study object.

In this study, the effect on digestion of an up to 3-fold increase of intake above maintenance was investigated in goats at different stages of lactation. The response of relevant digestive variables like MRT, digestibility, gut fill and – as a particularity of this study – also faecal particle size was evaluated.

2. Materials & Methods

2.1 Animals, housing and diet

Eight female Saanen-type goats (German Improved White Goat breed; initial live weight 60 kg) were fed a diet with a constant proportion of 50% chopped grass hay (21.0 ± 3.46 mm discrete mean (dMean)) and 50% concentrate (0.82 ± 0.16 mm mean particle size (MPS)) at three food intake levels (2.73, 1.82, and 0.91 kg dry matter (DM) per day) representative for different stages in lactation (peak lactation, late lactation, and dry). The periods of trial were conducted at day 42-50 (high intake), day 159-167 (medium intake), and after lactation/before new pregnancy (low intake). Table 6 shows the nutrient and chemical composition of hay and concentrate. All goats were adult and without known dental problems. The animals

were fed twice daily at 07:30 and 14:30, water was available ad libitum. During faecal collection the goats were kept in metabolism crates.

Table 6: Nutrient and chemical composition of grass hay and concentrate; Means ± SD are based on 3 observations for each value

Nutrient composition		Grass hay	Concentrate
Lucerne meal			32.9
Wheat middlings			13.9
Oats grain			10.7
Wheat grain			9.3
Soybeans	% of DM		8.7
Barley			5.9
Sunflower expeller			5.9
Beet pulp			5.2
Oats huskmeal			3.0
Molasses			0.9
Chemical composition			
Ash		98 ± 27.1	90 ± 0.6
CP		112 ± 26.5	170 ± 5.0
EE		26 ± 4.6	44 ± 0.6
NDFom	g/kg DM	501 ± 28.1	315 ± 5.5
ADFom		325 ± 12.7	188 ± 3.2
ADL		52 ± 4.0	47 ± 4.4
Starch		-	188 ± 5.1
24 h gas production	ml/200 mg DM	45.1 ± 1.7	49.0 ± 1.4
ME_{rum}	MJ/kg DM	9.3 ± 0.2	10.8 ± 0.1

DM: dry matter
CP: crude protein
EE: ether extract
NDFom: neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash
ADFom: acid detergent fibre expressed without residual ash
ADL: acid detergent lignin
ME_{rum}: metabolisable energy for ruminants

2.2 Experimental procedures

The length of each experimental period was 22 days including a 14 day adaptation period and an 8 day period for collecting samples. Two markers for estimation of digesta retention time were offered and ingested deliberately at day 15 with a small proportion of morning concentrate (15 g of Cr-mordanted fibre (1-2 mm; marker for small particles) and 1.1 g of cobalt(III)ethylene diamine tetraacetate (Co-EDTA; marker for solutes) per animal (Udén et al., 1980)). Samples of feedstuffs were taken on 33 occasions during the sampling period. Faecal samples were collected for 8 days at intervals of 4 h (day 1-3), 6 h (day 3-5), 8 h (day 6-8) and finally 12 h (day 9). Samples were dried directly and kept separately for analysis, while for nutrient and faecal particle size analysis a pool-sample was created from 10% proportions of each sampling interval and stored frozen.

The goats were milked twice daily. Milk samples for fat, protein and energy analysis were taken weekly as a pooled sample of morning and evening milking.

2.3 Analytical methods

2.3.1 Mean retention time

Faecal samples were consecutively dried for 24 h at 60°C and 100°C and ground (1 mm sieve). For Cr and Co analysis, 0.2 g of the milled sample was weighed into vessels and 4 ml of 65% HNO_3 plus 2 ml of 30% H_2O_2 were added. Samples were then macerated for 1 hour using a microwave (CEM; MarsXpress). After filtration the atomic absorption spectroscopy (AAS) was used for analysis.

The MRT in the total gastro-intestinal tract (GIT) was calculated following Thielemans et al. (1978):

$$MRT = \sum (c_i \times dt \times t_i) / \sum (c_i \times dt)$$

where MRT = mean retention time [h], ci = marker concentration in the faeces at time i [mg/kg DM], dt = length of time interval which represents the marker concentration ci [h] and ti = time after marker application (middle of time interval which represents the marker concentration ci) [h].

2.3.2 Calculation of dry matter gut fill

Dry matter gut fill was estimated according to Hollemann and White (1989):

$$V = Vn + \frac{Vn \ x \ A}{2(1-A)}$$

where V = DM gut fill [g DM], A = the (fractional) digestibility of the diet and Vn = the indigestible DM gut fill [g DM] (Vn = faecal output [g DM/h] * MRT [h]).

2.3.3 Chemical composition

For chemical analysis, faecal samples were freeze-dried. Feed and faecal samples were milled through a 1 mm sieve. Chemical analysis was done according to VDLUFA (2007) for DM (method 3.1), ash (method 8.1), crude protein (CP) (method 4.1.2; Dumas method; instrument FP-328, LecoEnterprise, St. Joseph, Michigan, USA) and starch (method 7.2.3; enzymatically). Ether extract (EE) was analyzed after acid hydrolysis using an ANKOM Extractor (Ankom technology, Macedon, NY, USA) according to AOCS (2009), Am 5-04 official method. Neutral detergent fibre (NDFom; not assayed with a heat stable amylase and expressed exclusive of residual ash), acid detergent fibre (ADFom; expressed without residual ash), and acid detergent lignin (ADL) were analysed following Van Soest and Robertson (1985). Feed samples were also evaluated with the Hohenheim gas test; that measures in vitro the 24 h gas production under ruminal conditions (Menke et al., 1979).

The metabolizable energy for ruminants (ME_{rum}) of the concentrate was calculated following GfE (2009)

ME_{rum} (MJ/kg DM) = 7.17 - 0.01171 ash + 0.00712 CP + 0.01657 EE

+ 0.00200 starch - 0.00202 ADFom

+ 0.06463 gas production (24 h)

and ME_{rum} of hay was calculated following the formula for grass products of the (GfE, 2008).

ME_{rum} (MJ/kg DM) = 7.81 + 0.07559 gas production (24 h) – 0.00384 ash

+ 0.00565 CP + 0.01898 EE – 0.00831 ADFom

In both formulas, units are g/kg DM for ash, CP, EE, starch and ADFom, and ml/200 mg DM for gas production.

2.3.4 Faecal particle size

Faeces, hay and concentrate were wet sieved (sieves of 16, 8, 4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm mesh size) according to Kovács et al. (1997a). All samples were soaked in water before sieving to release individual particles (hay for 10 min, concentrate for 30 min, faeces over night in a fridge). Sieving was conducted using an electric sieve shaker for 10 min with a water flow of 2 l/min sprayed on the top sieve. The amplitude of the sieve shaker was adjusted at 2 mm. The MPS was calculated from the distribution of the particle fractions on the sieves by an exponential model developed by Fisher et al. (1988) using the non-linear model procedure of SAS 9.2 (SAS Institute, 2007).

$$R = 100 \times e^{-(s^a - bs)}$$

R = particle size data expressed as cumulative percent weight oversize

s = screen size [mm]

a and b = estimated constants

The model was adapted following Kovács et al. (1997b) to enhance the number of steps between the sieve with the largest and the smallest pore size for the calculation of MPS

$$\text{Mean size} = \frac{\sum_{i=1}^{1000} step \ x \ R' \ x \ (0.063 + i \ x \ step)}{\sum_{i=1}^{1000} step \ x \ R'}$$

where Step = (L − 0.063) / 1000, L = double the aperture of the largest sieve [mm] and R' = first derivative of R (cumulative percent weight oversize); R' = 100 x $e^{(bs-s^\wedge a)}$ x (b-as$^{(a-1)}$)

The dMean was calculated according to Fritz et al. (2012) for hay samples. There was a major amount of particles that remained on the sieve with the biggest pore size which made the MPS smaller. This effect was balanced by using the length of the biggest particle as upper limit in the calculation of the dMean.

2.3.5 Milk

The protein content was analysed following the official methods § 64 (LFGB, 2009) using the Kjehldahl treatment. The fat content was measured following Gerber. The energy content of the milk was analysed by bomb calorimetry.

2.3.6 Statistics

Data were tested for the influence of feed intake via ANOVA, according to the equation:

$$Y_{ij} = \mu + \alpha_i + \varepsilon_{ij}$$

where

Y_{ij} = the observed response (dry matter intake);

μ = the population constant, common to all observations;

α_i = the effect of intake level (i=1-3);

ε_{ij} = the residual error.

Polynomial contrasts (Bewick, 2004) were used to test for linear and quadratic effects. If both were found to be significant, the contrast (linear or quadratic) with the considerably (at least one order of magnitude) lower P-value was considered to be present (Abdelqader et al., 2009).

3. Results

A clear influence of food intake level on digestive variables was evident from the data. Mean values and standard deviation at different periods are shown in Table 2, indicating an increasing effect for MPS, gut fill and digestible organic matter intake (DOMI), and a decreasing effect for MRTparticle, MRTsolutes, selectivity factor (SF) and digestibility of OM and NDFom. The effect of intake was linear in all cases.

Table 7: Influence of intake on digestive variables

	low intake	medium intake	high intake	P ANOVA	Plin	Pquad
MPS (mm)	0.53 ± 0.02	0.55 ± 0.02	0.59 ± 0.02	<0.0001	<0.0001	0.4906
MRTparticle (h)	71 ± 8.9	47 ± 4.8	31 ± 2.6	<0.0001	<0.0001	0.0006
MRTsolute (h)	48 ± 4.0	35 ± 4.3	31 ± 2.4	<0.0001	<0.0001	0.0041
SF	1.5 ± 0.1	1.3 ± 0.1	1.3 ± 0.2	<0.0062	<0.0030	0.1724
OM dig. (%)	68 ± 2.1	65 ± 1.1	59 ± 2.1	<0.0001	<0.0001	0.0218
NDFom dig. (%)	49 ± 3.4	47 ± 2.7	40 ± 2.9	<0.0001	<0.0001	0.0834
Gut fill (g/kg BW)	1866 ± 106.8	2474 ± 71.8	3178 ± 161.0	<0.0001	<0.0001	0.3000
DOMI (g/d)	550 ± 17.1	1081 ± 17.3	1487 ± 53.5	<0.0001	<0.0001	0.0006

MPS: mean particle size (mm)
MRTparticle/ solute: mean retention time of particle/ solute phase (h)
SF: selectivity factor
OM dig.: digestibility of organic matter (%)
NDFom dig.: digestibility of neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash (%)
DOMI: digestible organic matter intake (g/d)
Plin, quad: P-value of linear and quadratic effect (polynomial contrasts)

Linear regressions of absolute values with intake level indicated an increase of 0.03 mm for MPS and of 656 g DM for gut fill per unit of intake above maintenance (UIAM). The OM digestibility was estimated to decrease by 4.1%, while MRTparticle was reduced by 16 h/UIAM (Table 8). Expressed as percentage change of initial value, MPS increased by 5.7% and gut fill by 35% per UIAM, while OM digestibility decreased by 6.1% and MRTparticle by 22% per UIAM.

Table 8: Linear regressions of percentage and absolute changes of digestive variables at different intake levels

	Linear regression of percentage change (level 1 = 100%)	R^2	P	Linear regression of absolute change	R^2	P
MPS (mm)	5.7x + 94	0.5189	< 0.0001	0.03x + 0.5	0.6239	< 0.0001
MRTparticle (h)	-22.2x + 118	0.8407	< 0.0001	-16.04x + 84.3	0.7812	< 0.0001
MRTsolute (h)	-17.6x + 115	0.8330	< 0.0001	-8.407x + 54.6	0.7614	< 0.0001
SF	-6.91x + 105	0.3451	0.0025	-0.1071x + 1.582	0.3017	< 0.0001
OM dig. (%)	-6.1x + 107	0.7462	< 0.0001	-4.121x + 72.3	0.7534	< 0.0001
NDFom dig. (%)	-9.2x + 111	0.6375	< 0.0001	-4.559x + 54.4	0.6109	< 0.0001
Gut fill (g/kg BW)	35.4x + 64	0.9395	< 0.0001	656x + 1194	0.9570	< 0.0001
DOMI (g/d)	85.4x + 18	0.9836	< 0.0001	469x + 102	0.9874	< 0.0001

MPS: mean particle size (mm)
MRTparticle/ solute: mean retention time of particle/ solute phase (h)
SF: selectivity factor
OM dig.: digestibility of organic matter (%)
NDFom dig.: digestibility of neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash (%)
DOMI: digestible organic matter intake (g/d)
Plin, quad: P-value of linear and quadratic effect (polynomial contrasts)

The part of the particle fraction smaller than 0.063 mm (microorganisms, cells from the GIT and very small food particles) was at 23.5 ± 2.5% at low, 22.8 ± 1.72% at medium and 22.0 ± 1.81% at high intake. Average lactation curve turned out as expected with great increase of milk yield in the first two weeks of lactation up to 4 kg per day, followed by a slow decrease until day 116 (3.6 kg/day). The decline of daily milk yield down to 2.6 kg/d was related to the switch from high to medium intake level. After day 121 again a slow decrease in daily milk yield can be observed down to 2.1 kg/day. While body weight and maintenance energy requirements remained nearly constant during trial period, total energy requirements increased markedly due to lactation by 85.2 % from low to medium, and by 161.1 % from low to high food intake.

Table 9: Energy requirements of lactating and dry goats (Maintenance requirements for goats 450 kJ/kg BW$^{0.75}$ according to GfE (2003))

Intake level	low	medium	high
BW (kg)	58.0	58.1	60.7
food intake (kg DM/day)	0.91	1.8	2.7
milk yield (kg/day)		2.1	4.0
milk DM (g/kg)		111	110
CP in milk (g/kg DM)		256	244
EE in milk (g/kg DM)		285	283
milk energy content (MJ/kg)		2.49	2.46
Maintenance energy requirements (MJ/day)	9.5	9.5	9.8
Energy requirements for milk production (MJ/day)		8.7	16.4
Total energy requirements (MJ/day)	9.5	18.2	26.2
Multiples of maintenance		1.9	2.6

BW: body weight
DM: dry matter
CP: crude protein
EE: ether extract

4. Discussion

The digestive process in herbivores can be understood as the interplay of variables like intake, retention time, food comminution and gut fill, influencing each other and resulting in variables relevant for the performance of an animal, like digestibility or – even more relevant – intake of digestible OM. Effects of these factors can be studied particularly well in trials with varying intake levels.

4.1 Methodological considerations

4.1.1 Trial design

In the planning of a trial it is generally desirable to distribute treatment levels equally over all trial periods. The intention of such design is to level out any potential effect of trial period, and the approach allows the quantification of such effect in the later statistical analysis. Colucci et al. (1989; 1990) measured the effect of species (cattle and sheep), intake (maintenance and ad libitum) and type of diet (forage:concentrate ratios) on passage rate and digestibility. However, options for designing trials in this

way are limited if, like in this study, lactating individuals of a species with a significant seasonal component in breeding like goats are in the focus.

Since the relation of feed intake motivation (hormonally triggered via mechanisms of medium to long term feed intake regulation) and actually ingested food can be considered critical (particularly regarding the initial chewing while feeding) differences in this relation are expected to have the potential to influence results.

4.1.2 Size of the increase in feed or DM intake

Besides examples like huskies, experiencing a 3- to 4-fold increase in energy requirements when working as sledge dogs under harsh environmental conditions (Meyer and Zentek, 2001), lactating dairy cows are among the first candidates for a maximal increase in energy requirements; in high yielding cows (35 L milk/day), the energy requirements are raised >4-fold maintenance level (Kirchgeßner et al., 2011). However, the corresponding increase in food intake will be on the level of 3- to 4-fold maintenance only, since animals will mobilize body stores to some extent to meet their energy requirements. In this trial, starting from maintenance level, a 3-fold increase in food intake was achieved in dairy goats without acceptance problems. Even at the highest intake level, the daily portion was ingested completely by all animals.

It has to be kept in mind that such increases will probably not be possible on a forage-only diet, but only in diets with significant concentrate proportions. Apparently, chewing capacity becomes limiting at some level of forage intake per day. Long forages (lucerne or grass) require chewing activity of steers of at least 60 up to >100 min/kg DM, while concentrate (ground material) typically induces chewing times of 10-20 min/kg DM (Sudweeks et al., 1981). In consequence, the forage proportion of the diet used becomes important when comparing studies. Besides the principal

distinction between ground concentrates and long fibrous forages, forage type can also take some influence (e.g. Sudweeks et al. (1975; 1981)), legumes like clover requiring less chewing effort than grasses for example.

