How Understanding the Digestive Process Can Help Minimise Digestive Disturbances Due to Diet and Feeding Practices

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Introduction

Since its first domestication, believed to be around 5000 BC, the role of the horse in society has varied according to man's requirements. Initially, the horse was kept principally for its flesh but soon became used for transport. The first example of a man on horseback is believed to be the bone engraving of the Susa horseman dating from 2800 BC. Selective breeding meant that by the 10th century BC horses had become essential to the skilled horseman turned warrior. Horse racing developed in parallel with horse riding.

Horses are fundamentally nonruminant herbivores, which means that they are suited to eating high fibre diets due to continual microbial fermentation within the caecum and colon. The horse evolved to eat mainly grass with some other herbage and when available 'wild' cereals and other starch-containing feedstuffs.

Domestication, and an increasing demand for horses to perform at levels that require energy intakes above those able to be provided by their more 'natural' diet of fresh forage, has resulted in the common inclusion of cereal grains and their by-products as well as supplemental fat in many horse diets. This has led to many benefits but also has the potential to result in problems. This paper will very simply and briefly outline the digestive processes of a horse and highlight areas where dietary imbalances or inappropriate feeding practices may be disadvantageous.

The optimal feeding of horses is a combination of art and science. The science provides the information about the digestive and metabolic processes, the nutrient requirements and the principles behind feeding practices, etc. The art is the ability to convert this theory into practice for the individual horse, its needs, likes and dislikes. Fortunately for us, many horses are able to survive and prosper because of, or despite, the diets we feed them. Although good nutrition cannot improve the basic ability of a horse, poor nutrition may impose limitations on its performance. An understanding of the digestive processes of the horse helps us to appreciate how we should feed it, in order to maintain health and performance and minimise gastrointestinal disturbances caused by inappropriate feeding regimens.

For ease of discussion throughout this paper 'concentrate' meal will refer to a nonroughage meal which could consist of cereal grains with or without other feedstuffs or compound manufactured feeds such as coarse mixes or nuts/pellets.

An Overview of the Digestive System of a Horse

The horse's digestive system really should be thought of as being in 2 sections. The first section has similarities to the pre-caecal digestive system of a monogastric animal such as the dog, man or pig. The second section is more like the rumen of a cow. This has profound effects on the way we need to think about feeding the horses in our care. However, the horse is neither a dog nor a ruminant or even a direct combination of both. It is unique and needs to be considered as such.

Precaecal: Monogastric-like

Prehension

Food is grasped using a combination of the lips, the tongue and the teeth. The lips are relatively strong, mobile and sensitive and they can be selective in choosing food - so much so that food can be held by the top lip, cut by the incisors and then rejected. One advantage is that it reduces the chance of foreign body ingestion. One disadvantage is the habit of selective grazing and in some horses the ability to sift out small particles in feed such as the vitamin and mineral pellets.

Mastication

The jaw movements involved in chewing are quite complex and incorporate both lateral and vertical components. The jaw sweeps 60,000 times a day when grazing. Horses do not ruminate and naturally take in relatively small amounts of feed at each bite, then chew. They tend to take 2 or 3 bites at one site and then move slightly, i.e. they are often referred to as 'trickle feeders'.

The duration of feed intake depends on the type of feed and the size of the animal. The jaw movements in horses at grass are relatively wide and long but when eating hay, and in particular cereals or pelleted feeds, the movement is confined. This increases the chances of developing lateral and medial hooks and speeds up the time of ingestion.

The horse's jaw is designed for eating while the head is down towards the ground. Feeding hay from haynets or hayracks has been suggested to increase the risk of developing cranial and caudal hooks on the dental arcade. The nature of the feeds fed to horses will dramatically influence the chewing rate and speed of ingestion. The average 500 kg horse will chew approximately 3400 times/kg of hay consumed taking about 40 min but just around 850 times/kg of oats and take just about 10 min (ponies take longer). This can have knock-on effects: the more concentrate feed that the horse is fed the less time the horse will spend eating and potentially the more time that it has to become 'bored'. This in turn may lead to the development of certain behavioural abnormalities.

