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Invited Review

Physiological adaptations of ruminants and their potential relevance for production systems

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ABSTRACT - Herbivores face the dilemma that the level of feed intake is negatively related to factors that determine digestive efficiency, such as thoroughness of ingesta comminution by chewing, and retention of digesta in the digestive tract. Ruminants have evolved particular adaptations to solve this dilemma. Most ruminants share the characteristic of "digesta washing": fluid moves through their digestive tract faster than particles, thus effectively washing very fine particles, such as bacteria, out of the digesta plug. As the forestomach is followed by auto-enzymatic digestion, this allows a continuous, increased harvest of microbes from the forestomach. True rumination only evolved twice, in the camelids and the true ruminants. These both evolved a density-dependent sorting mechanism based on physical separation of the digesta by the process of flotation and sedimentation, ensuring that the process of rumination is applied to large particles. Differences in this sorting mechanism might facilitate a faster digesta processing in true ruminants as compared with camelids. The hallmark of ruminant digestive anatomy is the omasum, in which the fluid required for both digesta washing and the reticular separation mechanism is re-absorbed. In ruminants of the tribe Bovini, the omasum has reached the largest size and this group has a particularly great forestomach fluid throughput. Increasing the degree of digesta washing even more should increase microbial harvest from the forestomach and reduce the susceptibility to acidosis. At the same time, it should result in a metabolic state of the microbiome more tuned towards biomass production and less towards methanogenesis. Enhancing the forestomach fluid throughput by selective breeding could represent a promising way to further advance the productivity of the ruminant digestive tract.

Key Words: cattle, digesta washing, foregut fermenter, microbial harvest, microbiome

Introduction

Domestic ruminants are special. In contrast to domestic pigs, camelids, or horses, they belong to a family (Bovidae) that comprises an enormous extant variety of more than 100 species (Fritz et al., 2009b). This difference in species diversity between bovids on the one hand, and suids, camelids, or equids on the other hand, has been interpreted as a result of a displacement of previously more speciose large herbivore groups by ruminants (Janis et al., 1994). Ruminant species cover a large variety of ecological niches and hence display a large variety of morphophysiological adaptations (Hofmann, 1989; Kay, 1989; Woodall and Skinner, 1993; Beuchat, 1996; Cain et al., 2006; Zerbe et al., 2012). On the one hand, certain production systems, in particular more extensive systems, sometimes might benefit from employing this existing variety of ruminant species to increase the overall efficiency of resource use (Arsenault and Owen-Smith, 2002; Odadi et al., 2011; Riginos et al., 2012), but not always (Prins and Fritz, 2008). On the other hand, one could consider the variety of existing ruminant morphophysiologies as a pool from which one might choose certain traits as targets for selective breeding in domestic ruminant breeding programs (Clauss et al., 2010b). This short review is concerned with this latter option.

In particular, our approach focuses on digestive physiology. Evidently, any characteristic could be chosen as a target for selective breeding. For example, given the variety of dental traits (Archer and Sanson, 2002; Heywood, 2010; Kaiser et al., 2010) and hypsodonty (Mendoza et al., 2002; Damuth and Janis, 2011; Jordana et al., 2012) in ruminants, one could consider breeding domestic ruminants for more complex and higher-crowned teeth, if there was evidence that the production potential of domestic ruminants was constrained by the durability of their teeth. Given the variety of muzzle width (Gordon and Illius, 1988;

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Janis and Ehrhardt, 1988; Tennant and MacLeod, 2014) in ruminants, one could consider breeding domestic ruminants for wider muzzles to enhance their foraging efficiency, if muzzle width was identified as a constraint. The focus we place herein on digestive physiology is, at the moment, a subjective one.

Basic ruminant digestive physiology

Herbivore digestive physiology can be conceptualized as the dilemma to maximize feed intake while also maximizing diet quality and diet digestibility (Hume, 2005). The level of feed intake is typically negatively related with digesta mean retention time (Müller et al., 2013), a major determinant of digestibility. The intake-retention time relationship can be modulated by gut capacity (Clauss et al., 2007) and the retention time-digestibility relationship can be modulated by particle size reduction (i.e., chewing efficiency; Clauss et al., 2009d).

