Ruminant Physiology

by Dr Christina Marth

Ruminants belong to the suborder **Ruminantia** within the order **Artiodactyla** (even-toed hoofed animals). In this suborder, there are 66 living genera and 164 living species.

Most domestic ruminants, including cattle, sheep, goats and buffalo, belong to the family **Bovidae**. Other examples for ruminants are the deer family (deer, moose, elk, caribou), antelopes, the giraffe family (giraffes and okapi) and the **Camelidae** (camels, dromedaries, llamas, alpacas, vicunas).

All ruminants have **forestomachs** serving as **fermentation chambers.** As the name suggests, this group of animals **ruminate** (*Latin*: chewed over"). There are variations in size and shape of the non-glandular forestomach chambers, but all provide a place for bacteria to **break down complex plant carbohydrates** that mammals would otherwise be unable to digest. This allows for a **high energy yield from low energy food** (e.g. grass). Their ability to ruminate also means that they can eat quickly and **ruminate later**, potentially in a safer surrounding. The disadvantages of making use of low energy food are the need to **consume large amounts of food** and the **complicated, highly-regulated digestive process** required to extract this energy. To make the most use out of the ingested food, digesta needs to be separated so that large particles are re-masticated, gas can be eructated, and the liquid portion can move on to the omasum.

Some of the **main functions** of the ruminant forestomachs are:

- To serve as a **fermentation chamber** for microbes
- To **mix and separate ingesta** appropriately
- To allow built-up **gas to escape**
- To **buffer the rumen** content to maintain an optimal pH for the microbes while conserving water and electrolytes.

While Bovidae have three forestomachs plus one glandular stomach, Camelidae only possess three chambers. They are missing the omasum-equivalent. Chambers 1, 2 and the first two thirds of chamber 3 serve as fermentation chambers, while the glandular section is confined to the last third of chamber 3.

Rumen fermentation and absorption

To break down cellulose and hemicellulose, mammals require bacteria as their own enzymes are unable to do so. The **cellulolytic bacteria** are **strict anaerobes** that break down these plant structures into simple sugars that provide them with energy. The end products of their metabolism are **volatile fatty acids (VFA)**, primarily **acetate, propionate** and **butyrate**. These VFA are **absorbed** through the forestomach wall and supply about **60-80% of the ruminant's dietary energy**. **Rumen papillae** make this process more efficient by increasing the surface area for absorption. The rumen is lined with **stratified squamous epithelium** capable of absorbing VFA, as well as water and electrolytes, while being robust enough to withstand the abrasive forces of the rough ingesta.

Another source of energy are the rumen bacteria themselves once they get flushed into the intestine with other digesta. Rumen microbes can combine nitrogen from ammonia or urea with parts of the simple sugars derived from cellulose to **produce all essential amino acids**. These can then be absorbed by the cow, if the bacteria end up in the intestine.

As VFA are acids, the normal rumen pH relies on a balance between their production and absorption. If the rumen bacteria suddenly gain access to a grain-rich diet, VFA production increases rapidly and the rumen pH drops. In addition, bacteria specialised in **starch digestion** rapidly increase in number and mainly produce **lactic acid** as the end product of their metabolism. Lactic acid is nearly 10 times stronger than acetate and in combination with other VFA, it can make the **pH drop below 5.7**. Below this point, the physiological rumen flora is dying, and the rumen epithelium may get damaged releasing bacteria and their toxins into the blood stream. This condition is referred to as **rumen acidosis**. If grain is introduced into a ruminant's diet more slowly, bacteria that utilise the lactic acid can help stabilise the system.

Other populations in the rumen ecosystem include a small population of **fungi** that help break down lignin (a woody plant part) and **protozoa**, eukaryotic cells that generally live by ingesting bacteria and each other. Protozoa are a good biomarker for a low rumen pH, as they die rapidly in an acidic environment.

Rumen motility

The content of the rumen needs to be moved around so that **bacteria can reach** the fibres they are digesting. In addition, ingesta needs to be **separated** through selective cranial and caudal movements. This allows for **regurgitation** of inadequately digested material so that they can be more thoroughly chewed, **eructation** of the large amounts of gas produced during fermentation (~ 60 L per hour) and the **transport of adequately digested material** towards the omasum and abomasum.

Each type of contraction is controlled as a **distinct reflex** through the **vagal nerve** and executed through the **two perpendicular layers of smooth muscle fibres**. The nature of the muscle "bands" which encompass the ruminant stomach explain the directions of the contraction sequences.

In cows and sheep, the rumen ingesta forms **three distinct layers** – a **raft** of fibrous material floats on top of the rumen **fluid**, in which particle size decreases from dorsal to ventral. On top of the raft, a **gas cap** can be found. In **most other ruminants**, this layering of rumen ingesta is not present and **fibres of all sizes are continuously mixed**.

