# Veterinary Bioscience: Digestive system

## Lecture 23 – The role of microbes in digestive function

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## Key words

Foregut fermenter; ruminant; hindgut fermenter; bacteria; nutrition; volatile fatty acids; carbohydrates; rabbits; guinea pigs; kangaroos; herbivores


## Intended Learning Outcomes

At the end of this lecture you should be able to:

- Compare the roles of microbes in the digestive function of different domestic animal species, and explain how disruption of the microbiome can result in disease.
- Explain the role of microbes in the digestive processes of hindgut and foregut fermenting animals.
- Discuss the relative advantages and disadvantages of microbial digestion in the foregut and hindgut.

## Introduction

This lecture considers the role of bacteria in the digestive function of various different species, although it is primarily the herbivores where bacteria are essential for digestion of plant non-structural carbohydrates. Herbivores have developed several different systems for accommodating their intestinal microbiota in different parts of the digestive tract, and the advantages and disadvantages of having bacterial digestion in the forestomach or the hindgut can be compared. In all cases, while intestinal bacteria bring great benefits to the animal, disruption of normal microbiota can cause quite severe disease.

## Role of intestinal bacteria in carnivores

Although dogs and cats do not rely on bacteria for breakdown of food material to release substrates for energy production, they do possess a complex microbiota in their colons (anaerobic bacteria normally predominate). There is some variation in microbiota with different diets and environmental conditions, and there is evidence for some degree of bacterial fermentation with volatile fatty acid production and subsequent colonic absorption. Vitamins such as vitamin K and $B_{12}$ may also be produced, although their absorption from the colon may be limited. Two major beneficial roles of the colonic microbiota may be to promote proliferation of intestinal epithelial cells and to help prevent the colonisation and proliferation of harmful bacterial species within the intestine.

## Why do herbivores rely on bacteria for their digestion?

The foods of ruminants, mainly forages and fibrous roughages, contain carbohydrates which consist mainly of β-(1,4)-linked polysaccharides such as cellulose, which cannot be broken down by mammalian digestive enzymes. Bacteria however, have enzymes which can break these bonds and release simple sugars that they then convert to volatile fatty acids (VFAs). These are passively absorbed into the blood stream (or in some cases metabolised in the gut wall) and can be converted to glucose and other useful molecules in the liver. Therefore, special systems of digestion have been evolved that uses the aid of microbial actions on food. Other carbohydrates such as hemicellulose can also be degraded, although the extent depends on the degree of encrustation with lignin, which is indigestible to gut bacteria as well as mammalian enzymes. Secondly, the microorganisms synthesise essential amino acids that may not be present in the diet, and also the bacteria are net producers of water soluble vitamins (B group vitamins and vitamin K) which may be insufficient in the herbivore diet.

## Foregut fermenters

Foregut fermenters include cattle and sheep (true ruminants), camels and alpacas (atypical ruminants) and kangaroos (which are not ruminants; see below). Foregut fermenters have evolved a special system of digestion that involves microbial fermentation of food prior to its exposure to their own digestive enzymes. The reticulo-rumen of ruminants provides a continuous culture system for anaerobic bacteria, protozoa and fungi. The food is partially fermented to yield principally volatile fatty acids, microbial cells and the gases methane and carbon dioxide.

[*Fermentation is defined as the breakdown of carbohydrates to either alcohols or organic acids and carbon dioxide by bacteria, yeasts or a combination thereof, under anaerobic conditions*].

The volatile fatty acids produced in the rumen from carbohydrate fermentation (principally acetic, propionic, and butyric acids) are mainly absorbed through the rumen wall. The microbial cells, together with undegraded food components, pass into the abomasum and small intestine, where they can be digested by enzymes secreted by the host animal.