The exceptional reduction of ingesta particle size that functional ruminants achieve is the hallmark of ruminant digestive physiology (Fritz et al., 2009a), which allows them to increase intake (as compared with non-ruminant foregut fermenters) without compromising digestibility (Schwarm et al., 2009; Clauss et al., 2015). This increased chewing efficiency is not achieved by a particular dental design, but by a density-depending sorting mechanism in the forestomach, which separates the small particles from the large ones that are then regurgitated to be masticated again (i.e., rumination) (Lechner-Doll et al., 1991). Although merycism (i.e., regurgitation and re-mastication) and the presence of comparatively fine digesta particles have been reported in non-ruminant foregut fermenters such as kangaroos (Schwarm et al., 2013; Vendl et al., 2017) and proboscic monkeys (*Nasalis larvatus*) (Matsuda et al., 2011; Matsuda et al., 2014), true rumination linked to a sorting mechanism and with a physiologically fixed motor sequence (Gordon, 1968) only evolved twice, in the camelids and the taxonomic ruminants. While there appears to be no functional difference in the forestomach particle sorting mechanism between these two functional ruminant groups (Dittmann et al., 2015b), a major difference between them is the generally lower metabolism and lower feed intake in camelids (Dittmann et al., 2014). This may be linked to a less efficient morphophysiological design of their sorting mechanism (Dittmann et al., 2014; Dittmann et al., 2015b; Pérez et al., 2016); however, conclusive physiological studies are lacking.

In taxonomic ruminants, the particle sorting mechanism is based on a flotation-sedimentation mechanism in the reticulum (Sutherland, 1988; Baumont and Deswysen, 1991), for which a high moisture content is an important prerogative (Clauss et al., 2009b; Hummel et al., 2009; Clauss et al., 2017). The sorting mechanism automatically leads to the outflow of the fluid from the reticulum together with small particles. This fluid could represent a burden on the enzyme-secreting function of the abomasum and small intestine (that would have to compensate for the dilution effect with increased secretion rates). The omasum has been interpreted as the organ that reabsorbs this fluid and hence facilitates an efficient sorting mechanism and a great fluid throughput linked to high feed intake (Clauss and Rössner, 2014).

With this great fluid throughput, the ruminant forestomach displays a similar characteristic to most other foregut fermenters (with the exception of primates): a relatively faster movement of fluid vs. particles, (i.e., a “washing” or “flushing” of the forestomach contents; Müller et al., 2011). It has been claimed that an important effect of such a “digesta washing” is the efficient harvest of microbes from the forestomach (Hummel et al., 2008b; Müller et al., 2011; Hummel et al., 2015).

Comparative ruminant digestive morphophysiology

Although morphological differences of the digestive tract between ruminant species had been known for a long time (Garrod, 1877; Neuville and Derscheid, 1929; Langer, 1973), it was the seminal, comparative works of Hofmann (1973; 1988; 1989) and, to a less well-known extent, of Kay (1989), that placed these differences in a comprehensive ecological framework. This framework suggested convergences between feeding types (browser, intermediate feeder, grazer). Many of the resulting hypotheses were later corroborated by statistical evaluations (Pérez-Barbería et al., 2004; Clauss et al., 2008a; Meier et al., 2016). However, in many cases, correlations of investigated characteristics with the percentage of grass in the natural diet included substantial scatter, though being significant. The major challenge in these studies was not the statistical evaluation, but the development of an explanatory concept of biological validity.

Explanatory approach I: fibre content of forages

In the initial concept, Hofmann (1989) considered the major difference between grass and browse to be the general fibre concentration, with lower values in browse. However, empirical data on the fibre concentration in rumen contents in specimens of different feeding types did not support this hypothesis (Woodall, 1992). Instead, the proportions of different fibre types (hemicellulose, cellulose, lignin) were demonstrated to differ between grass and browse forages, as well as the fermentation behaviour of these forages (Hummel et al., 2006). This in turn links to hypotheses of grazers requiring longer digesta retention times and hence a larger rumen (Clauss et al., 2003; Clauss et al., 2010a). However, many other differences between grazers and browsers cannot be logically linked to fibre characteristics. For example, there is no logical concept why a high-fibre diet should be linked to small salivary glands or why a low-fibre diet should be linked to a more voluminous large intestine, as proposed in Hofmann (1989).

Explanatory approach II: various characteristics of forages and different niche characteristics

Various differences between forages might be linked to differences characterising the anatomy and physiology of browsers and grazers. Among these properties of forages might be their growth form, their spatial arrangement, the heterogeneity of their harvestable units, their physical resistance to mastication, and their content of phytoliths and secondary plant compounds (reviewed in Clauss et al., 2008b). Corresponding adaptations of ruminants include those related to oral and dental processing (Archer and Sanson, 2002; Clauss et al., 2008a; Heywood, 2010; Kaiser et al., 2010; Meier et al., 2016) or behavioural foraging strategies (Searle and Shipley, 2008). Other components of observed differences that had also been originally linked to the feeding type differences, such as the length of intestinal sections (Hofmann, 1989), were probably best explained by concepts completely unrelated to feeding types (Woodall and Skinner, 1993).