In this study, faecal particle size was used as a measure for food comminution. However, it should not be forgotten that average particle size in the rumen probably has an even higher significance for digestion, since a major part of digestion occurs there. In trials measuring both, Udén and Van Soest (1982b) found values of 1.5 and 0.5 mm for rumen and faeces of goats respectively; Kovács et al. (1997b) report a slightly larger difference of 1.8 (rumen) vs. 0.5 mm (faeces) at steers. Based on these studies, a factor of 3.3 (3.0-3.6) appears to be a reasonable value for calculatory estimates of average rumen particle size from faecal data.
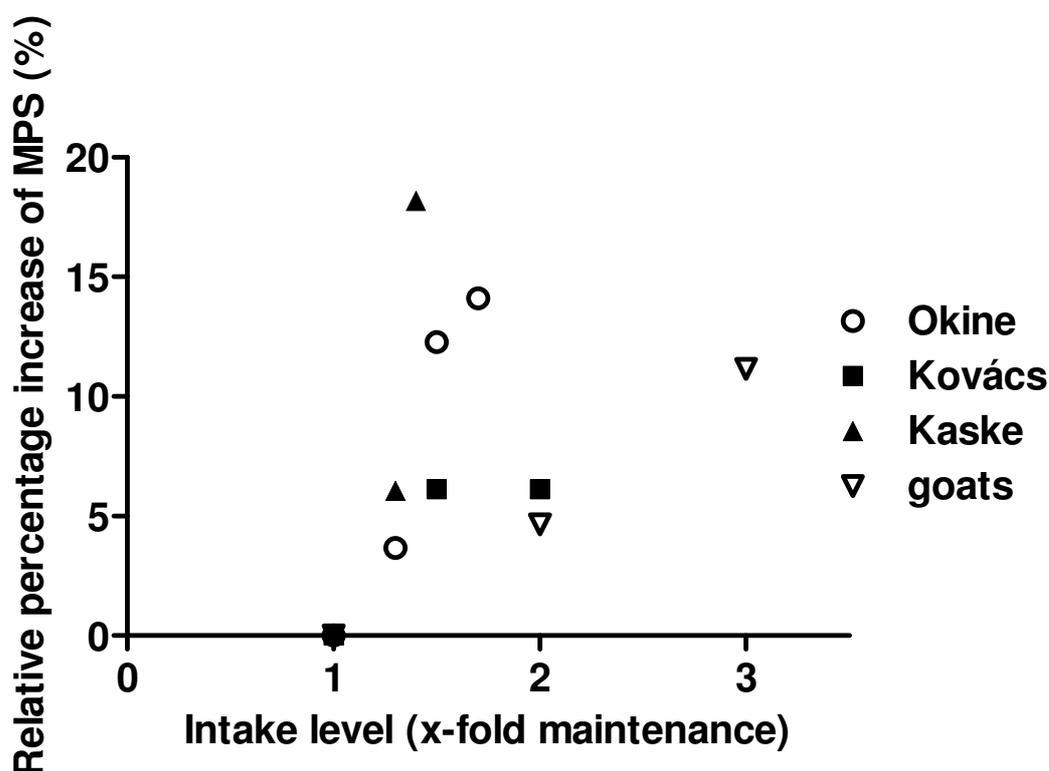
Fig. 8: Percentage increase of MPS at different food intake levels for cows fed a forage-based diet with an increase of 3.7, 12.3, 14.1% (Okine and Mathison, 1991b), for steers fed a mixed diet (silage + concentrate) with an increase of 6.1% (Kovács et al., 1998), for sheep fed long hay with an increase of 6.1, 18.2% (Kaske and Groth, 1997) and the goats fed a mixed diet with an increase of 4.7, 11.2% (hay and concentrate)

4.2 Size of corresponding changes - Comparison of ruminant studies

While many studies have investigated changes of digestion with intake level, far less have included changes in faecal particle size (Table 10/ 11), a variable of particular interest in this study. Probably changes in digestibility have been investigated best. In models a decrease of digestibility by 4% per multiple of maintenance intake was estimated (NRC 1978, 1989). Newer models use a variable factor , while in (NRC (2001), as cited in GfE (2003). The results for goats of this study (a decrease of digestibility of 4.1%/UIAM for OM and of 4.6%/UIAM for NDFom; in units of digestibility) are in line with such considerations. While the drop in OM digestibility in the study of Okine and Mathison (1991b) of 13% is surprisingly high, those found in the same study for NDFom (3.6%) or by Kaske and Groth (1997) for OM (3.7%) support the estimation of 4%/UIAM. What can be expected is that the effect should be larger in cell wall dominated feeds than in those with a higher fermentation rate (Tyrell and Moe, 1975).

For retention times, Lechner-Doll et al. (1991) give a rough estimation that doubling intake will result in a 20-40% decrease of MRT. Between different studies, some variation are present (e.g. related to diet type or the range of intake levels investigated, e.g. 0.5- to 2-fold maintenance vs. 1- to 3-fold maintenance): In this study, a rather comprehensive decrease of 16 h/UIAM was estimated for MRTparticle, while in others, considerably lower values were estimated (3 h/UIAM in Okine and Mathison (1991b) and 7 h/UIAM in Kaske and Groth (1997).

Table 10: Comparison of changes in digestive variables with increasing food intake

Intake*	Animal	MPS (mm)	MRTparticle (h)	OM dig. (%)	NDFom dig. (%)	Rumination chews	Study
1	dairy cows	1.63[A]	59.4[a]	76.4	60.1	24.5 min/kg DMI	(Okine and Mathison, 1991b)[1]
1.3		1.69[A]	59.1[a]	73.7	58.6	25.9 min/kg DMI	
1.5		1.83[A]	58.8[a]	71.6	59.3	23.7 min/kg DMI	
1.7		1.86[A]	56.9[a]	66.7	57.1	23.3 min/kg DMI	
1	steers	0.49[B]	55.3[b]			24.6 min/kg DMI[e]	(Kovács et al., 1997b; Rothfuss, 1997)[2]
1.5		0.52[B]	44.5[b]			25.1 min/kg DMI[e]	
2		0.52[B]	39.3[b]			26.5 min/kg DMI[e]	
1**	sheep	LP 5.3[C] SP 49.6[C]	63.9[c]	57.6		27.7 chews/g DMI	(Kaske and Groth, 1997)[3]
1.3		LP 7.5[C] SP 47.8[C]	47.3[c]	55.9		25.7 chews/g DMI	
1.4		LP 9.2[C] SP 49.0[C]	53.5[c]	59.8		24.2 chews/g DMI	
1	dairy cows		F: 66.6[d] C: 40.5[d]		64.9		(Colucci et al., 1982)[4]
3.5			F: 40.5[d] C: 25.8[d]		61.6		
1	dairy cows		F: 42.7[d] C: 30.0[d]		57.4		(Colucci et al., 1982)[5]
2.5			F: 32.7[d] C:22.1[d]		55.9		
1	goats	0.53[B]	71[d]	68	49		This study[6]
2		0.55[B]	47[d]	65	47		
3		0.59[B]	39[d]	59	40		

MPS: mean particle size (mm)
MRTparticle: mean retention time of particle phase (h)
OM dig.: digestibility of organic matter (%)
[*] multiples of maintenance energy requirements
[**] experimental period (EP) I; 60-80 d post conceptionem
[A] Weighted average
[B] Mean particle size (mm)
[C] DM retained on sieves; LP > 1mm pore size, SP > 0.25 mm, Rest < 0.25 mm (% of total DM)
[a] calculated as the reciprocals of the fractional passage rates
[b] Titanium oxide
[c] plastic particles
[d] Cr-mordanted fibre
[e] Means of values measured for 12 h periods (day and night)
F forage; C concentrate
[1] diet: 100% forage (chopped to 6 cm; 40:40:20 bromegrass, timothy, alfalfa)
[2] diet: 43:25:32 ryegrass silage, maize silage, concentrate
[3] diet: 100% forage (long; Lolium spp.)
[4] diet: 16:16:68 maize silage, lucerne haylage, concentrate
[5] diet: 41:41:18 maize silage, lucerne haylage, concentrate
[6] diet: 50:50 chopped grass hay, concentrate

Table 11: Linear regressions of digestive variables at different intake levels in three studies

		MPS [mm]	MRTparticle [h]	OM digestibility [%]	NDFom digestibility [%]	Rumination intensity
Okine and Mathison (1991)	abs	0.36x + 1.26	-3.23x + 63.0	-13.2x + 90.35	-3.60x + 63.72	-2.22x + 27.41[1]
	R^2	0.9298	0.7341	0.9337	0.7115	0.3351
	rel	21.84x + 77.49	-5.43x + 106.0	-17.39x + 118.30	-5.98x + 106.0	-9.09x + 111.90[1]
	R^2	0.9295	0.7325	0.9337	0.7047	0.336
Kaske and Groth (1997)	abs		-7.19x + 60.60	3.73x + 53.07		-11.77x + 40.82[2]
	R^2		0.1500	0.1545		0.9954
	rel		-13.35x + 111.5	6.62x + 92.51		-40.69x + 140.90[2]
	R^2		0.1521	0.1595		0.9953
Kovács et al. (1997a; 1997b)	abs	0.03x + 0.47	-16.0x + 70.37			1.90x + 22.55[1]
	R^2	0.750	0.9608			0.9304
	rel	6.12x + 94.90	-28.90x + 127.20			7.72x + 91.67[1]
	R^2	0.7500	0.9609			0.9304

MPS: mean particle size (mm)
MRTparticle: mean retention time of particle phase (h)
OM dig.: digestibility of organic matter (%)
NDFom dig.: digestibility of neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash (%)
[1] min/ g DM
[2] chews/ g DM

As mentioned in Van Soest (1966) and as cited in Van Soest (1988), faecal particle size must be considered to increase with food intake. A considerably lower increase (5.7%/UIAM) was found in this study compared to others (22% in Okine and Mathison (1991b) and 37% in Kaske and Groth (1997). In contrast, in Kovács et al. (1997a) a much smaller increase was found, happening mainly between the 1-fold and 1.5-fold maintenance levels. For the data on particle sizes it is most obvious that diet composition (concentrate:forage ratio) takes influence on the relation of feed intake and digestive variables. Chewing efforts (total chewing/day) of the different diets based on data of Sudweeks et al. (1981) resulted in chewing efforts for cows of 100 min/kg DM, based on data of Kaske and Groth (1997) at 100% grass hay; 92 min/kg DM, based on data of Okine and Mathison (1991b) at 40% brome grass hay, 40% timothy hay, 20% lucerne hay; 68 min/kg DM based on data of Kovács et al. (1997a) at 43% grass silage, 26% maize silage, 31% concentrates; and 56 min/kg DM based on this study at 50% grass hay, 50% concentrate. While a further standardisation of the relation of faecal particle size and intake regarding the forage level/chewing effort appears logic, it is hampered by the differences in wet sieving methodology (set of sieves), and was therefore omitted in this study.

The boundaries within which a herbivore can function reasonably and the overall robustness of a digestive system regarding increasing intake vary between species (Clauss et al., 2007b). In this context attention may be put to the fact that the changes in the digestive variables are never of the same size than respective change in intake level: Doubling intake does not result in doubling passage rate Lechner-Doll et al. (1991). Herbivores will work only within reasonable boundaries, but within these, additional intake will always pay in terms of increased energy intake, since the additional intake will always highly compensate any decrease in digestibility. In our study, DOMI increased with intake level at a rate of 85% per intake level (Table 8). In

this contribution - for the range of intake levels investigated – changes with intake were estimated to be linear. Given the results of the post hoc tests (estimated significant linear effects for all variables), there is good reason to believe that this is appropriate for the range of intake levels investigated in this study. However, it is also obvious that like in most biological variables the regression line has to approach a maximum at some point, therefore deviating form linearity. Fully exploited chewing capacity is generally considered to be a major factor for an upper intake limit of forage-rich diets.

4.3 Mechanisms at work at the "intake level - digestive variable"- interface

Obviously the variables of physiological output outlined above can be considered to represent the major currency in any evaluation of the effectiveness of a herbivore at different intake levels. However, further understanding of the underlying mechanisms leading to these changes (like chewing behaviour or gut motility) is desirable.

4.3.1 Chewing

In terms of chewing efforts, it is obvious that related to a unit of feed, time spent chewing or number of chews are usually negatively correlated to intake level (Welch, 1982). This is in agreement with the results of Okine and Mathison (1991b) (~9% less chewing time per kg DM per unit of maintenance intake) and Kaske and Groth (1997) (~41% less chews per kg DM per unit of maintenance intake) (Table 10/ 11); interestingly, in the study of Kovács et al. (1997b), an opposite trend was found.

The results of Blanchard (2005) on an increase in chewing frequency at rumination at lactation (= higher food intake) from 1.04 chews/s to 1.21 chews/s may be interpreted as an adaptive response to the higher chewing burden during lactation. The same trend was evident in other studies (Welch and Smith, 1969, 1970, Welch et al., 1970), where chewing rate increases at a higher food intake level.

4.3.2 Passage

Besides food comminution, mechanisms realizing an increased gut passage via changes in gut motility are of interest. In principle, gut passage depends on size and shape (Poppi et al., 1980a), and specific gravity of particles, with maximum passage rate for particles with a specific gravity of 1.2 - 1.4 (desBordes and Welch, 1984, Kaske and Engelhardt, 1990, Welch, 1986). Since density and size are influenced by rumination, the decrease of chews per feed unit at higher intakes should rather induce a prolongation of retention time; since the opposite is the case, other mechanisms must over-compensate this delay in bringing particles in the right condition for rumen outflow. The process accelerating passage may include a component not actively influenced by the animal (like a higher gut fill, leading simply to a higher "pushing out" of particles) or a more active one, including some adaptive changes of the animal´s physiology like a higher gut motility or earlier opening of abomasum. It is generally agreed upon that frequency of rumen cycles is not increased, but rather the amount of outflow per rumen cycle (Okine and Mathison, 1991a). Any of such actions could be triggered by more mechanical stimulation of the rumen wall via more particles and/or via hormonal changes related to the metabolic/reproductive status of the animal.

5. Major findings:

• Intake level had an increasing effect on MPS, DOMI, gut fill; and a decreasing effect on MRTparticle, MRTsolute, digestibility of OM and of NDFom.

• Per level of maintenance, the change of MPS was on the size of 5.7% of the initial value, while MRTparticle decreased by 22% as related to the initial value and digestibility decreased by 4.1% of OM digestibility.

Chapter 3

Food particle processing in rabbits and its relation to intake level

Abstract:

Due to relatively high energy requirements (per unit body mass) and their generally high reproductive output, small herbivores can be expected to experience particular challenges in terms of food processing. Rabbits use the caecum as fermentation chamber and for selective retention of well fermentable substrates, which sets them apart from many other larger hindgut fermenters. In this study the effect of an increase in intake level (1x and 2x maintenance level, representing an intake of 113 and 224 g dry matter/d) on several digestive variables was evaluated at a constant diet of 50% chopped grass hay and 50% concentrate. Digestive variables measured were mean retention time of particles and solutes (MRTparticle and MRTsolute) and mean faecal particle size (MPS). Digestibility of organic matter (OM) and cell wall (neutral-detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash ; NDFom) could only be evaluated for the lower intake. In addition, food particle breakdown was evaluated via particle size distribution in food, different parts of the digestive tract (stomach, caecum, colon) and faeces for maintenance intake. Greater intake decreased retention time (values always in the order low before high intake level: MRTparticle: 31 ± 2.5 h; 19 ± 3.1 h; P=0.0001; MRTsolute: 73 ± 2.2 h; 47 ± 3.2 h; P=0.0012), while MPS was only slightly increased (0.56 ±0.01 mm; 0.59 ±0.02 mm; P=0.073). On the low intake, OM digestibility was 58 ± 2.3%, NDFom digestibility 37 ± 3.6%, and digestible OM intake 60 ± 2.3 g/d. The discrete Mean (dMean) in food (10.8 ± 1.73 mm) was higher than that found within the gut (P<0.0001). The MPS in the stomach (0.68 ± 0.03 mm) was greater than the value in colon (0.59 ± 0.08 mm; P<0.0001) or faeces (0.56 ± 0.01 mm;

P<0.0001). As expected, the smallest particles were found in caecum (0.50 ± 0.01 mm; P=0.0082). While the change in retention time was considerable, the increase in faecal particle size was small when compared to ruminants. Some food comminution may occur after chewing in rabbits; however the effect is on the size of ~2% of total particle comminution only.

