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The effect of feed intake on digesta passage, digestive organ fill and mass, and digesta dry matter content in sheep (*Ovis aries*): Flexibility in digestion but not in water reabsorption

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ABSTRACT

The ruminant gastrointestinal tract (GIT) adapts to changes in diet quality or feed intake level, but studies that investigate changes in organ fill, tissue mass, and function simultaneously are rare. We used 3 groups of 7 mature sheep each, fed at different DM intake levels (range 25–64 g $kg^{-0.85}$ d^{-1}) for 3 weeks preceding slaughter. We determined the mean retention times (MRT) of a solute and two different-sized particle markers (and their ratios indicating particle sorting and digesta washing) in the reticulorumen (RR) and the GIT, total tract digestibility, as well as digesta wet mass, wet organ tissue mass, and the dry matter (DM) concentration of digesta in the indvidual GIT sections. As DM intake increased, digesta wet mass in the RR and spiral colon increased by organ distension. Simultaneous increases in digesta wet mass in the omasum and small intestine were parallel to increases in organ tissue mass. DM digestiblity, MRT in the RR, measures of the RR sorting mechanism ($MRT_{large particle}RR/MRT_{small particle}RR$) and RR digesta washing ($MRT_{particle}RR/MRT_{solute}RR$) all remained constant across intake levels. Whereas the DM concentration increased in the rumen with intake, it remained significantly lower in the reticulum than in rumen. DM concentration in the omasum and abomasum remained constant, but both MRT in the distal GIT and DM concentration in the spiral and distal colon digesta decreased with increasing intake, translating into higher fecal water losses. These results indicate that the flexibility of the mature sheep's GIT ensures constant digestive functions (such as digestibility, particle sorting, digesta washing) at different intake levels but does not compensate for greater fecal water losses at increasing intakes.

1. Introduction

The ruminant digestive tract fulfills a variety of functions (Clauss and Hofmann, 2014). These include microbial fermentation, which takes place in the reticulorumen (RR), the caecum and proximal colon, as well as aut-enzymatic digestion, which takes place in the abomasum and small intestine (Van Soest, 1994). Fluid moves through the RR at a faster rate than particles, thus 'washing' the digesta and harvesting microbes that are flushed into the lower digestive tract (Müller et al., 2011). A fluid-based sorting mechanism in the reticulum ensures that large particles are retained in the RR for further regurgitation and remastication via the process of rumination (Baumont and Deswysen, 1991; Lechner-Doll et al., 1991). Reabsorption of much of the fluid required for the reticulum sorting mechanism occurs in the omasum (Hauffe and Engelhardt, 1975; Holtenius and Björnhag, 1989). There is further reabsorption of fluids from the digesta in the spiral and distal colon that is unrelated to the reticulum sorting mechanism, but determines the ultimate fecal dry matter content (Woodall and Skinner, 1993). These differences in water reabsorption function are evident as variations in dry matter (DM) concentration of the digesta along the entire gastrointestinal tract (GIT), with a low DM concentration of digesta (%DM) in the reticulum but a high %DM in the omasum (Clauss et al., 2009), low %DM in the abomasum and the small intestine, followed by a gradually increasing %DM of contents through the colon (Hecker and Grovum, 1975; Clemens and Maloiy,

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1983). However, despite these known variations in fluid contents throughout the gut, as well as the importance of the particle sorting mechanism to overall gut function in ruminants, limited research has been conducted investigating how changes in feed intake levels affect fluid concentration within each gut compartment.

The effect of feed intake on various digestive functions in domestic ruminants is well documented (Ortigues and Doreau, 1995). For example, an increased intake typically leads to greater gut fill, a shorter digesta retention and a concomitant reduced digestibility (Colucci et al., 1982; Staples et al., 1984; Shaver et al., 1986). In particular, reduced digestibility in the RR has been reported when intake is elevated, but this may be partially or completely compensated by increased digestibility in the small intestine, caecum and proximal colon (Ortigues and Doreau, 1995). Of note, an increased intake also leads to lower colonic water reabsorption due to shorter colonic retention times (Blaxter et al., 1956; Castle, 1956; Grovum and Hecker, 1973). This might mean that the ruminants' intake capacity cannot be fully used if drinking water is limited, and could be one of several factors explaining the observation that water restriction can reduce voluntary food intake (*e.g.* Mousa et al., 1983; Jaber et al., 2004).

Changes in feed intake levels also influence organ sizes of the ruminant GIT. In studies on organ sizes, increased intake led to a general increase in GIT tissue wet mass (Burrin et al., 1990; Ortigues and Doreau, 1995; Fluharty and McClure, 1997; McLeod and Baldwin, 2000). These findings might lead to the expectation that digestive and water-saving functions should be maintained at higher feed intake levels via compensation in the corresponding tissue responsible for these functions. In particular with respect to colonic water reabsorption, a lack of distinction between individual colon sections in previous studies makes such interpretations difficult.