Explanatory approach III: a cohesive set of observations

Evident relationships between plant properties and the oral and dental processing apparatus notwithstanding, the observed differences between species in the anatomy and physiology of the forestomach and related structures still begged for a coherent explanation. In terms of anatomy, these included drastic differences in salivary gland size (Hofmann et al., 2008), intraruminal papillae distribution (Clauss et al., 2009c), height of the reticular crests (Clauss et al., 2010a), or omasum size (Clauss et al., 2006a). In terms of physiology, these related mainly to distinct differences in the relative retention times of fluids and particles in the reticulorumen (Hummel et al., 2005; Clauss et al., 2006b; Dittmann et al., 2015a). In the analyses of the adaptive values of these characteristics, we recently introduced the terms “moose-type” and “cattle-type” ruminants. Moose-type species are characterised by a low throughput of relatively viscous fluid (produced by large salivary glands) and a corresponding lack of stratification of rumen contents and intraruminal papillae gradient, low reticular crests, and small omasa. Cattle-type ruminants are characterised by a high throughput of a non-viscous fluid (produced by small salivary glands) and corresponding well-stratified rumen contents and an intraruminal papillae gradient, higher reticular crests, and larger omasa (to absorb the higher amount of fluid passing through the reticulorumen; cattle-type) (Clauss et al., 2010b). We chose this terminology to avoid circular reasoning when comparing the botanical composition of the diet (“browser-grazer diet”) with the adaptations of the species (“browser-grazer anatomy/physiology”).

Explanatory approach IIIa: maximizing stratification?

A first hypothesis developed to explain these patterns was based on the finding that rumen contents of a browser did not seem to stratify *in vivo* as previously reported for grazers (Clauss et al., 2001) and that, in captivity, browsing ruminants had larger faecal particles (i.e. a lesser particle size reduction efficiency) than grazing ruminants (Clauss et al., 2002). We note that both findings have been corrected since (Hummel et al., 2008a; Clauss et al., 2009a; Clauss et al., 2009b). Based on those early observations, a theory was developed that linked the throughput of great amounts of a low-viscosity fluid in cattle-type ruminants to adaptations whose ultimate objective was considered to be the enhancement of the natural tendency of grass forage to stratify in the rumen, thus facilitating a more efficient selective particle retention, size reduction via rumination, and hence digestibility (Clauss et al., 2003; Clauss et al., 2008b). When this theory was tested experimentally, however, results indicated that the particle retention and sorting mechanism did not differ fundamentally between a moose-type and a cattle-type species, even though differences in rumen content stratification, rumen fluid viscosity, and the relative rumen fluid throughput could be demonstrated (Lechner et al., 2010; Clauss et al., 2011; Lauper et al., 2013).

Explanatory approach IIIb: optimizing microbial harvest

Since then, our explanatory focus for the observed differences in fluid throughput and stratification has been on an optimization of digesta washing and hence harvest of microbes from the forestomach. This idea was first proposed by Hummel et al. (2008b) and has been elaborated since (Clauss et al., 2010b; Müller et al., 2011; Dittmann et al., 2015a). Hummel et al. (2015) demonstrated with an example calculation that because of the digesta washing effect, cattle-type ruminants could have a 10% higher microbial efficiency, quantified as the amount of microbial nitrogen produced in the rumen per unit of fermented organic matter.

The concept suggests that moose-type ruminants have adopted a strategy of defending themselves against secondary plant compounds by salivary tannin-binding proteins, which render the saliva comparatively viscous. Because the production of these proteins becomes the limiting step in saliva release, they have large salivary glands; yet, they do not achieve great amounts of saliva output. Lower amounts of saliva in combination with a high saliva viscosity reduce the tendency of rumen contents to stratify. Therefore, they lead to a homogenous intraruminal papillae formation pattern, make lower reticular crests understandable (to avoid complete emptying during reticular contractions that would cause a slow refilling of the reticulum because of the small amount of viscous saliva available), and do not require considerable omasal tissue for re-absorption (Clauss et al., 2010b).

Such moose-type ruminants are typically browsers. However, among the cattle-type ruminants, there is no clear association between the degree by which their characteristics are expressed and the percentage of grass in their natural diet (Codron and Clauss, 2010). In other words, the most extreme grazers are not necessarily the most extreme cattle-type ruminants. This was exemplified by Clauss and Hofmann (2014) listing a series of species from the taxonomic group of cattle, which have the most prominent cattle-type characteristics, yet consume higher amounts of browse (i.e., more "intermediate-type" diets) than strict grazers. This seeming contradiction could be resolved if the focus is no longer placed on adaptations to properties of the respective forages (grass or browse). Rather, we think that it is more promising to put the focus on an optimization of microbial harvest, which may be beneficial on any kind of forage. This new concept considers the different cattle-type ruminants as different stages in an evolution towards optimized microbial harvest from the forestomach.