It should be noted that food proteins are also broken down by the rumen bacteria – hydrolysed to peptides and amino acids. Some amino acids are further degraded to produce ammonia, although some of this can be utilised by the microbes to synthesize microbial proteins. Therefore, with most diets, the great majority of protein reaching the ruminant small intestine will be microbial protein, and this will be of fairly constant composition nutritionally. Very little will be undegraded food protein. The capacity of intestinal bacteria to digest lipids is rather limited. Triacylglycerols and phospholipids may be hydrolysed and converted to stearic acid. Bacterial lipids are also generated, and these will later be absorbed and may be incorporated into milk and body fat of ruminants.

***Types of rumen bacteria***

The rumen bacteria number between $10^{10}$ – $10^{11}$ per gram of rumen contents (75% of them attached to food material). Only a fraction of them have been identified, since many of them grow poorly in culture and only recently have molecular biological techniques been available to differentiate them definitively. However, there are probably many hundreds of different species; most are non-spore forming anaerobes. The normal rumen flora is established quite early in life, as early as six weeks of age in calves.

To break down the plant cell walls, digest the cellulose, release smaller carbohydrates and then convert them to volatile fatty acids, many different types of bacteria must work in an interactive way.
For example:

- Cellulytic bacteria (breaking down cellulose and cellobiose) include members of the family *Ruminococcus* spp., *Bacteroides* spp. and *Fibrobacter* spp. One of the fermentation products, succinic acid, must be converted by species such as *Selenomonas* spp. to propionic acid, which can be absorbed and utilised by the animal.
- *Streptococcus* spp. and *Lactobacillus* spp. break down starch and fructan carbohydrates to release glucose, fructose and lactic acid. Lactate and glucose are then metabolised by other species.

The total numbers of bacteria and the relative population of individual species varies with the animal's diet. For example, diets rich in concentrate foods promote high total counts and encourage the proliferation of lactobacilli. Also, antibodies secreted in the saliva can influence specific bacterial populations and help to keep numbers fairly constant.

Protozoa are present in smaller numbers than the bacteria ($10^6$ per ml), but may also contribute to digestion in the rumen. Fungi also play a role; they may invade the plant tissues and are capable of utilising most polysaccharides.

***Rumen environment***

Like other continuous culture systems, the rumen requires a number of homeostatic mechanisms. The acids produced by fermentation could reduce the pH of the rumen liquor drastically if not for the buffers present. Under normal conditions the pH is maintained at 5.5-6.5. Phosphate and bicarbonate contained in the saliva act as buffers. Also, the rapid absorption of acids helps to stabilize the pH. The osmotic pressure of the rumen contents is kept near to that of blood by the flux of ions between them, and the temperature in the rumen liquor is maintained between 38 and 42 °C. Oxygen entering the rumen with food is quickly used up to maintain the anaerobic environment, and undigested food components are removed (together with bacteria) by passage of ingesta through the reticulo-omasal orifice.

***The ruminant hindgut***
It should also be remembered that although the rumen is the pre-eminent place for the digestion of fibrous foods, the colon and caecum also sustain significant microbial populations. Volatile fatty acids are also produced and absorbed here. Ruminants have substantial capacity for hindgut fermentation, and this is useful for situations where large amounts of very fibrous forage are being fed, where undigested fibre from the rumen can undergo further bacterial action.

***Kangaroos***
Again, it is in the expanded foregut where bacteria and fungi are able to ferment food that the animal’s own digestive enzymes would not be able to break down. However, the kangaroo is not a true ruminant; instead is has a greatly expanded forestomach (much more developed than the saccus caecus in the horse), with sacculated (non-glandular) and tubular regions. Despite a herbivorous diet similar to ruminants which would be expected to release large quantities of methane through eructation, kangaroos release virtually none. The hydrogen byproduct of fermentation is instead converted into acetate, which is then used to provide further energy. Scientists are interested in the possibility of transferring the bacteria responsible from kangaroos to cattle, to reduce the greenhouse effects of methane release in the atmosphere. The bacteria have yet to be isolated.