1. Introduction

Maintenance energy requirements vary in relation to body size in a way that per unit body mass small herbivores have higher energy requirements for maintenance than larger animals (Kleiber, 1961). These relatively higher energy requirements may represent a particular challenge for small herbivores; although they can afford to select for a diet of higher quality, this feeding strategy is still focused on material relatively low in available energy and nutrients. Typically small herbivores follow the digestive strategy of a hindgut fermenter. The more efficient use of easily digestible nutrients like starch or protein via direct digestion by the animal in the small intestine largely compensates for the disadvantage of hindgut fermentation of extracting less energy from plant cell wall than does fermentation in the forestomachs of e.g. ruminants. Rabbits belong to a particular type of hindgut fermenter (Hintz, 1969), using the caecum as fermentation chamber (Sakaguchi, 2003). To be most successful, besides being selective their digestive strategy depends on a high food intake (Wallage-Drees and Deinum, 1985; Carabaño and Piquer, 1998), and on rapid passage of indigestible components while more digestible components are retained selectively (Björnhag, 1981). This applies to fine particles and solutes and microbes transform these substrates into volatile fatty acids which can be absorbed from the caecum and colon (Björnhag, 1972; Ehrlein et al., 1983). Concurrently large particles leave the caecum fast or do not enter it at all (Udén and Van Soest, 1982b), and are rapidly propelled through the colon and excreted as hard faeces. Rabbits are coprophagic animals (Madsen, 1939; Southern, 1940; Myers, 1955) which reingest the part of their faeces based on caecum content (soft faeces, incorporated directly from the anus) during resting periods. In contrast, the hard faeces are excreted during the active feeding period and are not reingested. Hard faeces contain large

particles and thus poorly digestible fibre (Cheeke, 1999) while soft faeces contain more microbial mass and less fibre (Chilcott, 1985; Sakaguchi, 2003; Pehrson, 2010). Selective retention of small particles and fluid in the caecum allows some microbial fibre digestion while hard faeces are passed through the digestive tract quickly without extensive fermentation. Tufarelli et al. (2010) exposed that different dietary particle sizes influence digestive variables like gut motility, diet digestibility and intestinal morphology significantly. Grinding of diet increases utilisation of diet; however a minimal proportion of 21% of large particles (> 0.315 mm) has been stated as mandatory for maximal performance in rabbits (Nicodemus et al., 1999).

Comprehensive food comminution is important for an effective digestive process in rabbits. Like other variables of digestive physiology this can be assumed to be influenced significantly by intake level. But while some information is available on this topic from ruminants like cattle (Okine and Mathison, 1991b; Kovács et al., 1997a; Kovács et al., 1997b; Kovács et al., 1998) and small ruminants ((Kaske and Groth, 1997); chapter 2), literarily nothing is known on the relations in non-ruminants like rabbits.

The aim of this study was to investigate the effect of different food intake levels on faecal particle size and retention times in rabbits. Lactation was chosen as period with highest energy requirements and thus highest food intake potential of the animals. Besides that, the distribution of particles at different compartments of the gastro-intestinal tract (GIT) was measured at maintenance intake level.

2. Materials and Methods

2.1 Animals, housing and diet

Four domestic rabbits *(Oryctolagus cuniculus)* with an average initial body weight (BW) of 3.79 ± 0.02 kg (non-lactating) and 4.27 ± 0.03 kg (lactating) were used in the intake trial (initially it was planned to use six rabbits, but two failed to deliver a litter successfully; values for these two animals on the maintenance intake level are available from appendix). All rabbits were adult (non-lactating = 8 months; lactating = 11 and 14 months) and without obvious dental problems. They were fed a diet with a constant proportion of 50% chopped grass hay (21.0 ± 3.46 mm discrete mean (dMean)) and 50% concentrate (0.59 ± 0.01 mm mean Particle size (MPS); see below for further explanation) at two food intake levels representative for maintenance and lactation intakes (113 and 224 g DM per day). Table 12 shows the nutrient and chemical composition of the diet. The concentrate was fed twice daily at 08:00 and 16:00, the hay was given in several smaller portions. Animals had ad libitum access to water. During the collection period they were kept in cages allowing separation and total collection of faeces. The litter (4 to 6 young) was kept in a severed nest box. Suckling was allowed twice daily at 08:30 and 16:30 and the mothers were weighed before and after nursing to estimate milk yield.

After this part of the study, all six rabbits were used in the determination of MPS in sections of the gastrointestinal tract (all at maintenance intake level).

Table 12: Nutrient and chemical composition of grass hay and concentrate; Means ± SD are based on 3 observations for each value

Ingredients		Grass hay	Concentrate
Lucerne meal			38
Wheat middlings			18.7
Soybean meal			12
Sunflower meal			10
Barley grain			8
Oats huskmeal	% of DM		6.3
Molasses			4.75
Soybean oil			0.5
Feeding lime			0.5
Monocalcium phosphate			0.2
Mineral and vitamin mix			1.25
Chemical composition			
Ash		95 ± 22.6	95 ± 0.6
CP		118 ± 28.2	190 ± 4.2
EE		25 ± 7.0	29 ± 0.4
NDFom	g/kg DM	519 ± 47.0	367 ± 10.1
ADFom		322 ± 32.8	206 ± 5.5
ADL		51 ± 1.0	58 ± 4.5
Starch		-	105 ± 3.4
24 h gas production (HGT)	ml/200 mg DM	45.3 ± 1.7	47.8 ± 1.2
ME_{rum}	MJ/kg DM	9.3 ± 0.5	10.8 ± 0.1

DM: dry matter
CP: crude protein
EE: ether extract
NDFom: neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash
ADFom: acid detergent fibre expressed without residual ash
ADL: acid detergent lignin
HGT: Hohenheim gas test
ME_{rum}: metabolizable energy for ruminants

2.2 Experimental procedures

The length of the experimental period at maintenance requirements was 22 days consisting of a 14-day period for adaptation and 8-day period for collecting samples. The length of the period during lactation was, adapted to the peak of lactation curve, 19 days including 14 days adaptation and a 5-day period for collecting samples, starting 3 days postpartum. Samples of feedstuffs were taken daily during the trial and were pooled. Faeces were collected quantitatively at intervals necessary for determination of digesta mean retention time (MRT). Two different markers were ingested by the animals on day 15 with a small proportion of morning concentrate. The animals were dosed with 2.7 g chromium(Cr)-mordanted fibre (1-2 mm particles) and 0.27 g cobalt(III)ethylene diamine tetraacetate (Co-EDTA; solutes) (Udén et al., 1980). To ensure total consumption, Co-EDTA was dissolved in water, mixed with the concentrate and the Cr-mordanted fibre and dried again before feeding (60°C, 6h). The faecal samples were collected at time intervals of increasing length (day 1-2: 4 h; day 3-5: 6 h; day 6-7: 8 h; day 7-8: 12 h). One part was dried at 60°C for 24 h and after that at 100°C for another 24 h, and then milled and stored for marker analysis; another part was pooled over the sampling period and stored frozen for wet-sieving procedure and chemical analysis.

After the litters had been weaned and the rabbits were back on maintenance intake level, they were sacrificed within 1.5 hours after morning meal. Total contents of stomach, caecum, and colon were taken and stored frozen. A representative part of the sample was used for wet sieving.

2.3 Analytical methods

2.3.1 Mean retention time

The Cr-mordanted fibre and Co-EDTA digestion for analysis was done by using a microwave (MarsXpress; CEM corporations, Matthews, NC, USA). 0.2 g of the milled samples (1 mm) was weighed into the vessels and 4 ml of 65% HNO_3 plus 2 ml of 30% H_2O_2 added, before the vessels were closed and the microwave could be started. After filtration, analysis was done by atomic absorption spectroscopy (AAS) following Behrend (1999).

The MRT in total GIT was calculated following Thielemans et al. (1978)

$$MRT = \sum(c_i \times dt \times t_i)/\sum (c_i \times dt)$$

(MRT = mean retention time [h]; c_i = marker concentration in the faeces at time i [mg/kg DM]; dt = length of time interval which represents the marker concentration c_i [h]; t_i = time after marker application (middle of time interval which represents the marker concentration c_i) [h]). In two animals at high intake, Co-EDTA had not been completely excreted by the end of the collection period. If this was the case, marker concentration was extrapolated to approximately 0 assuming exponential decay.

2.3.2 Chemical composition

Chemical analysis was done according to VDLUFA (2007) for dry matter (DM) (method 3.1), ash (method 8.1), crude protein (CP) (method 4.1.2; Dumas method; instrument FP-328, LecoEnterprise, St. Joseph, MI, USA) and starch (enzymatically; method 7.2.3). Ether extract (EE) was analyzed after acid hydrolysis using an ANKOM Extractor (Ankom Technology, Macedon, NY, USA) according to AOCS (2009) (Am 5-04 official method). Neutral detergent fibre (NDFom; not assayed with a heat stable amylase and expressed exclusive of residual ash), acid detergent fibre

(ADFom; expressed without residual ash), and acid detergent lignin (ADL) were analysed following Van Soest and Robertson (1985). Degradability of the feed samples was also evaluated *in vitro* with the Hohenheim gas test via 24 h gas production (Menke et al., 1979).

2.3.3 Digestibility and energy

Since total collection of faeces failed for the high intake trial, digestibility of organic matter (OM) was estimated using ADL as internal marker. A 5% disappearance of ADL in the digestive tract was assumed according to Nader and Robinson (2008). Digestible organic matter intake (DOMI) was calculated using the digestibility of OM and the intake of OM per day. The metabolizable energy for ruminants (ME_{rum}) of the concentrate was calculated following GfE (2009)

ME_{rum} (MJ/kg DM) = 7.17 - 0.01171 ash + 0.00712 CP + 0.01657 EE

+ 0.00200 starch - 0.00202 ADFom

+ 0.06463 gas production

The ME_{rum} of the grass hay was calculated following the formula for grass products of the GfE (2008).

ME_{rum} (MJ/kg DM) = 7.81 + 0.07559 gas production – 0.00384 ash

+ 0.00565 CP + 0.01898 EE – 0.00831 ADFom

Units for both formulae are g/kg DM for ash, CP, EE, starch and ADFom, and ml/200 mg DM for gas production.

2.3.4 Faecal particle size

The MPS of faeces and concentrate and the dMean of hay was determined using a wet-sieving procedure (sieves of 16, 8, 4, 2, 1, 0.5, 0.25, 0.125, and 0.063 mm mesh size) (Kovács et al., 1997a). All samples were soaked in water before sieving to separate all cohering particles (hay for 10 min, concentrate for 30 min, faeces over night in a refrigerator). Wet sieving was done for 10 min with a water flow of 2 l/min sprayed on the top sieve using a Vibrotronic Type VE 1 (Retsch Technology, Hanau, Germany). The amplitude of the sieve shaker was adjusted at 2 mm. The MPS from the data set was calculated by an exponential model developed by Fisher et al. (1988) using the NLIN procedure of SAS (2007).

$$R = 100 \text{ x } e^{-(s^a - bs)}$$

R = particle size data expressed as cumulative percent weight oversize

s = screen size [mm]

a and b = estimated constants

The model was adapted following Kovács et al. (1997b) to enhance the number of steps between the sieve with the largest and the smallest pore size for the calculation of MPS

$$\text{Mean size} = \frac{\sum_{i=1}^{1000} step \text{ x } R' \text{ x } (0.063 + i \text{ x } step)}{\sum_{i=1}^{1000} step \text{ x } R'}$$

Step = (L − 0.063) / 1000

L = double the aperture of the largest sieve [mm]

R' = first derivative of R (cumulative percent weight oversize)

R' = 100 x $e^{(bs - s^a)}$ x (b-as$^{(a-1)}$)

The dMean was calculated according to Fritz et al. (2011) for hay samples. There was a major amount of particles that remained on the sieve with the biggest pore size which made the MPS smaller. This effect was balanced by using the length of the biggest particle as upper limit in the calculation of the dMean.

2.3.5 Estimations related to energy metabolism of the study animals

Maintenance energy requirements expressed as digestible energy (DE) were calculated by multiplying metabolic body weight (MBW) with the factor 0.40 for non-reproducing does and 0.43 for lactating does (Xiccato and Trocina, 2010). ME could be estimated as 0.95 DE (Partridge et al., 1986; Xiccato and Trocina, 2010). Energy content of milk was calculated by a regression equation following Tyrrell and Reid (1965), modified by Nostitz and Mielke (1995) as follows:

$$E = 0.384 * F + 0.223 * P + 0.199 * L - 0.108$$

where E is the energy content (MJ/kg), F is the fat content (%), P is the crude protein content (%) and L is the lactose content (%) of the milk. Constant values for fat (15.2%), protein (10.3%) and lactose (1.8%) taken from Coates et al. (1964) were used in calculations of milk energy output.

2.3.6 Statistics

Differences between low and high intake level were tested for significance by paired t-test. Differences in particle size between food and different sections of the gastro-intestinal tract were tested for significance via ANOVA and consecutive Tukey-Kramer test. Level of significance was 5%. All tests were done using SAS 9.2 (SAS Institute, 2007).

3. Results

An influence of food intake level was found for all variables except for the faecal particle size (increase by 3.8%; P=0.073). The MRTparticle decreased by 38% (P=0.0001), and MRTsolute by 36% (P=0.0012) from low vs. high intake.
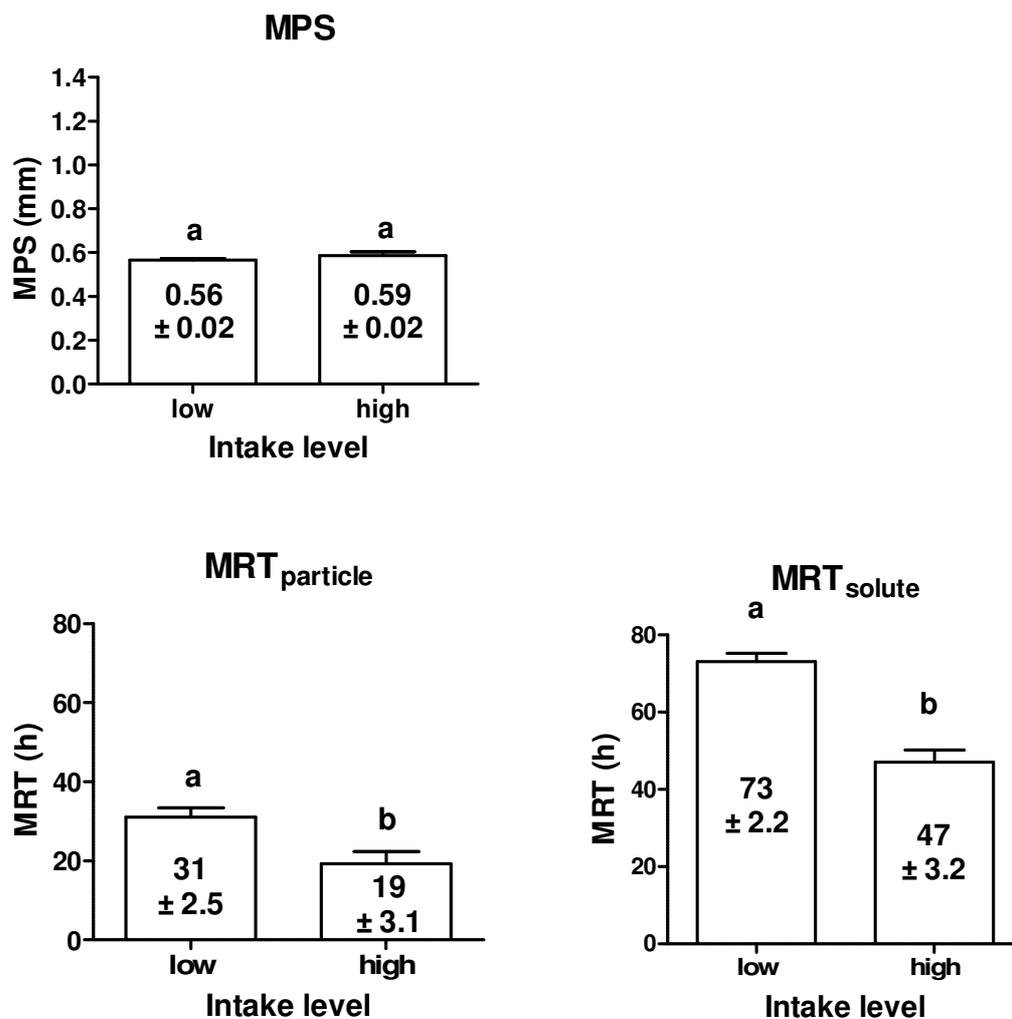
Fig. 9: Digestive variables of rabbits at two different levels of food intake. (MPS = mean particle size, MRTparticle/solute = mean retention time of particle/solute phase)