Digesta washing, microbial harvest, microbial metabolism

A variety of *in vitro* assays (Isaacson et al., 1975; Meng et al., 1999; Fondevila and Pérez-Espés, 2008) and *in vivo* experiments with domestic ruminants (Harrison et al., 1975; Wiedmeier et al., 1987b; Froetschel et al., 1989; Bird et al., 1993) support the concept that an increased fluid throughput through the rumen, in other words, an increase in the relative passage of fluid (as compared with particles) or an enhanced "digesta washing", increases the microbial yield from the rumen system (Figure 1). This is probably due to an increased microbial flow to the lower digestive tract. Additionally, the metabolic state of the ruminal microflora is most likely tuned to faster growth rates probably fuelled by a higher digestive capacity of the microbes, with the majority of microbial cells in the growth and reproductive stages (Isaacson et al., 1975; Hummel et al., 2015). Such a shift in microbial metabolism (Shi et al., 2014) might also lead to a decrease in methane yield (Isaacson et al., 1975; Van Nevel and Demeyer, 1979). This shift might occur because of an effect similar to the "partitioning factor" of feeds, that is, the degree by which they trigger energy transfer into microbial growth or into short-chain fatty acid and hence also CH_4 production (Blümmel et al., 1997; Moss and Newbold, 2000). A higher fluid throughput due to a higher saliva production should also be protective against acidosis. Carefully designed experiments are warranted to test the effect of differentially increasing rumen fluid throughput, by infusion of artificial saliva via fistula (Rogers et al., 1979), or by pharmacologically enhancing saliva production (Wiedmeier et al., 1987a; Wiedmeier et al., 1987b; Froetschel et al., 1989; Bird et al., 1993), not only on measures of digestive efficiency, pH, and microbial and methane yield, but also on the metabolic state (Shi et al., 2014) of the microbiome itself.

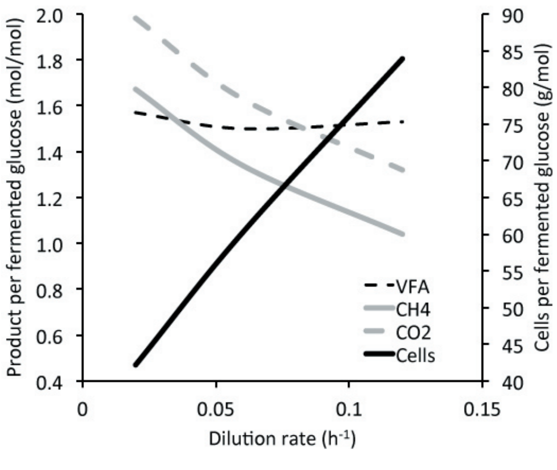

Figure 1 - *In vitro* experiment on the effect on increasing dilution rate (i.e., fluid throughput) on measures of microbial activity – volatile fatty acids (VFA), methane (CH_4), carbon dioxide (CO_2), and cell numbers. Note the decrease in methane and the increase in microbial biomass (cell numbers). Data from Isaacson et al. (1975).

Selective breeding for digesta washing?

It has been suggested that domestic ruminants could be selected for increased digestive efficiency, based on phenotypic characteristics of the way digesta moves through their digestive tract (Hegarty, 2004). Ruminants can actually be bred to differ in the mean retention time of digesta (Thompson et al., 1989; Smuts et al., 1995; Goopy et al., 2014). Variation in ruminal digesta retention time is currently considered the most likely explanation for the inherited differences in methane emissions (Pinares-Patiño et al., 2013). Frothy bloat in cattle is associated with decreased saliva production (Gurnsey et al., 1980) and decreased ruminal fluid passage rates (Okine et al., 1989). A report of a successful breeding program to reduce bloat susceptibility (Morris et al., 1997) therefore suggests that increased saliva flows can be achieved. Given the evidence from wild ruminants that not only retention time in general, but the difference between fluid and particle retention in the rumen is a species-specific and hence genetic/heritable characteristic, selective breeding for this measure would theoretically be feasible, if appropriate proxies could be found to evaluate phenotypes.

Conclusions

The diversity of ruminant species can be considered a catalogue of genetically fixed, morphophysiological characteristics that could, in theory, be exploited in domestic species by selective breeding. Some characteristics of that catalogue have most likely been selected indirectly during the process of breeding for phenotypes of high production value. For example, although reticulorumen volume is not a direct selection criterion, a particularly voluminous reticulorumen most likely results as an effect of breeding for phenotypes with a high intake capacity for a high milk yield. Other characteristics, such as those related to dental anatomy and durability, could be interesting in respect to intentions to prolong domestic ruminant lifespan. We propose that the characteristic of pronounced digesta washing and the associated microbial harvest and change of the microbial metabolism could represent a target for selective breeding that could further improve the efficiency of domestic ruminants.

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