## Hindgut fermenters

The advantages of having the majority of bacterial digestion in the hindgut is that not all food constituents are exposed to bacterial breakdown; good quality dietary protein, fats and non-structural carbohydrates can be digested and utilised by the animal in a similar way to the carnivores and omnivores. Therefore, the amount of easily digestible substrates such as starch reaching the hindgut is much reduced and it is mainly the indigestible fibre which is acted on by the bacteria. However, this does not only include structural carbohydrates such as cellulose; it also includes fructan carbohydrates from forage which are water soluble but cannot be broken down by mammalian digestive enzymes. On the down side, digesta may not be held in the GI tract for sufficient time to allow optimal/complete bacterial action. For example, when fed hay and concentrates, horses digest about 85% of organic matter that would be digested by ruminants.

***Horse***
A limited amount of fermentation occurs in fundic region of the stomach (saccus caecus). The large volumes of saliva produced by the horse help to provide an optimum pH in the proximal stomach. In this region, where the pH is around 5.4, there are normally approximately $10^8$ to $10^9$ bacteria per gram of ingesta. These bacteria, such as *Lactobacillus* spp. and *Streptococcus* spp. can withstand a fairly acidic environment, and can digest some starch and fructan carbohydrate and produce volatile fatty acids. However, in horses fed only one or two large meals per day, volatile fatty acid production in the stomach may contribute to gastric ulcers forming in the non-glandular parts of the stomach lining.

Most fermentation takes place in the hindgut, in the enlarged caecum (30 litres) and colon (60 litres). These organs contain bacteria and protozoa which digest the food constituents in a similar way to the rumen micro-organisms. Bacterial numbers in the region of $10^{10}$ per gram of ingesta, and more than 50% of equine faeces is contributed by bacteria (including bits of dead bacteria; on a dry matter basis). About 2–4% of the bacteria in the hindgut are cellulytic (cellulose digesting) and as in the ruminants, *Ruminococcus* spp. are the most important type, along with *Fibrobacter* spp. Fungi also help break down cellulose, and bacteria together with protozoa (more than 70 species) can digest pectins and hemi-cellulose; although the protozoa do not appear to play an essential role in digestion. Streptococci and lactobacilli are also present to convert starch and simple sugars to lactate. Diet and digesta have a major effect on bacterial populations, and numbers of specific species of micro-organisms may change by more than 100-fold during 24 hours when horses are fed discrete meals rather than grazing. The relative numbers of the different species are generally much less constant in the hindgut of the horse compared with the rumen of the cow.

***Rabbits and guinea pigs***
Rabbits are also hindgut fermenters, and have a large caecum (which may contain 40% of intestinal contents). The caecum has 10 times the capacity of the stomach. As stated above, the limitations of hindgut fermentation are that digesta may not be held in the GI tract for sufficient time and many products of digestion (particularly amino acids and vitamins) are not absorbed. Rabbits overcome this problem by practising coprophagy (the consumption of faeces).The rabbit has perfected this process by producing two types of faeces: the normal hard pellets (which are not eaten) and the soft faeces or caecotrophs, which contain well-fermented material from the caecum, and which are consumed. [*This is a higher degree of specialization than the coprophagy (reingestion of normal faeces) which is practised by many rodents*]. Caecotrophs contain microbes and products of microbial fermentation including amino acids, volatile fatty acids, and vitamins. A gelatinous mucous coating protects them from some of the stomach acid.

Guinea pigs (cavies) are also strict herbivores and are caecotrophic. The caecum is the largest part of the digestive tract, usually containing up to 65% of the gastrointestinal contents. It is large, thin-walled, and fills most of the left ventral abdomen (15–20 cm in length). Young cavies initially populate their intestinal tract by eating the sow's caecotrophs and pellets. Gut flora is primarily Gram-positive bacteria with many anaerobic *Lactobacillus* spp., coliforms, yeasts, and Clostridia may also be present in smaller numbers.