Such changes in digestibility and digesta retention, and in digestive organ masses, are usually not investigated in the same experiment. Therefore, we aimed to characterise such changes in the gastrointestinal system of a typical ruminant, the Merino sheep (*Ovis aries*) in a single experiment. This research was expanded from a related study that tested whether the fill of the entire digestive tract could be reliably estimated using measures of intake, digestibility and digesta mean retention time (Munn et al., 2015). That study offered the additional opportunity to examine how different gut sections respond to changes in feed intake in terms of tissue and content mass and fluid present in this content, and particularly with regards to changes in the dry matter concentration along the gut.

2. Materials and methods

This research was conducted at The University of Sydney Animal Reproduction Unit, Cobbitty, New South Wales Australia, under The University of Sydney animal ethics permit no. N00/6-2011/2/5564, and has been described in greater detail by Munn et al. (2015). Twenty-one mature, Merino breed wethers (*i.e.* castrated males; body mass [BM] 46 ± 5 kg) were kept on a forage-only diet of chaffed (chopped) dehydrated lucerne (*Medicago sativa*; D & R StockFeeds, Camden, New South Wales, Australia), with a stem length of 5–7 cm, and nutrient levels (in %DM) of approximately 18% for crude protein, 43% for neutral detergent fibre, 32% for acid detergent fibre, and 10% for crude ash. This diet was chosen because it could be obtained reliably, resembled whole forage insofar that it was of a particle size that required mastication both during ingestion and rumination, and was easier to handle than whole hay, especially with respect to measuring leftovers and guaranteeing complete intake in the animals that were fed restrictively. Animals were kept individually in open-sided pens and were randomly assigned to one of three feed-level groups; one group was offered *ad libitum* feed levels (2 kg offered with an average consumption of 1.6 kg), one group was offered a medium feed level of 1.1 kg daily (around 70% of average *ad libitum* intake), and one group was offered a low feed level of 0.8 kg daily (around 50% of *ad libitum* intake) of chopped lucerne hay per animal for 2 weeks. At the beginning of week 3 on their respective feed levels the digestibility and passage experiment commenced.

All animals were equipped with a fecal collection harness; feed was provided twice daily, at the total amounts mentioned above. Water was available *ad libitum* at all times. Intake was measured daily by weighing the feed offered and any feed not consumed; representative subsamples of the diet were dried at 103 °C to constant weight to determine dry matter content. Intake was expressed as dry matter intake (DMI, kg d^{-1}), and relative DMI (rDMI) on a $BM^{0.85}$ basis (g $kg^{-0.85}$ d^{-1}) (Hackmann and Spain, 2010; Müller et al., 2013). At the beginning of week 3, all animals received three passage markers (cobalt[Co]-EDTA as a solute marker, chromium[Cr]-mordanted fibre, 1 mm particles; lanthanium[La]-mordanted fibre, 20 mm particles). Markers were applied in liquid or moistened form into the mouth via syringe, restraining the animal until it had swallowed. One animal could not be dosed in this manner, and therefore analyses including retention measurements are based on n = 20 animals only. Co-EDTA and Cr-mordanted fibres were the same as used by Munn et al. (2012) and had been prepared according to Udén et al. (1980). Cell walls were prepared from chopped hay dried at 60 °C, ground through a 1 mm mesh and treated with neutral detergent (Van Soest et al., 1991) and wet-sieved through a series of Endicott (London, England) screens. Particles that passed through a 1 mm screen but trapped on a 500 μm screen were retained for mordanting with Cr. La-mordanted fibres were the same as used by Lechner et al. (2010) and had been prepared according to Schwarm et al. (2008), using hay particles hand-cut to 20 mm and treated with neutral detergent. Three fecal samples were taken before marker application for the marker baseline, and all feces defecated within defined intervals were collected for the subsequent 9 days: every 2 h in day 1, every 4 h in day 2, every 6 h in day 3, every 8 h in day 4, and every 12 h in days 5–9. Feces were weighed, and representative samples taken (at 10% of defecation weight) for passage marker analysis. Fecal samples were dried at 103 °C to constant weight to determine dry matter content.

One to 2 days after the last day of fecal sampling for MRT measurements, animals were slaughtered between 0800 h and 1000 h after their morning feed and body mass weighing, and were immediately dissected. Dissection was via a ventral incision and the GIT was removed. No particular care was applied to prevent mixing of dorsal and ventral rumen contents. All sections of the GIT were cleared of mesenteries and adhering adipose tissue. The stomach was separated cranially at the esophageal junction and caudally at the pyloric sphincter; the small intestine was separated from the caecum caudally at the ileocecal junction. The cecum was separated from the proximal colon, while the proximal colon was separated from the spiral colon at the beginning of the first spiral coil, and the spiral colon was separated from the distal colon and rectum after the last spiral coil. All compartments were weighed individually in full and empty state. For all parts of the intestines, emptying was achieved by carefully stripping contents out of the intestinal structures. The stomach was first weighed as a whole and then, the abomasum was removed and weighed full and empty after rinsing; then the omasum was removed and weighed full and empty after rinsing; subsequently, the reticular contents were removed individually through an incision along the cranial reticular curvature and weighed. Lastly, the rumen was opened and the contents were weighed as dorsal and ventral contents, as separated by the *ostium intraruminale*. The remaining reticulorumen was weighed