Motility patterns

To move the ingesta in the rumen, there are two types of contraction patterns differing in function and the direction of ingesta movement:

- The **primary (mixing) sequence**
- The **secondary (eructation) sequence.**

Rumination may occur during both mixing and eructation sequences.

Primary (mixing) sequences

These sequences commence with a **biphasic reticular contraction**, followed by the contraction of the **ruminal atrium and cranial pillar**, then the **dorsal surface** to the **caudal**, then **ventral rumen**.

The purpose of these sequences is the **mixing** of dry fibres with buffered saliva and bacteria to promote effective fermentation. The initial reticulum contraction directs liquid flow into the ruminal atrium and fibre flow to the dorsal rumen. Fine particles and liquid digesta are aspirated out of the rumen into the omasal canal. The liquid digesta of the ruminal atrium is directed into the dorsal sac, then the ventral sac and forward across the now relaxed cranial pillar. Hence, the direction of ingesta movement is: **cranial → dorsal → caudal → ventral → cranial**.

These contractions occur **about three times in every two minutes** and can be heard by placing a stethoscope in the **left paralumbar fossa**.

The thicker the **rumen raft**, the more it stimulates motility **promoting the mixing of ingesta**.

Secondary (eructation) sequences

Eructation sequences **commence similarly to the mixing sequence** with a biphasic contraction of the reticulum followed by the contraction of the ruminal atrium and then the dorsal sac. The difference arises during the **contraction of the ventral sac** when the **cranial pillar does not initially relax** forcing the **rumen content upwards** instead of cranial. This, in turn, leads to **compression of the gas cap**. The **dorsal sac contracts again** starting **caudally** and moving **cranially** which moves the **gas cap in front of the cardia**. When free gas is detected, the **cardia relaxes**, and the gas is forced into the **oesophagus** where it is transported upwards by **retrograde contractions** of the oesophagus. To prevent cows from burping and thus potentially attracting predators, part of the gas first **enters the trachea and the lungs** before being **exspirated** with the next breathing cycle. Inside the rumen, the contraction sequence finishes with another **contraction of the ventral sac,** this time with a relaxed cranial pillar allowing the ingesta to move forward.

The purpose of these contractions is both **mixing and eructation of gas** produced during fermentation. Most of the produced gas is **carbon dioxide**, while about **26% is methane**.

Eructation sequences generally occur after **every second to third mixing sequence**.

Rumination

Ruminants spend many hours re-processing their digesta. The **roughage quality** of the food will **determine** the **time** spent ruminating. **Grazing cattle** spend approximately **1/3 of their day ruminating** the coarse material floating on the surface of the reticulum and rumen contents. The objective of the rumination process is to **reduce the particle size** of the roughage to **improve the exposure to micro-organisms**. Fibres activate **mechanoreceptors** in the mucosa of the reticulum, rumino-reticular fold and the cardia to stimulate rumination. However, it may decrease or even stop if ruminants are disturbed or stressed.

Rumination involves:

- **regurgitation** of digesta
- **re-mastication** of the digesta
- the addition of more **saliva** to the ingesta
- subsequent **swallowing**.

Generally, regurgitation occurs in synchrony with the contractions of the reticulo-rumen at about one-minute intervals.

Rumination commences with the **contraction of the reticulum** resulting in the **flooding of the relaxed cardia** with partially fermented fibres. Simultaneously, the animal makes an **inspiratory effort against a closed glottis lowering** the **pressure** in the **thoracic oesophagus** sufficiently to allow any positive pressure in the rumen to eject the digesta. Once in the oesophagus, the bolus is propelled by **antiperistalsis**. Note that this is a very different reflex process to the vomiting reflex in monogastric animals. When the bolus arrives in the mouth, **liquid is squeezed out** and swallowed, before the bolus gets **re-insalivated** and **re-masticated**. Simultaneously, **the rumen undergoes a primary or secondary contraction cycle**. After the cycle has finished the bolus gets swallowed and re-enters the rumen.

Stimuli

Stimulation of several locations will cause reflexes leading to an increase in the frequency of reticulo-ruminal contractions. The afferent (sensory) information which is important in the regulation of ruminant motility arises from buccal, pharyngeal, oesophageal, gastric and intestinal locations.

Here are some examples:

- **Buccal and pharyngeal stimulation**: There are differences in the frequency of reticulo-rumen contractions when fresh food is ingested compared with when regurgitated digesta is being chewed.
- Stretch of the **oesophagus** or tactile stimulation of the oesophagus produces an increase in salivary gland flow rate and the frequency of contractions of the reticulum and rumen. Extreme distension can cause inhibition of movement.