The excretion curve of Cr-mordanted fibre showed a rapid excretion of the particle phase, while excretion curve of Co-EDTA showed several repeating small peaks.
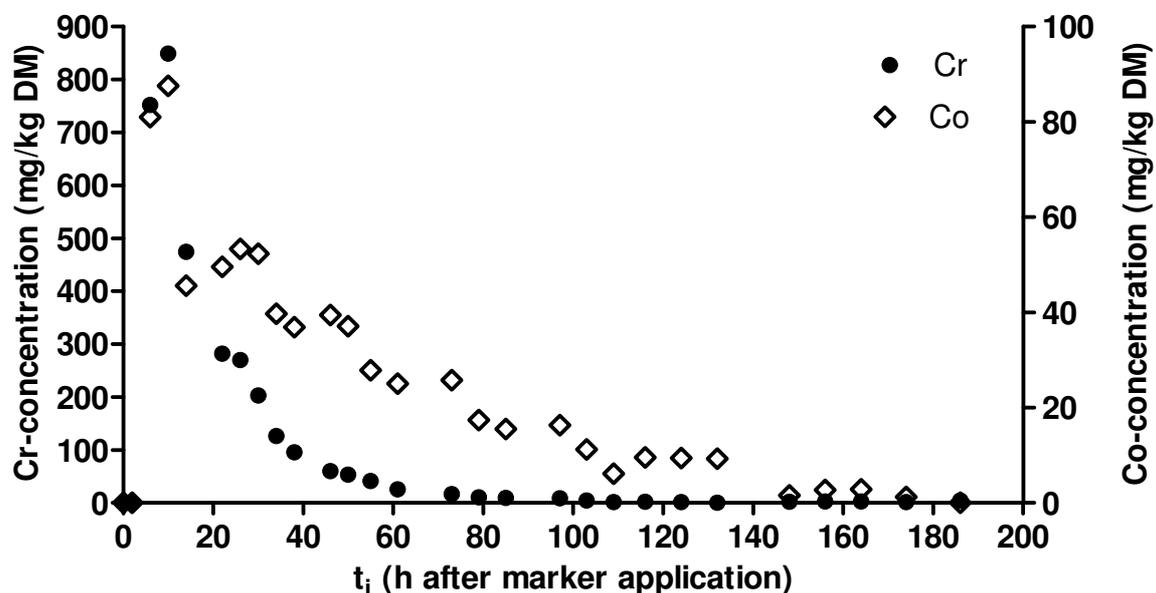
Fig. 10: Typical marker (Co-EDTA and Cr-mordanted fibre) excretion curve for rabbits

The digestibility of OM was 58.3% and the DOMI 22 ± 0.9 g/kg$^{0.75}$ (60 ± 2.3 g/d) on the low intake level. The digestibility of OM estimated via ADL was 55.4 ± 0.57% on low, and 58.2 ± 1.12% (P=0.020) on high intake level. The proportion of ADL in NDFom of faeces was lower on the low food intake level (low: 16.2 ± 0.01%; high: 17.5 ± 0.01%; P=0.027). Average lactation curve showed a lactation period of 22 ± 1 day. Milk yield increased rapidly in the first 10 days, from 30 to 120 g/day. Maximal daily milk yield was 177 g/d. The peak of lactation was achieved after 16.5 days, afterwards milk yield and willingness of mothers to nurse decreased markedly. While BW and thus maintenance energy requirements remained nearly constant during trial period, total energy requirements increased markedly due to lactation by 2.1 for average, and by 2.7 multiples of maintenance for peak lactation (Table 13).
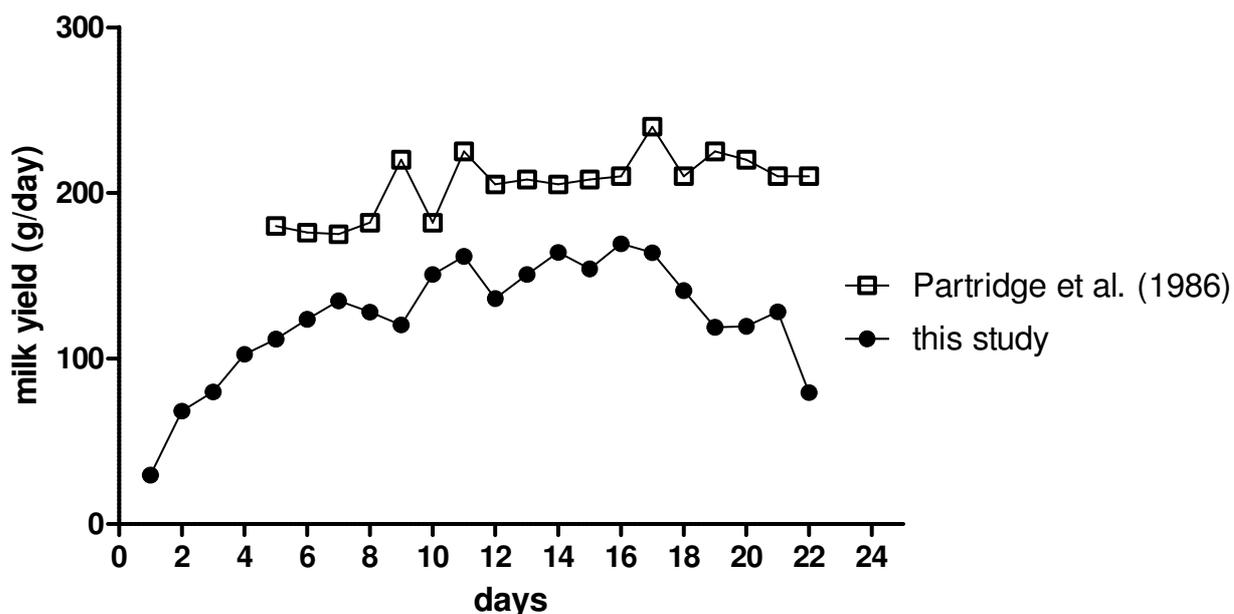
Fig. 11: Average lactation curves of rabbits from this study and literature (Partridge et al., 1986)

Table 13: Data on food intake and estimated average energy requirements of lactating and non-lactating rabbits; estimated milk production over lactation period was 2.5 kg with an average milk energy content of 8.4 MJ/kg (Coates et al., 1964)

	dry	peak lactation
Body weight (kg)	3.79 ± 0.02	4.27± 0.03
food intake (g DM/day)	111	220
milk yield (g/day)		178
Maintenance energy requirements (MJ ME/day)	1.4	1.5
Total energy requirements (MJ ME/day)	1.4	4.0
Multiples of maintenance		2.7

Mean particle size was 10.8 ± 1.22 mm in the diet, 0.68 ± 0.03 mm in the stomach, 0.50 ± 0.01 mm in the caecum and 0.59 ± 0.08 mm in the colon, the latter almost identical to MPS in faeces (0.56 ± 0.01 mm). Particle size in food was greater than in digesta (P<0.0001 for all comparisons); MPS in stomach was greater than in

caecum, colon and faeces (P<0.0001), and MPS in caecum (0.50 ± 0.01 mm) was lower than in colon and faeces (P=0.0082).
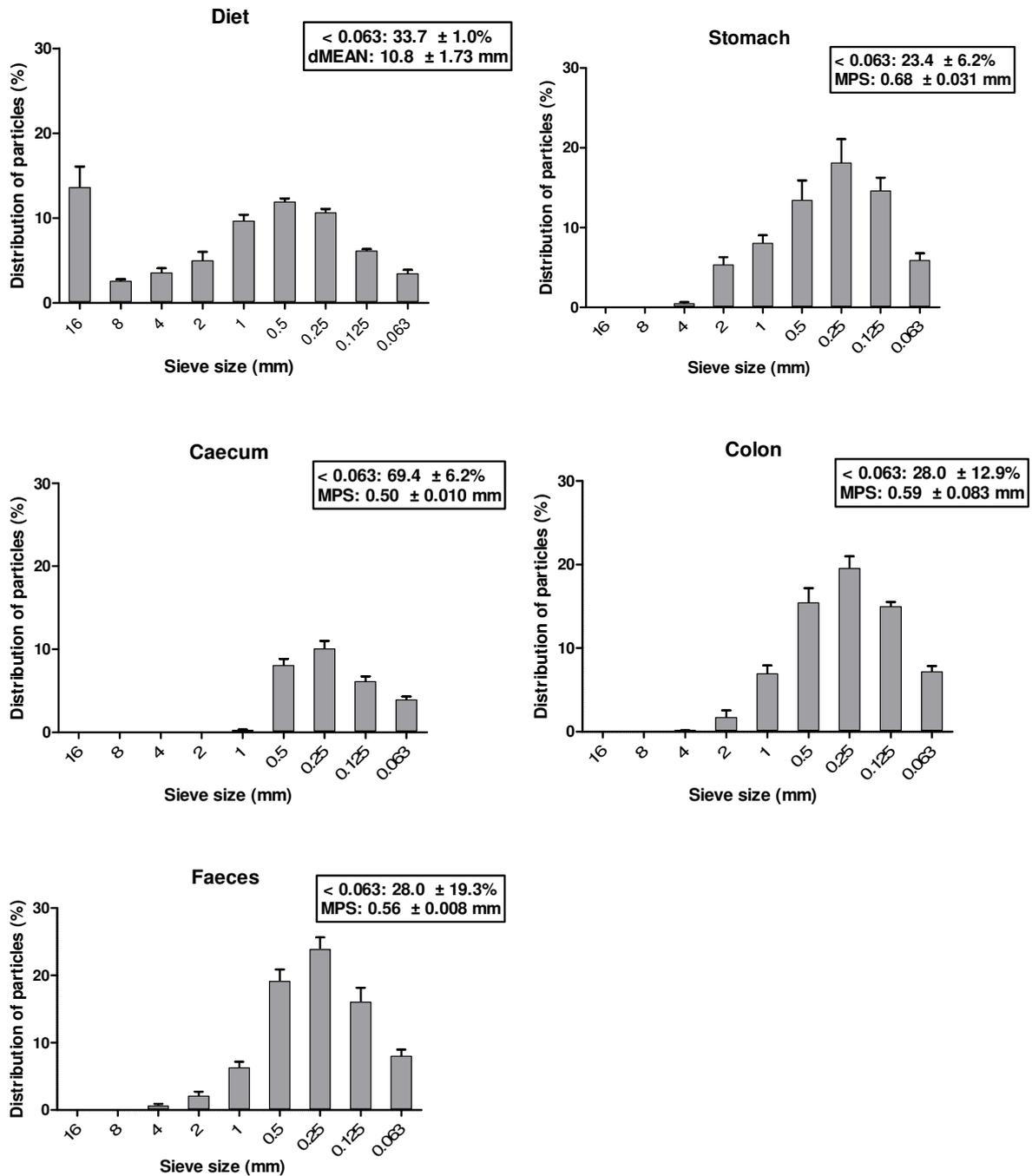
Fig. 12:   Average distribution of particles in a) the diet, b) stomach, c) caecum, d) colon, and e) faeces of rabbits; (Means ± SEM)

4. Discussion

4.1 Methodological considerations

Some methodological points of the study deserve mentioning. Like in most studies on particle size, the quantification of particle sizes has the lower limit of the smallest sieve size used in the trial (0.063 mm in this study); considerations focus on the particles retained on the sieves, and put less focus on the fraction passing the smallest sieve. This fraction probably represents heterogeneous components, since it can contain soluble material and microbial cells besides "true" digesta/food particles. While this fraction is considerable in many samples (in ruminants, it often represents approximately 50% of total faecal DM (Fritz, 2007)), it was particularly large in caecum content, but rather low (23-28%) in the stomach, colon and faecal samples of rabbits.

As mentioned in the Material and Methods section, digestibility of OM could not be determined reliably with total collection at the high intake (an unrealistically high value of 67% was calculated from the data, in comparison to 58% at the low intake). While the major reason for that must lie in sampling errors, a minor difference between the sampling periods appears to have been due to differences in hay quality according to estimations based on ADL (internal marker).

For the overall grading of this study, it is of interest how the intake and the increase in energy requirements as realized by the animals rank compared to other studies. The shape of the lactation curve was comparable to literature (Partridge et al., 1986; Nicodemus et al., 1999; Pascual et al., 1999a; Nicodemus et al., 2006; 2007) but milk yield was lower; this could be expected due to the use of primiparous does. Correspondingly, food intake was also lower with 220 g DM/day (74 g DM/kg$^{0.75}$ per day) in this trial compared with highest values in literature that were around 106 g DM/kg$^{0.75}$ per day (BW: 3.86 kg) on a diet containing 50% lucerne hay, 35% barley

grain and 12% soybean meal (Pascual et al., 1999a). Voluntary food intake of rabbits in this trial was about two thirds (64%) of maximal intake reported from literature. It will be interesting to see evaluations of food processing in rabbits at higher intakes than realized in this study.

4.2 Particle size in different parts of the GIT

It is generally assumed that the breakdown of large particles in diets is primarily achieved by chewing, while physical attrition and microbial breakdown in the gut are less important (Balch, 1971; Ehle and Stern, 1984). The merit of intensive diet comminution lies in an enlargement of the surface:volume ratio leading to improved microbial particle colonization and degradation and in a volume reduction facilitating a higher food intake. In rabbits, the particle size of digesta also has an important influence on caeco-colic motility (Björnhag, 1972; Bouyssou et al., 1988). Particles greater than 0.315 mm are propelled quickly out of the colon, while in contrast fine particles are retrogradally transported into the caecum, where accumulation, degradation and fermentation occur (see figure 13). Thus intense comminution by chewing plays a decisive role for digestion in rabbits; only fibre of very small particle size is flushed

Figure 13: Schematic view of the separation mechanism in the proximal part of rabbit colon during periods when hard faecal pellets are produced. Shaded squares represent particles larger than 0.1 mm. Empty squares represent finer particles (including microorganisms and water-soluble substances). PC= proximal (haustred) part of colon, FC= fusus coli (Björnhag, 1981)

into the caecum and can be degraded by microorganisms there. Caecotrophy itself actually does not seem to have much influence on overall faecal particle size, since the process does not involve any additional chewing (Gidenne and Lebas, 2006).

Based on the above considerations on rabbit digestive physiology, it is not surprising that in this study a smaller particle size was found in the caecum than in the colon (0.50 vs. 0.59 mm). In addition, the proportion of particles passing the smallest sieve (0.063 mm) was also higher for caecum than colon (69 vs. 28% of total DM). Also as expected, particle size in colon largely corresponded to faecal particle size. Udén and Van Soest (1982b) also found a larger particle size in hard pellets compared to caecum contents. On a first glance it seems surprising that the MPS in rabbit stomach is considerably higher than in colon and faeces. That seems to contradict the view of chewing as the by far most significant influence on particle size as implied by the findings of McLeod and Minson (1988) who stated that in steers 82% of large particle breakdown is caused by mastication (during feeding and rumination), while only 18% is related to chemical digestion and physical detrition. Actually Fritz (2007) also described a tendency (P<0.10) of particle size (geometric mean) in the stomach to be greater than in the colon for a rodent (the viscacha, *Lagostomus maximus*; 0.24 vs. 0.22 mm) and also for domestic rabbits (0.43 vs. 0.35 mm); anecdotically, even a larger difference between stomach and colon was found in two individual elephants (African elephant *Loxodonta africana*: ~3.8 vs. 1.9 mm; Asian elephant *Elephas maximus*: 4.2 vs. 2.2 mm) (Fritz, 2007). A clear decrease of MPS from stomach to colon could indicate a lower relevance of chewing compared with enzymatic digestion and detrition via friction, like demonstrated to be the case in marine herbivores feeding on aquatic and therefore very little lignified plants (Lanyon and Sanson, 2006).