Horses that bolt their food or who are unable to chew it properly are less likely to utilise their food efficiently. The grinding of whole grains is necessary for their optimal digestion in the small intestine. The intensity of the grinding of the roughage may be important for the passage of digesta through the ileocaecal-colic junction into the large intestine. Regular dental care is essential to maintain optimal mastication and steps should be taken to prevent horses from bolting their food such as adding short-chopped fibre or chaff.

Salivation

Saliva in a horse is produced in response to chewing a meal not in anticipation of a meal. This means that the more the food is chewed the more saliva it is mixed with and therefore the lower the DM content of the swallowed bolus. The amount of saliva secreted is believed to be dependent on the moisture content of the feed, the horse's speed of intake and the taste of the food. The level commonly quoted for an average 500 kg horse on a mixed hay/concentrate diet is around 12 litres/day but it has been suggested that on a very dry hay diet considerably more (up to 100 litres) may be produced. The typical DM content of a hay bolus is around 20% whereas that of a cereal-based feed bolus is more like 30-40%.

The occurrence of oesophageal obstructions has been thought to depend not only on the swelling capacity of the feedstuff but also the speed of feed intake and the size, nature and DM content of the boluses swallowed. The mucous content of the saliva helps lubricate the bolus but saliva contains little if any enzymatic activity and so no digestion *per se* occurs.

Stomach

As stated above, horses evolved to take in high-fibre diets in small amounts almost continuously, i.e. they are trickle feeders. The stomach volume of the adult horse is relatively small - between 9-15 litres. Ingested food is retained for about 20 min although the stomach is rarely fully empty as small amounts remain for several hours following a single meal. The stomach is relatively inelastic and has a finite capacity. The musculature is such that vomiting or gastric reflux is extremely rare and usually reflects a significant abnormality. The rate of gastric emptying is dependent on the square root of the volume. So effectively the larger the meal the more rapid the rate of gastric emptying. There is also a knock-on effect, as the food will then pass more quickly through the small intestine.

The stomach is divided into the 2 sections, which have both anatomical and physiological differences. In the cranial nonglandular section bacterial fermentation of the ingested feed starts. This mainly involves lactobacteria, which convert any available simple sugars or starches to lactic acid. This microbial activity and degradation is stopped when the gastric contents pass to the fundic gland region and mix with the acid stomach juice containing pepsinogen. When large concentrate meals are fed, the swallowed bolus has a higher DM content and the stomach contents have a higher DM content - there is slower and/or reduced mixing of the feed with the gastric juices and therefore an increased risk of dysfermentation. Whether this results in a clinical or subclinical problem will depend on the amount of available sugars and starches and the individual microbial population, etc.

Small Intestine

The saliva of a horse contains little, if any, amylase and there is little actual digestion that occurs in the stomach of most horses. Most digestion therefore occurs in the small and large intestine. The main functions of the pancreatic secretions are to neutralise the acid chyme and to provide proteolytic, amylolytic and lipolytic enzymes. Naturally, the horse would graze for 16-18 h per day and evolved without a gall bladder; bile being secreted continuously as the food passes through the gastrointestinal tract. Bile helps to alkalise the digesta and the bile acids are required for emulsification and digestion of lipids. Most fatty acids are absorbed into the lymphatics but some of the medium chain triglycerides may be absorbed directly into the bloodstream. Although the pancreatic enzyme, amylase, hydrolyses starch to disaccharides and trisaccharides these have to be further metabolised by the mucosal enzymes before the resultant hexoses can be absorbed. Mucosal enzymes are also important for protein digestion and absorption. We tend to feed our horses fundamentally for energy and then adjust the diet to ensure that all other nutrients are provided. Practically, certain nutrients in a horse's diet provide the energy intake for that individual following conversion of their chemical energy to other forms of chemical energy, mechanical energy and heat. Dietary energy is provided to the horse by 4 principal dietary energy sources:

1. Hydrolysable carbohydrates e.g. starch.
2. Cellulose, pectins, hemicelluloses, etc. (i.e. nonstarch polysaccharides: a component of dietary fibre).
3. Fats ('normally' less than 3% total feed intake but most horses are able to digest and utilise fat efficiently; however, it is not usually recommended to feed at more than 10% of the diet and any supplemental oil should be introduced gradually).
4. Proteins (not a nutritionally preferred option as an energy source as they are ergogenically inefficient; nitrogen must be removed, as excess protein is not stored, resulting in increased water requirements and potentially higher ammonia levels in the stable).