- Passive stretch of the **reticulum** and **reticulo-rumen fold** causes contraction of the reticulum.
- The **rumen** is particularly important as a site of reflex modification of gastric and oesophageal motility, salivary secretion and rumination. Both inhibition and excitation have been shown. Gaseous distension of the rumen invokes reflex eructation.
- Increase in levels of acid (fall in pH) in the **abomasum** increases reticulum contractions.
- Tactile stimulation of the abomasal mucosa will produce a contraction of the reticulum.
- Distension of the **duodenum** generally inhibits reticulo- ruminal motility.

Control of motility

The alimentary tract of all mammals is composed of smooth muscle for most of its length (except for varying parts of the oesophagus and the anus). Regulation of the ruminant digestive tract motility is a smooth muscle control action.

There are two types of movement of the reticulo-rumen:

- **Intrinsic contractions** consist of low amplitude waves travelling in the **smooth muscle** wall of the reticulo-rumen and occur even when the nerves to the reticulo-rumen are severed. The local **myenteric plexus** controls these contractions. Local reflexes in conjunction with the intercellular communication channels (gap junctions) are important in regulating rumen motility.
- **Extrinsic contractions** occur only when the **vagal or splanchnic nerves** are intact. These powerful contractions are initiated by burst of activity in the vagal nerves originating in the gastric centres of the medulla oblongata.

Intrinsic contractions

Smooth muscle is normally a **spontaneously active** tissue contracting continuously in a slow and rhythmic fashion. It will alter the rate and force of contraction in response to local mechanical stimuli. Two separate mechanisms exist in the gut which allow intrinsic or spontaneous rhythmical activity:

- **intrinsic myogenic contractions** caused by smooth muscle cells.
  The basis of the myogenic contraction is the **inherent instability** of the smooth muscle cell membrane (a **'leaky' membrane**) which depolarises spontaneously. Through intercellular communications occurring at **tight junctions** between the cells, the signal spreads slowly to neighbouring cells. This intrinsic communication between adjacent smooth muscle cells is sufficient to produce peristalsis which simultaneously involves all the circular layer muscle cells in a localised region contracting.
- **intrinsic neurogenic contractions**: contractions dependent on the fine nerves running in the wall of the gut.

Extrinsic contractions

The extent of peristalsis in smooth muscle fibres is further controlled by higher centres through the **autonomic nerves** and can be altered by circulating **hormones, local stimuli** and **reflexes**.

The **autonomic nervous system** involving the release of acetylcholine from the **parasympathetic nerve endings** and noradrenaline from the **sympathetic nerve endings**. These bind with membrane receptors in the cell membrane of the smooth muscle cells or the **myenteric plexus** cells and produce alterations in their activity. **Acetylcholine increases motility** while **noradrenaline decreases motility**. The **vagus nerve** is the predominant nerve of the parasympathetic system, while the **splanchnic nerves** are sympathetic.

Gastric groove

The gastric groove is a specialised region of the reticulum which is formed from reticular and omasal smooth muscle and oesophageal muscles. The groove can be formed into a **tube** between the oesophageal orifice and the reticulo-omasal orifice, by contraction of the muscles forming the two lips. Contraction of the oesophageal groove results in a passage which ensures that any swallowed material is kept out of the reticulo-rumen.

An immature ruminant swallowing saliva can have this material go into either the reticulo-rumen or the omaso-abomasum. Any swallowed plant material should go to the rumen. When the lamb/ calf is suckling, the **milk protein must be directed to the abomasum** for acid hydrolysis. The gastric groove responds with **reflex** actions which depend on the **stimulation of taste and mechano-receptors** in the **buccal and pharyngeal cavities**.

In the adult animal the groove remains open so that ingesta can be transferred to and from the oesophagus, reticulum and rumen. However, adult animals retain the oesophageal groove reflexes. If they swallow salts, both mineral and metallic, the groove will contract and direct the contents towards the abomasum. This can be used during treatments.

The gastric groove reflex is controlled by the vagus nerve.

Salivary secretion

The major salivary glands found in most mammals are also found in ruminants, but their activity varies considerably. Of the three main paired salivary glands: the **parotid**, the **mandibular** and the **sublingual**, the **parotid is the most altered in ruminants** when compared with the monogastric animals.

These adaptations are an integral part of the optimisation of the ruminant digestive system for their diet. The functions and secretions of the salivary glands ensure that **digestion** occurs as completely as possible and **homeostasis** is ensured. In addition to the common functions of saliva, such as keeping mucosal surfaces moist and predigesting and moistening of the food, saliva in ruminants also has the function of securing rumen acid homeostasis. An adult cow produces about **100-150 L of saliva each day**.