The correct starting point for considerations of the contribution of chewing on food comminution is obviously particle size in food. If this is followed for the rabbits of this study, the picture is that a particle size of 10.8 mm in the diet (0.59 mm for concentrate and 21.0 mm for hay) opposes 0.68 mm in stomach and 0.56 mm in faeces, which indicates that at least 98% of total comminution is performed before the material leaves the stomach (which can be considered to be due to chewing activity dominantly), and only the remaining 2% were due to chemical or physical detrition in post gastric sections of the gut. If compared to data for ruminants (McLeod and Minson, 1988), this would indicate a comparable if not greater contribution of chewing to total particle comminution in rabbits.

For the further decrease of particle size from stomach to faeces, another point may be relevant. Results of investigations on the development and prevention of gastric ulcera in pigs point to a positive role of larger particles in prevention (Maxwell et al., 1970). This is interpreted convincingly as an effect of particle stratification in the stomach, which has a protective effect on sensible parts of stomach mucosa by preventing too intense direct contact with stomach secretions of low pH (Grosse Liesner et al., 2009; Kamphues, 2011); in consequence this implies the presence of some selective retention of larger particles in the stomach, leading to enrichment of larger particles in this section of the GIT. These larger particles may leave the stomach only after some chemical weakening of their fibrous structure, which could lead to a higher MPS in this section of the gut, which is not necessarily linked to the process of particle comminution. In fact, colon contents and faeces included some particles retained on the 4 and 2 mm sieve but in lower concentrations than in the stomach.

4.3 Influence of intake - comparison with ruminants

Fibre content of a diet is negatively correlated with MRT and OM digestibility, and chopping of roughages increases digestibility for rabbits (Laplace et al., 1977; Gidenne, 1992; Sakaguchi, 2003). Several groups working with ruminant herbivores found at increased intake a decreased retention time and associated with that a decrease of diet digestibility (Kennedy and Murphy, 1988; Kaske and Engelhardt, 1990; Rothfuss et al., 1997). The decrease of food comminution with increasing intake (Okine and Mathison, 1991b; Kovács et al., 1997a; 1997b; 1998) can also contribute to a decrease in digestibility.

Table 14: Comparison of changes in digestive variables at increasing food intake level (x-fold maintenance intake)

Intake level	Animal	MRTparticle (h)	OM dig. (%)	NDFom dig. (%)	Study
1.0	Pony	30.5[a]	58	42	(Pearson, 2001) [1]
2.2		21.3[a]	58	38	
1.0	Donkey	39.8[a]	66	54	
1.8		32.8[a]	63	47	
2.0	Pigs		80.8		(Parker and Clawson, 1967) [2]
4.0		[b]	78.8		
6.0			78.7		
1	Cattle	59.4[c]	76.4	60.1	(Okine and Mathison, 1991b)[3]
1.3		59.1[c]	73.7	58.6	
1.5		58.8[c]	71.6	59.3	
1.7		56.9[c]	66.7	57.1	
1	Rabbits	31[a]	58.3	36.8	This study [4]
2		19[a]			

MRTparticle: mean retention time of particle phase (h)
OM dig.: digestibility of organic matter (%)
NDFom dig.: digestibility of neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash (%)
[a] chromium mordanted fibre
[b] chromium oxide; cumulative excretion (day):
intake level 2: 1.0 (1), 26.2 (2), 84.3 (3), 96.2 (4), 93.2 (5), 99.0 (6), 100 (7);
intake level 4: 9.6 (1), 82.1 (2), 93.2 (3), 95.8 (4), 94.9 (5), 100.8 (6), 100 (7);
intake level 6: 28.1 (1), 95.4 (2), 95.2 (3), 99.9 (4), 94.9 (5), 99.7 (6), 100 (7).
[c] calculated as the reciprocals of the fractional passage rates
[1] diet: 100% short chopped, molassed, alfalfa hay
[2] 100% fortified barley-soybean meal diet
[3] diet: 100% forage (chopped to 6 cm; 40:40:20 bromegrass, timothy, alfalfa)
[4] diet: 50:50 chopped grass hay: concentrate

Since in rabbits diet comminution by chewing can be considered at least as important as in ruminants, the question arises which influence intake level takes on this relation. To our knowledge no systematic data exists on the relation of intake and particle breakdown for non-ruminants to date; therefore the rabbits of this study can be considered a "model" for the whole class of non-ruminating herbivores, although the particularities of their particular digestive system obviously need to be kept in mind.

It is hypothesised that intake has a stronger influence on MPS in non-ruminants than in ruminants due to some compensating influence of rumination and selective retention in the rumen. However, the results of this study indicate the opposite: Between maintenance and 2-fold maintenance intake during lactation, no increase in particle size was found in rabbits (3.8 %; P=0.073) compared to goats (6%; chapter 2). Although the available evidence is based on a small data base, the few results yield a relatively clear pattern. An explanation for this pattern is more challenging: Why was MPS less influenced in rabbits than in goats in this study? Two points have some explanatory potential: Chewing in ruminants as a two-stage process (chewing during feeding and rumination) is influenced by the availability of particles for the rumination process, responsible for approximately two thirds of the total particle comminution due to chewing (McLeod and Minson, 1988). The availability is mainly determined by their retention in the rumen (which increases the likelihood for the particle of being ruminated). If higher gut fill leads to a higher probability for larger particles to leave the rumen and therefore to escape further (repetitive) rumination, MPS in faeces will increase. A second point not necessarily exclusive to the first may be related to maximal daily chewing times: Daily rumination time is usually thought to be limited at some point (8-9 h) (Van Soest, 1994) which is hard to overcome by the animal, while daily feeding time in rabbits (~ 4 h according to Maertens (2010))

appears to leave ample space for adaptive prolongation of feeding time without compromising an advantageous food amount/chewing time ratio at higher intakes. In general, significant changes in faecal particle size should result from changes in chewing rate (in terms of chews/g DM), particularly in non-ruminants. It can be assumed that in this trial chews per unit of food were not changed considerably due to higher food intake.

While faecal particle size changed surprisingly not with intake in rabbits, passage time of particles and solute decreased markedly by 39% and 36%.

Table 15: Linear regression of percentage and absolute changes of digestive variables at different intake levels

	Linear regression of percentage change (level 1 = 100%)	R^2	P	Linear regression of absolute change	R^2	P
MPS	3.79x + 96.21	0.5536	0.0343	0.02x + 0.54 [mm]	0.4553	0.0664
MRTparticle	-39.14x + 139.10	0.9691	<0.0001	-12.04x + 43.02 [h]	0.8642	0.0008
MRTsolute	-35.90x + 135.90	0.9702	<0.0001	-26.24x + 99.25 [h]	0.9683	<0.0001
SF	-4.55x + 104.60	0.0855	0.4821	-0.02x + 0.44	0.0260	0.7031

MPS = mean particle size
MRTparticle/ solute = mean retention time of particles/ solute
SF = selectivity factor

The linearity of the response to an increase in intake was assumed in these calculations, which is implied by the results on goats in chapter 2. The digestive strategy of rabbits includes rapid excretion of low digestible fibre, and selective retention of highly digestible parts like solutes and fine particles in their fermentation chamber (Franz et al.) (see figure 10). Fine particles are defined as particles shorter than 0.315 mm (Nicodemus et al., 1997) which aligns with our findings for particle distribution in caecum (see figure 12). However in this study, there were also particles found on the sieve with a pore size of 0.5 mm. This may be related to the

fact that samples were taken during feed intake, when large particles can be located directly behind the ostium caecocolicum. Large particles are also very important in rabbit digestive system because of their influence on gut motility and intestinal morphology like crypt depth of colon and villus height of duodenum (Tufarelli et al., 2010). Following Nicodemus et al. (1999) a minimal proportion of 21% particles (>0.315 mm) is needed to get maximal performance in rabbits. A lack of such particles results in reduced colon motility thus reduced retrograde transport of highly digestible small particles into the caecum, and ultimately poor utilisation of the diet independent of diet quality. A comparison of digestive variables of this trial with that of other hindgut fermenters (pony, donkey, pigs) and ruminants (dairy cows) showed some heterogeneity in passage rate and digestibility of OM and NDFom (Table 16). It can be expected that changes in digestibility with increasing intake are less pronounced in herbivores realizing a lower fibre digestibility only (like equids or lagomorphs), because digestibility of easily digestible fractions will be less influenced by a decrease of MRT.

Table 16: Linear regression of digestive variables at different intake levels for different species

Species		MRTparticle [h]	OM-dig. [%]	NDFom-dig. [%]	Source
Pony	abs	-7.67x + 38.17		-3.33x + 45.33	(Pearson, 2001)[*]
	rel	-25.13x + 125.10		-7.93x + 107.9	
Donkey	abs	-8.75x + 48.55	-3.75x + 69.75	-8.75x + 62.75	(Pearson, 2001)[*]
	rel	-21.99x + 122.00	-56.81 + 156.80	-16.21 + 7.17	
Pigs	abs		-0.53x + 81.53		(Parker and Clawson, 1967)
	R^2		0.7856		
	rel		-0.65x + 100.90		
	R^2		0.7856		
Cattle	abs	-3.23x + 63.0	-13.2x + 90.35	-3.60x + 63.72	(Okine and Mathison, 1991b)
	R^2	0.7341	0.9337	0.7115	
	rel	-5.43x + 106.0	-17.39x + 118.30	-5.98x + 106.0	
	R^2	0.7325	0.9337	0.7047	

[*] no R^2 because of only one value per intake level

MRTparticle: mean retention time of particle phase (h)
OM dig.: digestibility of organic matter (%)
NDFom dig.: digestibility of neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash (%)

4.4 Solute marker excretion pattern and coprophagy

On a first glance the results on retention times in rabbits are more than surprising: It is a constant result for ruminants that MRTparticle is at least slightly (and usually considerably) longer than MRTsolute; the opposite was true for the rabbits of this and other trials (e.g. Franz et al. (2011)). Obviously, this behaviour actually reflects the particularities of the particle dynamics in the rabbit GIT as outlined above, like reflux of soluble nutrients and very fine particles, but selective excretion of larger particles (1-2 mm particles should be considered large particles in this context). The excretion of Co-EDTA showed a particular curve shape. Repeated small peaks in the decreasing part of the excretion curve are best explained as the results of events of soft faeces re-ingestion and in fact, this excretion pattern has been suggested as proof of coprophagy in rodents (Clauss et al., 2007a). The MRTsolute as measured in rabbits represents a somehow theoretical value therefore, since most material

normally included in the ingesta fraction flushed into the caecum probably is fermented rather fast, and will therefore disappear via digestion and not show up repeatedly in faeces (only indigestible markers will be re-ingested several times). Connected to this, even though long sampling periods were chosen, it happened that some rabbits still excreted measurable marker concentrations at the end of the sampling period. It would be interesting to figure out how long the clearance of a defined proportion of fine particles (< 0.315 mm) is. The possibility of an iterated intake of substances solved in ingesta opens interesting aspects for veterinary pharmacy, reaching from an unexpectedly low clearance of substances excreted via the gut to the potential of making benefit from the "depot-effect" for drug agents that are gastro-resistant and thus protected against rapid digestion.

5. Major findings:

- Intake level had a considerable effect on ingesta passage in rabbits, MRTparticle decreased by 39% and MRTsolute by 36% per level of maintenance intake

- There was no effect of doubling intake on MPS.

- Overall, particle comminution can be considered to be largely (~98%) due to chewing activity. The higher MPS of particles in the stomach compared to colon/faeces was surprising, but probably can be explained partly by some selective retention and therefore accumulation of long particles in the stomach.

General Discussion

Comparison of different methods to measure particle size

The general basis for a comparability of parameters estimating average particle size from wet sieving studies is given if the same rate of water-flow and the same length of sieving time were used. This can represent a problem, because there is no standard sieving method and the analysis can differ between groups therefore. There are several possible methods to calculate the average particle size based on the results of the wet sieving procedure (Kovács et al., 1997a). As listed below these are the modulus of fineness (MOF) (Poppi et al., 1980a), the discrete mean that is the weighted average (dMEAN), the continuous mean particle size (cMEAN) (Fritz et al., 2012) and the mean particle size (MPS) (Fisher et al., 1988; Kovács et al., 1997b), which all have their assets and drawbacks. The MOF is calculated by the formula:

$$MOF = (\Sigma p_i \times f_i)/100$$

Where p_i is the percentage fraction retained on the sieve i and f_i is an assigned factor. The sieve with the smallest pore size gets the factor 1, the next smallest pore size gets the factor 2 and so on. A resulting MOF of 1 means, that all particles were retained on the sieve with the smallest pore size, a bigger MOF stands for a higher amount of bigger particles. The comparability of the calculated MOF between different studies is only given, if (additionally to the aforementioned conditions) the same number of sieves with the same pore sizes were used. The advantage of the MOF over the other methods is that it is dimensionless, which avoids any misunderstandings, that the calculated particle size represents the real size of particles and not the pore size of the sieve where the particles were kept.

The dMEAN is calculated by the formula:

$$\text{dMEAN} = \sum_{i=1}^{n} p_i \times [s(i+1)+s(i)/2]$$

Where p_i is the percentage fraction retained on the sieve i and s_i is the pore size of the sieve i in mm. This method produces sufficiently exact results using an equal number of sieves with equal pore size. For the cMean, average particle size is estimated from the area under the curve of a regression function that was fitted to a cumulative oversize data set (Fritz et al., 2012); based on the fit of the data, it applies different regressions. The calculation of the MPS is explained in Materials and Methods of the chapters 2 and 3; while the approach is comparable to the cMean, is applies just one particular regression equation to all data. The advantage of this method over the dMEAN is the heightened preciseness of the result by the implementation of smaller steps and over the MOF in the better comparability between different studies. The approach of the cMean and the MPS can be considered comparable in their preciseness. The decision which calculation method should be used is dependent on the type of data set. The cMean appears more convenient for comparisons between several species (potentially varying considerably in the distribution of particles over sieves), while the MPS is preferable for several foodstuffs or food intakes at one species, representing a more gradual change in the distribution of particle sizes. Table 17 shows the results of chapter 2 and 3 of this thesis calculated with the aforementioned methods without the cMean, which was omitted because of the present data set. While the percentage differences between the low, medium and high intake level at goats using the dMEAN method were clearly higher (15.8/ 26.3%), the differences using the MOF method were very little (2.7/ 4.4%) compared to the MPS method (4.7/ 11.2%). These differences between the methods were much smaller in the rabbit trial due to the altogether lower

variation between the low and high intake level. As it seems, the dMEAN method leads to an overestimation of the influence of larger particles on the average result while the MOF overestimates the influence of small particles, both compared to the MPS method.

Table 17: Comparison of wet-sieving results calculated by three different methods (mean particle size [mm]; discrete mean [mm]; modulus of fineness)

maintenance intake	MPS	dMEAN	MOF
goats			
1fold	0.53	0.38	2.94
2fold	0.55	0.44	3.02
3fold	0.59	0.48	3.07
Increase (%)	4.7/ 11.2	15.8/ 26.3	2.7/ 4.4
rabbits			
1fold	0.56	0.38	3.08
2fold	0.59	0.39	3.15
Increase (%)	-*	2.6	2.3

* 3.8%; P= 0.073

The part of the fraction that passes the sieve with the smallest pore size is not considered in all methods estimating average particle size. It contains microorganisms from the fermentation chamber, cells from the gastrointestinal tract and solutes (all fractions not depending on food comminution), but also very small food particles. It has to be kept in mind that this fraction is not considered in the mentioned indices of average particle size as outlined.

Maximum feed intake level from literature and our trials

The rabbits were fed restricted (dry matter intake (DMI) low: 41 g/kg$^{0.75}$ BW per day; DMI high: 74 g/ kg$^{0.75}$ BW per day) during the trial period. These values result from the voluntary feed intake at maintenance requirements and the voluntary intake of rabbits in literature. Stott (2008) compared several digestive variables of European

hare *(Lepus europaeus)* and European rabbit *(Oryctolagus cuniculus)* fed ad libitum at maintenance energy requirements. Here the rabbits consumed 48.4 g/kg$^{0.75}$ body weight (BW) per day, which is similar to the maintenance intake level of the rabbits in this thesis. For ad libitum intake during lactation there were found several data between 105.8 g/kg$^{0.75}$ BW per day of a pelleted diet containing 50% Alfalfa hay, 35% barley grain, 12% soybean meal and 3% minerals (Pascual et al., 1999a), 118.4 g/kg$^{0.75}$ BW per day of a pelleted diet containing 62% alfalfa hay, 15% barley grain, 15% soybean meal, 0.45% wheat bran and 7.55% minerals (Pascual et al., 1999b), and 141.3 g/kg$^{0.75}$ BW per day of a pelleted diet containing 60% forage 35:35:30 alfalfa hay, sunflower hulls, wheat straw and 40% concentrate (Nicodemus et al., 2007). The difference between the amounts of ingested food in literature compared to the trial in this thesis is obvious. The reason behind this is probably that the rabbits in our trial were primiparous with lower average milk yield compared to the animals in the abovementioned studies.