The basic digestive processes (enzymatic degradation of proteins, fats, starches and sugars) are similar to those of other monogastric animals BUT the activity of most of the enzymes in the chyme, in particular amylase, are lower than in other monogastric animals. The horse, therefore, has a limited capacity to digest starch in the small intestine. The exact limit does seem to vary with the individual and although feeding high-starch diets may result in increased levels of amylase the increases are not marked. Values of around 2 g starch/kg bodyweight per meal have been suggested in the literature to be the maximum that should be fed in any one meal. Large concentrate meals may, therefore, result in an increased rate of gastric emptying, increased gut transit time and decreased digestion of the available starch within the small intestine.

Fluid Shifts

Adult horses, around 500 kg bwt, secrete more than 100 l of fluid per day into this pre-caecal section of the gastrointestinal tract i.e. around 70-100 ml/min. When large meals of either pellets or cereal grains are fed infrequently a transient state of hypovolaemia occurs as a result of meal-stimulated upper gastrointestinal secretions. Within 1 h of feeding ponies there has been shown to be on average a 15% loss in plasma volume. In quick or greedy feeders this can be up to a 24% loss. Slow feeders compensate while they eat and the resultant volume losses are therefore small. These changes in plasma volume are not seen when frequent small meals are fed.

Slowing down quick and greedy feeders can obviously be advantageous. The provision of supplemental chaff at an appropriate length may be beneficial.

Exercising, especially for quick-feeding and greedy horses, soon after they have eaten a large nonforage-based meal may not be advisable as they are already in a state of relative dehydration. In addition:

- Glucose peaks around 1-3 h post a meal which is associated with a rise in insulin. If the horse is exercised at this point one may see a drop in blood glucose during the first stages, which may not be desirable (the brain can only use glucose as a fuel) and may retard the release of free fatty acids into the circulation (so the horse has to rely even more on stored glycogen, potentially resulting in a quicker onset of fatigue).
- Large full sections of the gastrointestinal tract may restrict the space available for lung expansion.
- Following a meal, blood flow is diverted to the gut to enable the products of digestion to be efficiently utilised - this may reduce the blood flow to working muscles and other organs where it may be better employed.

Caecum/Colon: Rumen-like

Digestive Processes

Ingesta moves through the small intestine (SI) quite rapidly, reaching the caecum within 45 min and much of the ingesta will reach here within 3 h of eating. The rate of passage will depend on the nature of the feedstuff and the way in which it is fed. Small particles, ground and pelletted types of feed tend to move more quickly through the large intestine than fresh grass. Fibrous feeds such as hays tend to have the slowest passage of all.

It is important to note that if the nutrient value of a particular feed depends on its degradation in this section of the gut, it should ideally remain within this section for sufficient time to enable the process to be effective. So if a particular feed relies on slow fermentation for its digestion and it takes 100 h of fermentation before 50% of its nutrient value is released, and yet it only remains in the large intestine for 50 h, then its real value to the horse is decreased from its theoretical one.

The large intestine does not have mucosal enzymes and does not have any significant active transport mechanisms for hexoses and amino acids. Digestion and absorption of residual carbohydrates relies instead on microbial action and absorption of the end products of microbial fermentation. The intensity of these processes depends on the amount and the temporal influx of fermentable material arriving from the small intestine. If fed appropriately, a high proportion of the available starch ingested can be degraded to glucose before absorption in the small intestine (unless for example the digestive capacity of the SI is overwhelmed). However, a proportion of the starch and, depending on the extent of lignification, a varying proportion of the dietary fibre, will be subjected to microbial fermentation, primarily in the large intestine, producing predominantly short chain or volatile fatty acids. These can be used directly as an energy fuel by the gut cells themselves, etc but the majority is absorbed and converted to either glucose or fat. This is ultimately less efficient than obtaining energy from carbohydrate sources directly via glucose.