Salivary gland secretions are controlled by both **parasympathetic and sympathetic stimuli**.

Parotid saliva, by volume, is the most important secretion. **Parasympathetic innervation** causes a **profuse flow** with **low protein content**. The latter is only slightly increased by sympathetic stimulation. Stimulation of many receptors in the buccal cavity, pharyngeal cavity, oesophagus, reticulum, rumen, omasum and abomasum can increase parotid salivary flow. These stimuli can be stretch, tactile or chemical. Any **mastication** (including during rumination) results in an **increased flow rate**.

Parotid saliva is a very nearly **iso-osmotic buffered medium** based on levels of bicarbonate in the secretion. It buffers well between pH 6 and pH 7. It assists in the maintenance of the alkaline rumen medium by buffering the VFAs produced by rumen fermentation. In contrast to other species, there are almost no enzymes such as amylase in ruminant parotid saliva.

The composition of **mandibular gland secretion** is more variable. Stimulation of the **sympathetic nerves** causes its normally clear secretion to become very **viscous and opaque**. This sympathetic secretion is very rich in **mucopolysaccharides** which produce a stable foam if shaken.

Comparison of parotid and mandibular gland salivary secretions at a glance:

PAROTID	MANDIBULAR
Consistent serous secretion	Mucous secretion (after sympathetic stimulation)
strongly buffered (pH 6-7)	weakly buffered
Spontaneous flow	No spontaneous flow
Daily Output (sheep - both glands) 3 - 8 litres	Daily Output (sheep - both glands) 0.4 – 0.8 litres
Reflex stimulation of flow from mouth, oesophagus and reticulo-rumen.	Reflex stimulation of flow almost exclusively from buccal region in the mouth.

Water & electrolyte balance

Due to the very large water reserves held in the ruminant forestomach, water and salt regulation is very important. Reductions in the volume of the rumen can result in inefficient digestion and resultant loss of condition. Water is sourced from drinking free water or milk, from moist food, or from oxidation of food. It is lost in respiration, faeces, urine and sweat. **Faeces** is the most serious potential water loss accounting for **20 to 30% of the total water loss**. This varies between species: While a 350 kg bovid excretes 10 L of faecal water per day, a camel on a similar diet only excretes 5 L per day. Part of this difference is the amount of faecal material produced but part is the water content. Water content in faeces in ruminants can be reduced to 60%. Genetically adapted animals can reduce this value further. **Most livestock have to drink at least every second day**.

Even with regular water intake, continuous loss of water and salt from the rumen along with the digested food material would quickly result in a dehydrated animal. Systems are required to recover as much of the liquid lost from the rumen as possible. The **omasum** is the first site of liquid recycling. **Absorption of water from the inflowing rumen contents** retains some of the liquid. The digesta cannot become too dry or they will not pass through to the abomasum, which requires a water-based slurry on which acid hydrolysis can occur. Thus, further absorption must take place in more distal parts of the gut.

Water and salt that have been recovered from the rumen into the blood stream must be recirculated into the rumen. The **parotid glands act as the re-circulators of salt and water**. The volumes of iso-osmotic saliva which are produced by both parotids is enough to nearly completely replace the entire volume of the rumen in 24 hours. This is one reason for the large quantities of saliva produced and the reflex link between the salivary glands and gastric motility.

Even though the salivary glands are working almost continuously to recycle salt and water, there are breakdown products which must be removed from the blood (such as urea). For this to be able to occur there must be some loss of liquid and salt through the **kidneys.** Compared to many other species, ruminants have a much higher protein content in their urine, *i.e.* a more concentrated urine. In experiments where sheep have been fed while undergoing heavy water diuresis, the urine flow will stop as soon as the animal begins to eat. This shows that even in the kidney, there are **reflex effects of gastric activity**.

Conclusion

Digestive physiological processes are intimately involved in the homeostatic mechanisms in the ruminant. The special needs of the fermentative digestive process require special adaptations to ensure proper control. Motility is complicated by the requirements to ruminate, eructate and to swallow. Gastric reflexes must ensure that digesta travels in the correct directions either down the alimentary tract or retrogradely for re-processing. Mixing must be maintained and gas levels must be controlled. The entire content must be buffered and kept at a suitable liquid level. Salivary glands are specially adapted to act as water and salt recyclers as well as the primary hydrators of food.

Bibliography

Reece. Dukes' Physiology of Domestic Animals. 13th edition (2015). Wiley Blackwell Publishing.

Cunningham and Klein. Textbook of Veterinary Physiology. (2007) 4th edition. Saunders.

The ruminant animal digestive physiology and nutrition. Church DC Ed. (1988). Eaglewood Cliffs, Prentice Hall Publishers.

J. Patterson, lecture notes (2017)