The goats were also fed restricted (DMI low: 0.91 kg (33 g/kg$^{0.75}$ BW) per day; DMI medium: 1.82 kg (66 g/kg$^{0.75}$ BW) per day; DMI high: 2.73 kg (98 g/kg$^{0.75}$ BW) per day) during the trial period. These values result from experience from previous trials with goats fed ad libitum at maintenance energy requirements and during lactation and a comparison with literature (Goetsch et al., 2001).

Comparison of digestive parameters and energy output via lactation at the trials

The results of the work in hand allow some comparisons between hindgut and ruminating foregut fermenters. The MPS at both species was on the same level during maintenance intake. This is salient because body weight of goats and rabbits

in the trials had evidently no effect on faecal particle size at low intake (0.53 vs. 0.56; Table 17). Only at high intake level there was a difference between the goats that excreted bigger particles (4.7% bigger at 2fold and 11.2% bigger at 3fold maintenance intake) than the rabbits (no difference [3.8%; P-value= 0.072]). The goats with much higher body weight were expected to show markedly bigger faecal particles than rabbits. But ruminants comminute food particles more intense than all hindgut fermenters including the caecum fermenters because of rechewing (Fritz et al., 2009) what results in smaller faecal particles. The importance of this and of selective retention of the rumen fades at highly increased gut fill and bigger particles leave the rumen. So this explains the increase in faecal particle size at ruminants, but it does not explain the small change in MPS at the rabbit trial. Small particles and fluid are retained in the rabbit caecum while large particles are passed fast through the colon (Pickard and Stevens, 1972). While this represents a very effective strategy to utilize dietary nitrogen, this strategy detains the rabbit digestive system of utilizing the dietary fibre in fraction. A diet with large amount of fibre can therefore poorly be digested by a rabbit (Sakaguchi and Hume, 1990; Sakaguchi, 2003). Differences between food intake levels at caecum fermenters are much more pronounced regarding the mean retention time. Equal at both, rabbits and goats, is the decrease of mean retention time (MRT) at increasing food intake level.

Table 18: Digestive variables at maintenance and increased food intake level due to lactation at ruminants (dairy goats) and caecum fermenters (rabbits)

| | Maintenance food intake | | | Increased food intake | |
	goats	rabbits		goats	rabbits
MPS (mm)	0.53	0.56	Difference low vs.	+ 11.2	*
MRTparticle (h)	71	31	high intake level	- 45.1	- 38.7
MRTsolute (h)	48	73	(%)	- 35.4	- 35.6
OM digestibility (%)	67	58		- 10.4	
NDFom digestibility (%)	50	37		- 20.0	
Total energy requirements (MJ/d)	6.2	1.0		+161.1	+246.4

MPS: mean particle size (mm)
MRTparticle/ solute: mean retention time of particle/ solute phase (h)
SF: selectivity factor
OM dig.: digestibility of organic matter (%)
NDFom dig.: digestibility of neutral detergent fibre, not assayed with a heat stable amylase and expressed exclusive of residual ash (%)
* 3.8%; P-value= 0.072

Noticeable at rabbits is the much longer fluid retention time compared to the particle phase, which is partly due to caecotrophy, but mostly due to the selective retention of fluids in the caecum of the animals. This distinguishes caecum fermenter from ruminants and the remaining hindgut fermenters. Ruminants retain large particles until their size is reduced below a certain threshold, which results in a particularly high fibre digestibility (Blaxter et al., 1956; Kaske and Engelhardt, 1990). Digestibility of OM and NDFom at maintenance intake level was clearly lower in rabbits than in goats. That difference results mainly on the difference in abilities to utilize the fibre fraction of the diet (Udén and Van Soest, 1982a). Incidentally it should be pointed out, that goats consumed a different concentrate as rabbits while the hay and the forage:concentrate proportion was identical in both trials. The ruminant selective retention again has, regarding to the digestibility of diet, the advantage over the rabbit digestive tract. In caecotrophic animals seems the fibre digestion to be antagonistic to the utilization of nitrogen (Sakaguchi, 2003). Digestive variables of four small hindgut fermenters showed that fibre digestibility was related mainly to their turnover time of large particles in the caecum. The MRT in the whole digestive

tract played a minor role. Additionally showed the species with most effective selective retention of fluid and fine particles the lowest fibre digestibility (Sakaguchi et al., 1987).

The total energy requirements increased at both species markedly during peak lactation compared to maintenance. Both had additional needs of 2.7fold maintenance intake, but rabbits consumed 1.34 MJ per metabolic body weight (MBW; $kg^{0.75}$) while goats did consume 1.20 MJ per MBW. The smaller rabbits consume more energy per unit body mass compared with a larger species like goats. This is a result of variation of maintenance energy requirements in relation to metabolic BW (MBW) (Kleiber, 1961). Larger animals need less energy per body mass than small animals.

The milk yield of the goats in the trial (chapter 3) is markedly higher than the average daily yield of native goat breeds (Salama et al., 2003) and is on the same level as recorded at other dairy goat breeds like the alpine goat (Goetsch et al., 2001) and therefore comparable to the requirements of dairy cows. One of the basic problems of high yielding dairy cows is the inability of the animals to cover their energy requirements sufficiently by food intake without intense body weight reduction and reduced reproductive performance (Dobson et al., 2007). While on the one hand less energy is needed for harvesting forage than preparation of grass by chewing for swallowing and digestion (Pérez-Barbería and Gordon, 1998), long forage particles are on the other hand essential for rumen activity (Woodford and Murphy, 1988). Therefore it is not only important to adjust the total amount of forage in a ruminant diet to retain the structure important for rumination, but also to adjust the average particle size to avoid an additional load of the energy budget by excessive chewing.

Relationship between chewing behaviour and MPS

Pérez-Barberia and Gordon (1998) defined the chewing effectiveness (CE) as the reduction of a defined amount of food with controlled particle size after a known number of chews. Factors influencing the CE are the tooth effectiveness (TE), related to the molar occlusal surface area, molar occlusal contact area, and the length of the enamel cutting edges of the occlusal surface. An additional factor is the chewing behaviour, including variables like chewing rate, time spent chewing and the ability to ruminate. The type of diet is important because of differences in resistance to comminution and because cell wall contents and silicates lying on the forage influence teeth surface and thus ingested particle size (Hummel et al., 2011). Constant factors of the CE are the TE and the effect of the digestive strategy, like rumination or hindgut fermentation (Chai et al., 1984; Fritz et al., 2009). Chewing behaviour and bolus size change due to intake level resulting in bigger particles at increased food intake (Kovács et al., 1997b; Pérez-Barbería and Gordon, 1998).

Comparison of MPS and energy output at trials with allometric regression from literature

The comparison of the results from the trials with the calculated results from the review shows some differences, especially for the goats (Table 19). The measured values are 2.3fold higher for milk yield and 2.2fold higher for energy requirements. The probable explanation of this effect lies in the used dairy goat breed and their physiological high milk yield, because the calculations in the review are based on wild animals. Considering the rabbit data, trial results are lower but in the same range as the calculated values.

Table 19: Comparison of variables from trial results and calculated by equation of literature review

	trial results		Calculated via review results	
	goats	rabbits	goats	rabbits
Average milk yield (kg/d)	3.30	0.12	1.46	0.20
Energy requirements due to average lactation (MJ ME/d)	18.29	2.83	8.31	2.45

Zusammenfassung

Der quantitative Zusammenhang zwischen Futteraufnahmemenge, Zerkleinerung des Futters mit den Zähnen und Partikelgröße der Nahrung im Verdauungstrakt und die Größenordnung resultierender Effekte auf weitere Verdauungsvariablen und den Energiegehalt des Futters von Pflanzenfressern wurden in der Vergangenheit kontrovers diskutiert. Es kann als gegeben angesehen werden, dass bei steigender Futteraufnahme die Zerkleinerungsrate der Ration und ihre Retentionszeit im Verdauungstrakt sinkt, und in der Folge davon auch die Verdaulichkeit des Futters. Zu diesem Ergebnis kommt auch die vorliegende Studie, deren Ansatz es ist, diesen Effekt quantitativ genauer zu beschreiben.

Studien, die die Partikelgröße im Kot in Abhängigkeit von der Futteraufnahme untersucht haben, wurden in der Vergangenheit bei domestizierten Wiederkäuern durchgeführt und haben erste Anhaltspunkte geliefert, um welche Größenordnung sich die Kaueffektivität pro Einheit gestiegenem Futteraufnahmeniveau ändert. Für Wildtiere ist es kompliziert solche Aussagen zu treffen, da nur selten genaue Angaben zur aufgenommenen Futtermenge vorliegen. In einer Literaturstudie der vorliegenden Arbeit wurde diese Lücke ausgeglichen über einen Faktor, der aus Milchleistung und Energiegehalt der Milch berechnet wurde und abschätzt, um wie viel der Energiebedarf laktierender Tiere über dem Erhaltungsbedarf liegt. Mit Hilfe dieses Faktors wurde der Anstieg der Kotpartikelgröße während der Laktation abgeschätzt, der je nach Körpermasse (KM) zwischen 8,5 (über 250 kg KM) und 15,5% (unter 100 kg KM) liegt. Dieser Effekt wurde außerdem bei kleinen Wiederkäuern (Ziegen) dargestellt. Durch Beprobung der Tiere in verschiedenen Laktationsstadien konnte eine maximale Variation der Futteraufnahmemenge erreicht werden; pro Einheit Futteraufnahmeniveau ergab sich für die Partikelgröße ein Anstieg von 6 Prozentpunkten, für die Verdaulichkeit ein Abfall von 4 Prozentpunkten und für die Passagezeit der Partikelphase ein Abfall von 22 Prozentpunkten. Vergleichbare Daten zu Dickdarmfermentierern liegen bisher nicht vor; in einem fast identischen Versuchsaufbau wurde ein kleiner Dickdarmfermentierer (Kaninchen) beprobt. Hier wurde bei Verdopplung der Futteraufnahmemenge kein Effekt auf die Kotpartikelgröße festgestellt, während die Retentionszeit der Partikelphase um 38% sank. Mit Proben aus Bereichen des Verdauungstrakts (Magen, Dickdarm) wurde der Anteil des Kauens an der Nahrungszerkleinerung bei Kaninchen als sehr hoch (~98%) eingeschätzt.

Summary

The quantitative relation between food intake level, comminution of the diet with teeth and the size of food particles in the gastro-intestinal tract (GIT), and the size of resulting effects on further digestive variables and therefore on food energy content for herbivores have been discussed controversially in the past. It can be assumed that at increasing intake level the rate of comminution of a diet and its retention time in the gastro-intestinal tract and in consequence its digestibility decrease. Results of this study confirm this and try to define this effect more precisely in a quantitative way.

To date, studies on the correlation of faecal mean particle size (MPS) and food intake level have been conducted on domestic ruminants basically. They conveyed first reference points on the size of the change of chewing effectiveness per unit food intake level. For wildlife such an assertion is hard to make since data on the amount of diet ingested are rare. In the present study, this gap was approached in a literature review; a factor calculated from yield and energy content of milk allowed an estimation of the size of the difference between energy requirements during maintenance and during lactation. This factor was used to estimate the increase of faecal MPS during lactation, which is apparently influenced by body weight (BW) (between 8.5% for over 250 kg BW and 15.5% for under 100 kg BW).. In own studies, this effect was investigated in more detail for a small ruminant (goat). A maximum variation in food intake level was achieved by taking samples at different lactation stages. An increase of intake by one unit of maintenance intake caused an increase of MPS by 6 pecentage units while digestibility decreased by 4 percentage units and mean retention time of particles (MRTparticle) by 22 percentage units. Because comparable data for hindgut fermenters is absent, a trial was done with a small hindgut (caecum) fermenter (rabbit). Here no effect of doubling the intake level on faecal MPS could be noted while MRTparticle decreased by 39%. Using samples of different parts of the GIT (stomach, colon) the proportion of chewing on total food comminution in rabbits was estimated to be as high as ~98%.

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Appendix

I: Dry matter of faeces, weight of sample taken for sieving, and dry matter retained on several sieves for wet sieving of goat samples

No. Animal	DM (%)	Weight of sample (g DM)	g DM								
			16 mm	8 mm	4 mm	2 mm	1 mm	0.5 mm	0.25 mm	0.125 mm	0.063 mm
Intake level 1											
95 – Monika	55.0	5.02	0	0	0.0479	0.2392	0.3055	0.8239	1.4786	1.3398	0.7851
74 – Nelle	53.1	5.21	0	0	0.0038	0.1399	0.3879	1.1541	1.6237	1.0558	0.6549
65 – Rika	52.7	4.98	0	0	0	0.2098	0.4050	0.7569	1.5654	1.1768	0.9060
73 – Mia	56.0	5.08	0	0	0	0.0998	0.5843	1.0403	1.4348	0.9821	0.8787
12 – Motte	53.0	4.75	0	0	0.0176	0.2788	0.2708	0.9378	1.4582	1.1689	0.8880
94 – Billi	52.6	4.69	0	0	0	0.2942	0.3858	1.0204	1.6667	0.9270	0.7260
97 – Fabia	50.5	5.10	0	0	0	0.2984	0.3756	1.0082	1.3019	1.1991	0.8368
2 - Christiane	55.7	4.85	0	0	0	0.2372	0.2325	1.1559	1.4908	1.0560	0.8477
Intake level 2											
95 – Monika	44.5	3.95	0	0	0.0358	0.3645	0.3942	0.7759	1.3871	1.3490	0.7136
74 – Nelle	47.2	4.23	0	0	0.0543	0.3363	0.4167	0.8113	1.4848	1.3466	0.5700
65 – Rika	45.1	4.53	0	0	0.0460	0.2893	0.4005	1.1136	1.3161	1.1762	0.6784
73 – Mia	45.9	4.62	0	0	0	0.3714	0.4258	0.8687	1.2798	1.3274	0.7470
12 – Motte	44.8	4.76	0	0	0.0217	0.3019	0.4450	0.8771	1.3477	1.3922	0.6344
94 – Billi	46.7	4.69	0	0	0.0570	0.3426	0.3606	0.8990	1.4140	1.3070	0.6399
97 – Fabia	46.2	4.85	0	0	0.0067	0.3667	0.4158	0.8428	1.2880	1.3494	0.7506
2 - Christiane	45.3	4.35	0	0	0.0221	0.3644	0.3606	0.7045	1.3464	1.4587	0.7632
Intake level 3											
95 – Monika	29.5	3.22	0	0	0.0975	0.3643	0.3333	0.9673	1.4044	1.0817	0.7715
74 – Nelle	30.2	3.08	0	0.0063	0.1032	0.2854	0.4727	0.8513	1.3901	1.0898	0.8210
65 – Rika	28.8	3.69	0	0.0041	0.0975	0.3165	0.4976	0.8796	1.3863	0.9824	0.8559
73 – Mia	29.4	3.56	0	0	0.0752	0.3615	0.4799	0.9075	1.2480	1.0053	0.9427
12 – Motte	30.1	4.06	0	0.0017	0.1035	0.3123	0.4267	0.9218	1.3438	1.1042	0.8061
94 – Billi	28.7	4.18	0	0	0.0955	0.3746	0.3455	0.9878	1.3415	1.1373	0.7378
97 – Fabia	29.6	3.15	0	0	0.0000	0.1491	0.8854	0.6671	1.2252	1.3062	0.7870
2 - Christiane	29.3	3.67	0	0	0.0464	0.3713	0.3759	0.7940	1.4562	1.1873	0.7890