Unlike in the ruminant, this microbial fermentation obviously occurs after the 'monogastric'-like section rather than before. This has a great impact on how we should feed a horse and explains in part why the horse and cow differ so much in their nutritional efficiencies and requirements. Microbial enzymes also break down undigested proteins and urea, which enter the large intestine. The main end product is ammonia, some of which is absorbed, but much of it is reutilised by the bacteria in the synthesis of bacterial protein stimulating bacterial growth. Microbial protein, which is synthesised in the large intestine, cannot be utilised to any great extent by the horse. This means that animals with a high demand for protein (foals, lactating mares and probably intensively exercising horses) must therefore be fed high quality protein which can be broken down and absorbed primarily in the precaecal section of the gut. Most of the water-soluble vitamins as well as the fat-soluble vitamin K are synthesised in the large intestine. The horse is able to utilise these so that oral supply is only necessary under certain circumstances (Pagan, 1999).

Water is predominantly stored in and absorbed from the large intestine. Different feedstuffs will have different water holding and releasing properties.

Fluid Shifts

It is important to note that there is a fluctuation in the bacterial populations in any meal-fed horse. The microfloral population within the hindgut does adapt to a certain extent to the type of feed being fed. However, if the dietary fluctuations are too marked or excessive starch/rapidly fermentable carbohydrates reach the hind-gut even in the concentrate-adapted horse, a significant change in the microbial population may have clinical consequences. Obviously the closer a feeding programme can get to the natural manner to which the horse evolved then the smaller the effect on the gastrointestinal tract homeostasis.

Starch Digestion

The upper part of the gastrointestinal tract has a relatively small capacity and the horse has digestive and metabolic limitations to high-grain, highly soluble carbohydrate diets. This has resulted in problems following domestication and the requirement for repetitive, intensive or prolonged exercise. Large grain meals may overwhelm the digestive capacity of the stomach and small intestine leading to the rapid fermentation of the grain carbohydrate in the hindgut and a decrease in the pH. A significantly decreased caecal pH may initiate a serious chain of events including a change in the microbacterial flora (excessive growth of those bacteria that can live under such conditions), a degree of lysis of those bacteria which can not live at such low pHs allowing the release of endotoxins, damage to the mucosa of the caecum and colon which in turn may allow the absorption of endotoxin, and various other pathogens with potential clinical consequences including colic, diarrhoea and laminitis.

pH in the hindgut following feeding either a concentrate or by hay based feed (Willard et al., 1977)		
Hours post feeding	**Concentrate**	**Hay**
0	7.22	7.14
2	7.14	7.04
4	6.43	6.92
6	6.12	6.87

Hay or roughage-based diets do not result in such decreases in caecal pH but may not provide sufficient usable or net energy for many horses' needs. This is one of the main reasons that supplemental oil/fat has become so popular in recent years as a nonstarch energy source.

The extent to which cereal starch provides glucose or volatile fatty acids as the end result of digestion will depend on its precaecal and even pre-ileal digestibility which will, in turn, vary according to the feedstuff under consideration and the extent and nature of the processing to which it has been subjected.

Feedstuff	Processing	Approximate pre-ileal starch digestibility (%)
Oats	Whole	83.5
	Rolled	85
	Completely ground	97
Barley	Rolled	21.5
Corn/Maize	Whole	29
	Cracked	30
	Ground	46
	Popped	90

This means that, despite corn containing more starch than oats, weight for weight, if fed whole then less actual starch will be digested in the small intestine and more will reach the hindgut. Feeding large amounts of cornstarch is more likely to result in a significant decrease in hindgut pH and an increased risk of acidosis than if an equivalent amount of oat starch is fed.

Conclusion

In conclusion, a basic understanding of the digestive processes and how diet can have an impact can be very valuable when deciding how to feed horses optimally. The above provides a general overview of the relevant processes and points out a few areas where our feeding practices can be very influential.

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