***Birds***
Birds such as poultry have two caeca and a colon in which to ferment food residues; however, they gain little or nothing from hindgut fermentation when fed a commercial concentrate diet. Birds reared in a sterile environment with no microorganisms grow even better than normal birds, so in some situations the intestinal flora may be no advantage at all. The situation may be somewhat different in the wild, however.

## Disturbances of the intestinal bacterial flora

While bacteria are essential for the normal digestive function of herbivores (even more so than carnivores and omnivores), if the balance between the different populations of bacteria is not maintained within reasonable limits, then problems can arise which may have serious consequences for the animal. Growth of specific groups of bacteria at the expense of others (which may lead to the production of toxic metabolites) is prevented by the normal healthy gut flora.

***Ruminal acidosis in the cow***
Too much dietary non-structural carbohydrate (starch in cereal grains) entering the rumen over a short period of time can severely disrupt the balance of bacteria in the rumen, and in some cases lead to a potentially lethal acidosis. More commonly in cattle feedlots we see subacute (less severe) rumen acidosis, which decreases feed and energy intake. The starch is easily fermentable by streptococci and lactobacilli and this leads to the production of lactic acid within the rumen, which lowers the pH below 5.5 and starts to kill off other bacteria. The acidity may also cause inflammation of the rumen mucosa (rumenitis) and impair VFA absorption and rumen motility.

***Carbohydrate overload in the horse***
As in the rumen, the optimum pH for microbial activity in the caecum is around 6.5, and this also promotes VFA absorption. Normally very little starch escapes digestion in the small intestine and reached the bacteria in the caecum and colon. However, if a horse gets into a grain store and gorges itself on oats or barley (or grain-based concentrates) then the mammalian digestive enzymes are overwhelmed and most of the starch will be available for rapid fermentation in the hindgut. Numbers of streptococci and lactobacilli can increase

dramatically (100- to 1000-fold) within a few hours, and again lactic acid production results, leading to death of other bacteria.

The major problem in horses is that they are very sensitive to the inflammatory effect of bacterial cell wall toxins. As the acid in the hindgut damages the sensitive mucosa, these toxins (there are about 4 million lethal doses contained in the GI tract of a normal horse) enter the blood circulation. This causes a 'toxic shock syndrome' (endotoxaemia) which causes circulatory disturbances, organ failure and laminitis (detachment of the suspensory structures within the hooves).

***Enteritis in guinea pigs***

Common disorders in guinea pigs include anorexia due to hindgut dysbiosis (a change in microbiota) and motility, and diarrhoea. Changes in diet, stress, illness or anesthesia may alter gut motility and/or gut microbiota, resulting in diarrhoea, but the most serious form is Clostridial enteritis secondary to antibiotic therapy. Certain antibiotics disrupt the normal gut flora in such a way that Clostridial bacteria can overgrow and produce very potent toxins. The resulting diarrhoea and dysentery may be fatal. This condition can also occur in horses, and care must be taken in selecting antibiotics for use in these species.

## Summary

***Advantages of microbial digestion in the foregut:***

- Large quantities of food can be stored rapidly for later mastication and fermentation
- Bacterial cell contents (a source of protein) are released at an early stage in digestion
- The main products of fermentation have ample opportunity to be absorbed in the remainder of the tract

***Disadvantages of microbial digestion in the foregut:***

- All food constituents are exposed to bacterial breakdown

***Advantages of microbial digestion in the hindgut:***

- Not all food constituents are exposed to bacterial breakdown
- Dietary protein, fats and non-structural carbohydrates can be digested and utilised by the animal in a similar way to the carnivores and omnivores
- The amount of easily digestible substrates such as starch reaching the hindgut is much reduced and it is mainly the indigestible fibre which is acted on by the bacteria

***Disadvantages of microbial digestion in the hindgut:***

- Only one opportunity to chew the food, therefore animals must chew thoroughly as it ingests feed
- Digesta may not be held in the GI tract for sufficient time to allow optimal/complete bacterial action
- Not all products of bacterial action will be absorbed (e.g. decreased amounts of bacterial amino acids absorbed)

## Further Reading

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