II: Marker concentration (CoEDTA and Cr-mordanted fibre) in faeces after application at three levels of food intake of goats

high intake level

marker concentration in faeces

d	t	95 – Monika		74 - Nelle		65 - Rika		73 - Mia		12 - Motte		94 - Billi		97 - Fabia		2 - Christiane	
		Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr
	(h)	(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)	
1	2	-0.01	0.00	8.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	6	6.45	1.61	7.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	10	181.23	45.31	89.02	72.78	67.67	34.39	105.16	84.98	58.84	51.64	48.37	18.85	44.27	27.04	104.55	74.38
	14	589.85	147.46	151.68	272.48	118.73	110.45	136.45	212.81	141.01	209.39	119.70	115.08	158.86	161.83	174.80	333.01
2	18	1010.91	252.73	156.06	348.49	137.70	238.84	131.21	315.98	124.05	260.08	143.47	328.13	155.61	421.37	164.57	346.74
	22	1428.58	357.14	129.51	354.85	109.83	256.19	99.59	322.42	96.14	289.81	110.33	444.26	119.72	417.18	115.53	349.26
	26	1512.73	378.18	91.15	357.30	79.91	249.41	84.78	343.56	82.81	319.96	84.92	458.61	74.60	419.30	87.69	303.01
	30	1547.09	386.77	69.60	339.11	65.96	248.58	74.37	337.73	66.28	304.09	82.89	451.65	71.02	399.82	69.43	300.80
	34	1479.47	369.87	60.76	329.83	51.97	231.12	59.15	330.89	58.25	276.23	66.86	413.48	56.77	354.43	55.10	281.10
	38	1291.70	322.92	39.95	254.41	41.11	209.09	36.23	238.89	37.75	220.29	44.17	375.34	47.37	291.59	33.91	209.89
3	42	974.95	243.74	29.79	183.69	23.16	171.83	26.99	223.13	28.23	190.91	30.07	363.96	34.46	214.41	28.94	183.62
	46	762.50	190.62	24.39	137.62	14.26	128.66	21.51	163.20	20.81	163.46	16.50	178.04	19.44	161.22	17.51	133.00
	50	628.30	157.08	17.03	137.78	8.68	110.00	20.85	126.58	16.72	143.20	11.30	135.60	18.99	99.80	16.03	128.03
	55	737.80	122.97	11.76	112.62	12.12	111.92	15.29	117.72	13.26	102.09	11.00	111.76	14.08	86.68	15.47	95.01
	61	568.17	94.69	11.53	78.02	9.81	97.71	10.36	90.44	11.88	88.43	11.99	85.98	11.25	66.25	10.01	76.05
4	67	445.51	74.25	7.98	48.60	8.89	72.34	7.02	61.23	8.25	67.53	8.39	66.58	8.70	34.04	6.82	53.50
	73	306.04	51.01	10.48	50.67	2.98	47.54	8.11	48.05	6.16	50.18	7.56	28.98	9.33	24.56	8.07	39.50
	79	205.99	34.33	0.45	46.25	1.98	38.12	6.17	38.97	6.17	46.95	4.49	20.57	8.01	33.50	6.83	32.96
	85	125.13	20.85	3.69	34.93	1.97	35.81	0.00	29.40	4.64	40.38	5.74	20.02	4.72	21.91	2.94	42.93
5	91	114.74	19.12	2.35	25.93	2.55	21.55	0.00	11.99	3.95	34.47	3.68	14.14	1.23	9.13	7.97	37.61
	97	71.07	11.85	3.57	24.15	0.64	14.38	1.01	10.45	2.90	23.74	2.40	12.19	0.21	7.10	6.59	34.72
	103	37.48	6.25	0.68	24.60	0.46	13.14	5.34	12.67	1.85	31.90	2.54	0.82	2.84	6.84	5.98	24.59
	109	22.67	3.78	3.86	24.91	1.97	10.12	4.45	14.27	1.12	16.30	0.90	0.00	0.21	4.89	5.69	10.82
6	116	50.57	6.32	5.87	23.24	0.00	3.41	1.59	5.54	0.89	13.92	1.49	0.73	0.36	4.27	2.77	7.92
	124	14.58	1.82	0.00	17.07	0.10	7.93	0.60	0.00	1.14	9.03	1.50	3.59	1.99	3.19	5.59	5.16
	132	22.84	2.86	0.00	15.30	0.00	3.99	0.00	2.56	0.96	5.86	3.11	0.00	2.66	2.98	0.00	3.31
7	140	19.59	2.45	0.00	12.37	1.27	0.00	0.00	0.71	0.67	1.72	1.67	0.00	0.00	2.74	0.00	6.66
	148	0.00	0.00	0.00	8.80	0.00	0.00	0.00	0.00	0.34	0.49	6.23	0.00	0.00	1.90	0.00	6.81
	156	24.95	3.12	0.00	4.65	0.00	0.00	4.59	0.00	2.14	0.43	0.00	0.00	0.00	3.29	0.00	0.00
8	164	0.00	0.00	0.00	4.69	0.00	0.00	0.00	0.00	1.05	0.33	0.00	0.00	0.00	2.08	0.00	0.00
	174	0.00	0.00	0.00	2.90	0.00	0.00	0.00	0.00	2.42	0.70	0.00	0.00	0.00	1.74	0.00	0.00
9	186	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

medium intake level

d	t (h)	95 – Monika Co (mg/kg T)	Cr	74 - Nelle Co (mg/kg T)	Cr	65 - Rika Co (mg/kg T)	Cr	73 - Mia Co (mg/kg T)	Cr	12 - Motte Co (mg/kg T)	Cr	94 - Billi Co (mg/kg T)	Cr	97 - Fabia Co (mg/kg T)	Cr	2 - Christiane Co (mg/kg T)	Cr
								marker concentration in faeces									
1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	6	5.74	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.95	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	10	5.61	0.00	0.00	0.00	7.87	0.00	13.79	-0.01	18.04	4.36	0.00	0.00	8.81	0.00	1.48	0.00
	14	64.70	9.26	46.20	18.23	77.58	41.36	86.41	34.84	78.74	74.93	9.78	0.00	72.58	48.92	80.37	71.95
2	18	100.78	47.75	114.19	163.43	114.23	149.79	108.49	125.42	90.59	137.54	77.52	33.54	96.74	148.91	93.82	205.11
	22	101.66	107.82	105.00	238.37	110.81	198.43	100.72	236.57	82.18	153.28	104.67	104.56	91.94	225.92	76.68	251.15
	26	91.43	143.13	88.61	255.99	89.21	204.31	78.87	237.01	73.68	166.55	91.89	175.40	77.91	275.67	72.59	269.41
	30	77.61	176.49	79.31	275.30	79.56	214.85	63.77	243.13	66.70	188.04	79.12	205.89	77.49	275.21	50.31	259.48
	34	63.23	205.56	66.92	274.04	77.14	216.01	60.50	236.47	58.66	193.82	65.34	267.32	68.93	278.19	49.08	257.06
	38	51.35	199.60	39.92	198.83	55.75	192.81	34.61	238.89	40.42	175.30	46.16	257.33	37.03	214.89	39.58	240.21
3	42	38.82	184.52	29.74	172.31	37.45	164.97	28.05	221.02	34.49	143.13	33.15	250.30	24.89	200.04	29.03	209.73
	46	31.60	177.08	24.27	146.62	30.15	140.74	27.15	181.74	26.89	125.98	33.30	219.04	19.05	157.94	22.59	171.79
	50	25.03	164.46	20.40	139.55	22.33	117.88	17.84	142.43	22.77	114.18	22.35	175.28	18.16	125.37	16.26	148.93
	55	20.59	158.19	16.31	131.96	18.95	112.57	15.73	133.55	17.16	118.09	13.56	162.34	14.74	117.23	16.17	137.09
	61	15.83	123.62	12.87	115.48	17.22	106.66	10.26	101.39	8.55	108.96	15.53	149.92	11.53	104.88	12.77	106.05
4	67	14.07	98.33	9.95	60.88	13.65	82.24	5.32	69.11	10.56	100.83	11.40	122.44	7.25	56.03	10.64	73.96
	73	10.71	72.28	3.73	48.90	9.60	57.35	4.12	50.53	10.40	72.08	6.12	74.71	3.15	34.62	8.36	52.24
	79	14.16	66.62	3.91	48.75	6.64	52.58	2.80	49.89	7.42	69.07	4.62	49.79	1.56	29.48	7.82	34.92
	85	10.58	61.11	2.00	40.25	6.83	42.33	2.11	37.22	8.98	54.80	4.13	47.40	0.31	30.57	10.10	30.32
5	91	8.96	42.99	0.00	28.73	6.28	32.01	0.39	21.68	7.71	44.86	1.85	31.89	0.93	11.66	9.25	0.00
	97	8.03	37.06	0.20	14.77	7.28	25.61	0.00	18.64	6.66	31.96	0.98	16.76	2.06	10.67	6.16	0.00
	103	6.59	26.06	2.41	8.90	5.45	23.72	0.00	15.20	5.88	28.57	2.09	11.38	0.00	6.50	4.69	0.00
	109	10.31	20.43	0.20	9.91	3.49	17.17	0.00	9.10	4.43	26.23	1.93	10.13	0.00	2.35	2.38	0.00
6	116	1.31	11.26	0.00	4.47	3.87	0.00	0.00	5.38	8.18	23.05	1.34	0.00	0.00	0.00	0.69	0.00
	124	1.19	9.46	0.20	6.76	2.73	0.00	0.00	3.77	3.53	12.65	0.36	0.00	0.00	0.00	0.00	0.00
	132	2.95	6.96	0.00	0.83	4.57	0.00	0.00	4.84	1.66	8.18	0.12	0.00	0.00	0.00	0.00	0.00
7	140	2.90	0.00	0.20	0.00	1.71	0.00	0.00	0.00	1.07	8.52	1.95	0.00	0.00	0.00	0.00	0.00
	148	1.22	0.00	0.00	0.00	5.26	0.00	0.00	0.00	0.00	6.65	0.00	0.00	0.00	0.00	0.00	0.00
	156	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.52	0.00	0.00	0.00	0.00	0.00	0.00
8	164	0.00	0.00	1.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	174	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
9	186	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

low intake level

marker concentration in faeces

d	t (h)	95 – Monika Co (mg/kg T)	95 – Monika Cr	74 - Nelle Co	74 - Nelle Cr	65 - Rika Co	65 - Rika Cr	73 - Mia Co	73 - Mia Cr	12 - Motte Co	12 - Motte Cr	94 - Billi Co	94 - Billi Cr	97 - Fabia Co	97 - Fabia Cr	2 - Christiane Co	2 - Christiane Cr
1	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.52	0.00	0.00	0.00
	14	0.00	0.00	19.74	0.00	23.72	0.00	2.92	0.00	31.23	4.82	0.00	8.46	11.34	2.39	33.48	13.58
2	18	58.44	41.48	144.42	105.72	92.10	23.91	101.56	18.23	135.96	28.74	5.37	10.42	111.41	30.90	153.06	117.10
	22	118.33	209.62	184.07	285.51	177.52	127.41	217.15	124.82	191.11	109.82	109.32	57.49	172.82	130.28	178.47	312.01
	26	125.38	125.81	192.52	379.41	194.16	206.95	218.70	217.23	158.81	213.69	190.98	237.05	192.44	309.20	163.49	429.22
	30	142.31	284.18	193.57	449.69	190.95	266.37	191.30	270.52	152.18	263.63	184.26	304.85	176.73	403.25	156.55	510.32
	34	151.68	361.47	172.30	517.64	165.24	332.66	189.41	355.49	136.34	286.57	157.00	403.76	170.70	476.37	135.56	549.02
	38	148.61	385.34	158.93	539.26	145.79	360.16	172.22	443.48	124.80	289.76	152.55	457.13	162.53	477.19	128.60	577.19
3	42	130.77	404.63	141.86	514.25	140.07	432.96	156.56	449.65	113.84	301.82	133.92	507.17	123.52	487.00	122.62	506.98
	46	107.13	400.22	112.02	436.12	133.72	435.23	128.60	411.51	95.86	306.13	130.94	506.40	104.92	521.23	91.97	445.97
	50	89.59	412.24	87.67	410.19	108.43	434.01	102.74	403.23	78.09	323.04	118.07	506.69	83.96	511.75	72.70	391.79
	55	78.39	414.64	75.33	389.55	93.47	422.85	76.06	381.36	67.01	309.74	89.01	522.47	70.24	487.96	64.15	381.45
	61	63.63	400.99	62.47	375.06	78.30	400.52	74.35	374.25	60.02	270.27	87.51	510.85	58.69	393.05	54.89	334.23
4	67	60.91	380.96	52.15	345.55	68.59	363.54	69.37	334.84	44.47	225.48	65.88	481.51	44.34	307.33	42.47	273.90
	73	47.41	326.36	39.84	303.48	59.76	333.72	47.81	289.32	36.51	212.23	51.39	400.45	33.55	279.87	31.95	221.29
	79	36.69	272.01	33.17	258.46	48.78	291.66	38.91	263.40	24.75	175.17	41.32	334.40	27.80	256.05	21.20	178.44
	85	28.12	263.46	22.94	211.68	27.60	254.10	33.09	246.94	23.56	178.79	35.80	294.48	21.50	212.18	20.78	166.36
5	91	27.38	218.51	15.33	171.23	30.41	219.79	29.79	211.55	13.37	160.68	35.40	289.86	17.96	180.96	19.17	137.52
	97	17.88	186.08	13.05	127.44	30.19	182.33	21.94	171.67	10.88	126.93	23.85	215.52	15.18	140.51	15.76	106.82
	103	18.14	166.60	7.60	107.75	20.76	166.42	17.73	143.31	12.34	110.80	15.89	172.97	10.87	113.79	9.67	82.06
	109	11.51	142.84	6.38	93.85	14.83	145.25	16.45	126.44	12.09	110.05	13.26	160.59	8.73	98.64	9.11	77.25
6	116	16.90	125.13	3.24	81.69	12.01	122.09	11.91	116.01	8.87	100.91	13.41	148.16	4.95	88.36	6.15	61.91
	124	12.10	102.02	2.54	55.15	11.49	103.73	8.83	81.75	6.99	84.65	7.14	110.48	2.69	61.90	5.40	41.14
	132	6.60	65.81	1.11	55.44	6.02	85.74	7.61	71.37	6.66	73.08	3.01	86.56	0.70	53.17	0.00	18.87
7	140	3.94	57.01	1.80	48.10	3.53	76.65	7.27	63.10	5.02	54.64	2.39	80.43	1.34	36.22	0.00	0.00
	148	2.19	53.11	0.30	34.88	10.38	52.25	4.11	49.23	5.35	51.23	3.54	63.94	0.18	30.19	0.00	0.00
	156	2.90	40.32	0.00	26.66	5.23	47.96	2.83	37.38	4.32	41.21	0.00	56.26	1.00	28.97	0.00	0.00
8	164	0.71	26.05	0.00	19.35	5.54	41.84	1.57	31.01	0.00	36.24	0.00	52.06	0.30	19.59	0.00	0.00
	174	2.34	21.81	0.00	12.52	0.84	34.54	1.61	23.86	0.00	29.97	0.00	38.75	0.00	13.52	0.00	0.00
9	186	0.00	17.03	0.00	11.40	0.44	26.77	0.00	22.28	0.00	21.58	0.00	34.28	0.00	12.57	0.00	0.00
x	198		*15.83*		*13.1*		*19.4*		*20.03*		*20.72*		*19.28*		*8.79*		
	210		*11.82*		*9.8*		*14.8*		*15.53*		*16.61*		*14.42*		*6.31*		
	222		*8.83*		*7.3*		*11.3*		*12.04*		*13.31*		*10.78*		*4.53*		
	234		*6.59*		*5.5*		*8.6*		*9.33*		*10.67*		*8.07*		*3.25*		

x	t	95 – Monika		74 - Nelle		65 - Rika		73 - Mia		12 - Motte		94 - Billi		97 - Fabia		2 - Christiane	
		Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr	Co	Cr
(h)			(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)
246			4.92		4.1		6.6		7.23		8.55		6.03		2.33		
258			3.67		3.1		5.0		5.61		6.85		4.51		1.67		
270			2.74		2.3		3.8		4.35		5.49		3.37		1.20		
282			2.05		1.7		2.9		3.37		4.40		2.52		0.86		
294			1.53		1.3		2.2		2.61		3.53		1.89				
306			1.14		1.0		1.7		2.03		2.83		1.41				
318			0.85		0.7		1.3		1.57		2.27		1.06				
330							1.0		1.22		1.82		0.79				
342							0.75		0.94		1.46						
354											1.17						
366											0.94						

x = extrapolated

III: Dry matter, Fat, Protein and Energy content of goat milk during trial

Date	Animal	Dry matter (g/kg)	XP (g/kg DM)	XL (g/kg DM)	Energy (kJ/kg DM)
01.04.2009	12-Motte	982	217	333	23845
	2-Christiane	979	246	332	24402
	97-Fabia	-	-	-	-
	95-Monika	977	239	322	23845
	74-Nelle	964	253	335	24701
	65-Rika	971	233	311	23866
	73-Mia	967	250	285	23452
	94-Billi	976	251	278	23344
08.04.2009	12-Motte	950	214	321	24313
	2-Christiane	960	209	262	24577
	97-Fabia	960	203	321	24722
	95-Monika	958	230	306	23845
	74-Nelle	963	227	345	24714
	65-Rika	966	227	302	24160
	73-Mia	961	248	275	23190
	94-Billi	955	228	298	23558
15.04.2009	12-Motte	966	236	288	23125
	2-Christiane	957	235	281	23168
	97-Fabia	962	235	322	23978
	95-Monika	969	243	291	23090
	74-Nelle	951	238	293	23259
	65-Rika	967	248	267	22929
	73-Mia	952	247	253	22921
	94-Billi	965	261	254	22394
22.04.2009	12-Motte	116	227	312	23578
	2-Christiane	115	239	289	22381
	97-Fabia	117	227	315	23536
	95-Monika	113	266	272	22630
	74-Nelle	109	257	288	22978
	65-Rika	110	235	289	23097
	73-Mia	107	261	247	22430
	94-Billi	106	254	260	22897
28.04.2009	12-Motte	117	235	338	24019
	2-Christiane	115	237	298	23813
	97-Fabia	124	222	356	24766
	95-Monika	118	236	302	24176
	74-Nelle	111	233	294	23941
	65-Rika	112	236	308	24056
	73-Mia	109	243	259	22961
	94-Billi	106	248	289	23130
06.05.2009	12-Motte	113	224	282	23497
	2-Christiane	108	269	252	22769
	97-Fabia	114	235	295	23569
	95-Monika	110	252	282	23220
	74-Nelle	107	245	269	23116
	65-Rika	107	226	264	23343
	73-Mia	105	255	241	22492
	94-Billi	103	241	249	22685
13.05.2009	12-Motte	117	231	329	24184
	2-Christiane	107	265	283	23507
	97-Fabia	120	229	341	24519
	95-Monika	115	249	278	23723
	74-Nelle	113	238	316	23749
	65-Rika	113	234	297	23550
	73-Mia	108	258	260	22903
	94-Billi	107	254	296	23493

Date	Animal	Dry matter (g/kg)	XP (g/kg DM)	XL (g/kg DM)	Energy (kJ/kg DM)
20.05.2009	12-Motte	111	244	291	22890
	2-Christiane	108	257	259	22851
	97-Fabia	119	231	335	24300
	95-Monika	111	246	289	23087
	74-Nelle	108	240	300	23283
	65-Rika	107	246	309	23215
	73-Mia	105	265	268	22222
	94-Billi	101	248	280	22450
27.05.2009	12-Motte	111	247	262	23241
	2-Christiane	112	243	282	23685
	97-Fabia	116	255	272	23552
	95-Monika	110	268	264	22824
	74-Nelle	103	237	284	23463
	65-Rika	107		274	23222
	73-Mia	101	253	232	22486
	94-Billi	102	264	243	22221
03.06.2009	12-Motte	114	244	304	23627
	2-Christiane	115	262	268	22881
	97-Fabia	118	218	342	24282
	95-Monika	110	260	301	23099
	74-Nelle	107	245	292	23453
	65-Rika	110	250	278	23230
	73-Mia	104	270	251	22458
	94-Billi	104	263	258	22708
10.06.2009	12-Motte	111	236	291	23834
	2-Christiane	108	277	289	24307
	97-Fabia	113	252	288	23416
	95-Monika	107	253	272	22834
	74-Nelle	106	238	289	23751
	65-Rika	107	249	281	23839
	73-Mia	105	262	247	22424
	94-Billi	101	261	272	22789
17.06.2009	12-Motte	111	242	286	23138
	2-Christiane	110	265	269	23120
	97-Fabia	116	236	330	24099
	95-Monika	111	254	273	23281
	74-Nelle	106	240	298	23329
	65-Rika	107	250	284	23189
	73-Mia	101	261	261	22563
	94-Billi	100	260	365	22292
24.06.2009	12-Motte	113	248	289	23426
	2-Christiane	114	259	283	23254
	97-Fabia	114	235	310	23713
	95-Monika	110	264	265	23218
	74-Nelle	108	241	293	23273
	65-Rika	108	250	282	23308
	73-Mia	104	267	253	22945
	94-Billi	98.6	266	253	22747
01.07.2009	12-Motte	111	241	268	23507
	2-Christiane	111	268	283	23085
	97-Fabia	113	245	277	22959
	95-Monika	109	258	263	23034
	74-Nelle	105	236	290	23533
	65-Rika	104	250	258	22904
	73-Mia	107	269	241	22501
	94-Billi	106	222	307	23635

Date	Animal	Dry matter (g/kg)	XP (g/kg DM)	XL (g/kg DM)	Energy (kJ/kg DM)
08.07.2009	12-Motte	106	238	250	22942
	2-Christiane	109	247	293	23557
	97-Fabia	110	236	299	24192
	95-Monika	103	250	249	23033
	74-Nelle	100	238	284	23309
	65-Rika	102	237	271	22594
	73-Mia	98.2	282	207	21686
	94-Billi	100	283	227	22494
15.07.2009	12-Motte	109	229	303	23688
	2-Christiane	109	246	316	24648
	97-Fabia	116	228	342	24812
	95-Monika	106	245	284	23696
	74-Nelle	108	232	319	24425
	65-Rika	108	232	295	23987
	73-Mia	110	260	274	23245
	94-Billi	98.8	270	280	22738
23.07.2009	12-Motte	110	213	306	23540
	2-Christiane	109	239	294	23591
	97-Fabia	114	222	320	23987
	95-Monika	103	252	286	23129
	74-Nelle	107	312	322	23843
	65-Rika	106	234	290	23263
	73-Mia	108	250	276	23278
	94-Billi	96.9	252	278	22741
29.07.2009	12-Motte	107	231	285	23519
	2-Christiane	105	251	272	23035
	97-Fabia	106	227	326	23515
	95-Monika	99.9	255	287	22851
	74-Nelle	105	240	296	23508
	65-Rika	107	247	293	23481
	73-Mia	109	262	269	23469
	94-Billi	95	250	263	22470
05.08.2009	12-Motte	124	243	297	23388
	2-Christiane	113	269	272	22849
	97-Fabia	117	229	298	23677
	95-Monika	107	252	246	22245
	74-Nelle	111	244	285	23231
	65-Rika	111	256	276	22852
	73-Mia	118	262	253	22626
	94-Billi	101	266	274	22170
12.08.2009	12-Motte	113	252	297	23472
	2-Christiane	111	252	292	23532
	97-Fabia	114	249	258	23778
	95-Monika	114	253	292	23429
	74-Nelle	107	247	295	23742
	65-Rika	106	256	278	23108
	73-Mia	107	272	264	22892
	94-Billi	100	267	277	22940
18.08.2009	12-Motte	116	238	309	24056
	2-Christiane	116	265	295	23375
	97-Fabia	116	247	313	23866
	95-Monika	111	267	258	22929
	74-Nelle	116	243	312	23852
	65-Rika	111	258	284	23366
	73-Mia	119	262	268	23280
	94-Billi	104	262	270	22915
	12-Motte	116	238	309	24056
	2-Christiane	116	265	295	23375

IV: Dry matter of faeces, weight of sample taken for sieving, and dry matter retained on several sieves for wet sieving of rabbit samples

No. Animal	DM (%)	Weight of sample (g DM)	16 mm	8 mm	4 mm	2 mm	1 mm	0.5 mm	0.25 mm	0.125 mm	0.063 mm
							g DM				
Intake level 1											
1	46.3	4.8	0	0	0.0350	0.0935	0.2200	1.1055	1.3011	0.8706	0.4471
2	46.8	4.8	0	0	0.0248	0.0342	0.2485	1.0604	1.2646	0.6867	0.3605
4	44.6	3.6	0	0	0.0085	0.0795	0.1747	0.7497	1.0700	0.5783	0.2371
6	57.0	4.7	0	0	0.0179	0.0586	0.1898	1.0626	1.2404	0.6393	0.3750
Intake level 2											
1	45.1	2.4	0	0	0.0056	0.0313	0.1638	0.5319	0.5576	0.4350	0.1894
2	48.2	2.5	0	0	0	0.0224	0.1493	0.4583	0.5367	0.3195	0.1322
4	44.9	2.5	0	0	0.0074	0.0482	0.0838	0.5144	0.5531	0.3518	0.1457
6	46.8	2.5	0	0	0.0070	0.0430	0.1893	0.6284	0.8193	0.2884	0.1899
Stomach											
1	17.7	1.7	0	0	0.0051	0.1221	0.1086	0.2683	0.3420	0.3049	0.1505
2	24.1	1.9	0	0	0.0185	0.1241	0.1265	0.2589	0.3281	0.3383	0.1356
4	15.5	1.1	0	0	0.0084	0.0549	0.1170	0.1740	0.2472	0.1676	0.0690
6	25.2	1.8	0	0	0.0037	0.1056	0.2730	0.2461	0.3531	0.3441	0.1993
Caecum											
1	21.4	1.6	0	0	0	0	0.0089	0.1106	0.1972	0.1073	0.0690
2	19.5	1.5	0	0	0	0	0.0065	0.1320	0.1784	0.0920	0.0644
4	21.7	1.5	0	0	0	0	0.0030	0.1134	0.1399	0.0674	0.0592
6	24.1	1.7	0	0	0	0	0.0005	0.1849	0.1617	0.1308	0.0794
Colon											
1	27.3	2.1	0	0	0	0.0111	0.1324	0.3720	0.5026	0.2957	0.1633
2	24.1	2.4	0	0	0.0023	0.0131	0.1315	0.4470	0.4947	0.3845	0.1797
4	31.0	1.8	0	0	0	0.0114	0.1548	0.4468	0.4947	0.3745	0.1330
6	28.7	1.9	0	0	0	0.0488	0.0986	0.1914	0.3360	0.2917	0.1252

V: Dry matter of faeces, weight of sample taken for sieving, and dry matter retained on several sieves for wet sieving of rabbit samples

Sample	DM (%)	Weight of sample (g DM)	16 mm	8 mm	4 mm	2 mm	1 mm	0.5 mm	0.25 mm	0.125 mm	0.063 mm
							g DM				
hay*	87.4	2.8	0.7979	0.1740	0.1836	0.2397	0.3379	0.1740	0.0906	0.0221	0.0102
concentrate goats	90.2	10.2	0	0	0.1612	0.4241	1.0625	1.6807	1.5250	0.8167	0.4321
concentrate rabbits	89.4	8.1	0	0	0.0045	0.0873	0.7186	1.7759	1.9081	1.2352	0.7031

* hay was similar for both trials

VI: Marker concentration (CoEDTA and Cr-mordanted fibre) in faeces after application at two levels of food intake of rabbits

Level 1 (low intake)

d	t	marker concentration in faeces							
		1 – Verona		2 – Naddel		4 – Carina		6 - Hanni	
		Co	Cr	Co	Cr	Co	Cr	Co	Cr
	(h)	(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)	
1	2	0.00	23.37	0.00	21.99	0.00	0.00	0.00	0.00
	6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	10	61.45	1053.95	91.44	1028.43	72.69	1149.38	86.95	85.74
	14	62.22	665.60	83.36	670.42	59.90	534.37	892.58	97.87
2	18								
	22	36.88	388.84	58.43	347.96	57.17	300.29	436.64	88.98
	26	51.53	387.18	59.84	393.92	65.62	386.42	430.71	98.39
	30								
	34	37.89	301.64	53.17	263.05	52.11	230.03	282.66	58.66
	38	43.20	259.75	47.69	294.13	47.54	206.07	280.93	64.16
3	42								
	46	46.85	164.21	58.90	241.90	150.91	162.02		
	50	51.80	180.60	53.65	213.67	57.50	147.63	158.29	58.42
	55	31.59	113.39	38.65	127.12	35.74	65.39	126.77	97.77
	61	34.77	95.20	38.52	88.74	41.47	68.92	68.30	
4	67	28.43	56.23	40.06	79.16	52.44	56.98		
	73	46.96	62.64	30.72	64.10	57.61	43.78	49.30	55.80
	79	21.92	23.97	0.00	0.00	29.43	24.40	39.24	42.14
	85	25.98	22.91	21.69	42.57	37.18	26.49	37.26	39.62
5	91	31.43	26.62	41.11	36.80	40.03	19.35	24.43	29.82
	97	27.64	14.04	25.68	33.68	41.14	18.24	27.57	39.32
	103	29.03	7.91	25.01	30.38	41.25	10.65	16.88	40.61
	109	24.40	9.35	21.17	24.59	31.15	9.34	11.16	30.60
6	116	21.32	10.65	27.86	41.85	53.28	10.61	5.34	28.20
	124	24.36	3.88	95.60	35.85	34.09	12.69	6.29	32.98
	132	16.75	3.90	25.40	30.39	34.56	9.01	3.58	41.44
7	140	10.33	0.86	11.53	10.62	30.10	6.52	2.30	30.99
	148	10.75	0.00	20.14	10.56	29.71	6.40	4.44	28.65
	156	11.70	0.00	8.20	8.16	23.91	7.60	1.24	17.82
8	164	10.98	0.00	8.06	10.00	22.81	7.16	0.10	15.85
	174	16.49	0.00	14.99	7.92	20.13	6.44	0	14.38
9	186	3.43	0.00	2.12	6.74	15.67	5.44	2.42	11.75

Level 2 (high intake)

d	t	1 – Verona Co	1 – Verona Cr	2 – Naddel Co	2 – Naddel Cr	4 – Carina Co	4 – Carina Cr	6 - Hanni Co	6 - Hanni Cr
	(h)	(mg/kg T)		(mg/kg T)		(mg/kg T)		(mg/kg T)	
1	2	12.64	9.85	0.00	31.15	0.00	25.50	0.00	0.00
	6	73.92	345.35	50.22	438.56	60.41	981.50	81.01	751.81
	10	99.09	287.23	56.66	255.13	68.80	791.69	87.56	848.80
	14	62.21	139.15					45.64	474.45
2	18								
	22			51.44	158.43	90.91	144.48	49.58	281.77
	26	68.47	117.65	49.89	158.69	69.50	112.35	53.30	269.65
	30	47.96	91.63	49.97	109.35	25.71	64.24	52.33	202.83
	34	119.47	50.88	41.90	70.56	35.40	48.74	39.68	126.26
	38					31.67	25.34	36.93	95.56
3	42	29.40	36.66	33.72	33.61				
	46	55.90	32.57	25.19	27.35	47.33	20.21	39.44	60.01
	50	34.77	31.86	30.94	18.10	31.66	20.29	37.11	53.45
	55	35.28	16.43	18.30	5.07	34.55	11.66	27.87	41.36
	61	33.56	13.67	20.47	5.94	30.74	8.64	25.04	25.53
4	67			13.55	0.00	55.48	8.73		
	73	28.35	6.56	16.39	0.00	25.60	3.68	25.80	16.56
	79	25.95	0.00	16.12	0.00	12.78	2.57	17.41	10.43
	85	18.06	0.00	16.68	0.00	13.97	0.30	15.54	9.46
5	91	31.43	0.00	26.47	0.00	17.55	1.72		
	97	28.13	0.00	15.44	0.00	14.25	0.00	16.32	8.47
	103	0.55	0.00	13.27	0.00	11.33	0.34	11.20	4.35
	109					9.53	0.54	6.10	1.72
6	116					15.27	1.72	9.52	2.34
	124					8.85	1.48	9.45	1.50
	132					3.51	0.00	9.28	0.00
7	140					4.92	0.00		
	148					5.10	0.00	1.58	2.14
	156					2.44	0.00	2.69	2.42
8	164					2.71	0.00	2.87	2.48
	174					3.60	0.00	1.21	1.32
9	186					0.42	0.00	0.00	4.46

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Erklärung

Ich erkläre:

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Bei den von mir durchgeführten und in der Dissertation erwähnten Untersuchungen habe ich die Grundsätze guter wissenschaftlicher Praxis, wie sie in der „Satzung der Justus-Liebig-Universität Gießen zur Sicherung guter wissenschaftlicher Praxis" niedergelegt sind, eingehalten."

Eva Findeisen

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