Recent advances in equine nutrition

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Summary

Ruminant *in sacco* techniques were used to measure feed degradability in the pre–caecal segment, caecum, and over the total tract of ponies. Optimal mobile dacron bag sizes were considered to be 10 x 60 mm with a pore size of 41µm, containing 350 mg of dry sample. Use of these bags enabled the quantification of pre–caecal NSP losses from botanically–diverse fibre sources; 16.4% of unmolassed sugar beet pulp NSP disappeared pre–caecally. Caecal outflow rate was measured using a pulse dose of chromium–mordanted feed and could be fitted with a simple exponential relationship which showed that the rate varied between 24 and 38.7% per hour depending on the feed marked. *In situ* degradation profiles were combined with those obtained with mobile bags. Together with rate of passage data from marker experiments, the degradability of hay and sugar beet pulp was estimated in different parts of the digestive tract of ponies.

Total tract apparent digestibility of barley starch, energy and organic matter was unaffected by micronising or extrusion. *In situ* studies showed that at mean retention times of 2, 3 or 5 h, DM degradability was greatest for micronised barley and the Effective Degradability values of starch were significantly higher ($P<0.05$) at 3 and 5 h compared to both rolled and extruded barley. Caecal parameters reflected these differences. The addition of rolled barley to a diet of hay cubes significantly ($P<0.05$) reduced caecal pH (6.24) and acetate and increased propionate; micronised barley depressed acetate and pH and increased propionate the least. The safe levels at which starch can be meal–fed to horses or ponies depends on the source of the starch, the level of intake and whether or not it has been effectively processed. Evidence presented suggested that micronising barley was more effective than extrusion in increasing pre–caecal starch digestion. Relatively low intakes of raw starch (about 2.4 g starch/kg body weight/meal) significantly ($P<0.05$) depressed caecal pH.

Introduction

The relative paucity of equine experimental models and the apparent reluctance to transfer ruminant methodologies to the equine are in part responsible for the lack of progress in the field of equine nutrition. Only recently have techniques that have been developed in pigs, cattle and sheep been adapted for use with equids. These fundamental techniques are the *in situ* incubation method, the mobile nylon bag method, the use of markers singly and in combination, and modelling.

Equine nutritional research has been underfunded because horses are perceived as leisure animals and have little value in agricultural terms and so it has received minimal Governmental support (Cuddeford 1991). As a consequence, compared with other domestic livestock, we know rather little about the digestive processes of the horse, its requirement for nutrients, the controls of food intake, the role of diet in disease and the nutritive value of feeds for horses.

This paper provides an overview of how techniques, developed for ruminant use, may be used to elucidate the digestive process in horses and shows how they have been applied in the determination of the sites of digestion of barley starch processed in various ways.

Application of ruminant techniques

Merits and demerits of using dacron bags

Using dacron bags (*in sacco* techniques) either for *in situ* studies or as mobile bags, provides very useful data. However, these data require careful interpretation since they provide measures of substrate disappearance from the lumen of the bag; degradation curves represent losses of material from bags over a period of time. Because degradation curves are time–based, they can give a dynamic, continuous impression of the degradation process. In contrast, digestibility trials give a point estimate of the apparent digestibility of a feed or a combination of feeds.

The importance of measuring degradability

Degradation curves give some indication of the rate and site of digestion whereas an apparent digestibility value gives no such information. The former is well illustrated by the *in situ* degradation curves for soya hulls and unmolassed sugar beet pulp reported by Stefansdottir *et al*. (1996); these reached the same asymptotic value but by very different routes. Total tract apparent dry matter digestibilities of three diets containing different forms of barley (rolled, extruded or micronised) fed 50:50 with hay cubes were 0.82, 0.82 and 0.83 respectively (McLean *et al.* 1999a). Thus, it would appear that each barley type was digested to the same extent but in fact, there were significant changes in caecal pH (McLean *et al*. 1998a). These were measured 5 h post–feeding and showed that rolled barley resulted in a pH of 6.26 which was significantly ($P<0.05$) less than that for the extruded barley (pH 6.38). These differences suggest that the pre–caecal degradation of the rolled barley was less than that of the extruded barley. There is no doubt that any starch that passes into the caecum and beyond will be readily degraded, but the consequences for the animal would be that less glucose would be absorbed and that caecal function may be compromised. Thus, a total tract value may conceal factors of biological significance to the animal.

The use of *in situ* methods to determine degradability

The *in situ* technique has been modified for use in the horse caecum as described by a number of authors (Applegate and Hershberger 1969; Miraglia *et al*. 1988; Drogoul *et al*. 1995). Variations in procedures that influence the results obtained when using this technique in ruminants have been extensively studied and were recently reviewed by Huntington and Givens (1995), but have not been fully evaluated in equids. However, Hyslop *et al*. (1999a) have recently reported a methodology based on the use of 6.5 x 20 cm *in situ* bags, containing 16 mg of feed per cm^2, incubated in the caeca of mature pony geldings (mean weight 285 kg). A complete exchange method (Paine *et al*. 1982) was used to evaluate two different incubation sequences: forward (3, 5, 16, 8, 24, 48 h) and reverse (48, 24, 8, 16, 5, 3 h). This technique involves placing two *in situ* dacron bags into the caecum for the prescribed period of time, they are then removed, the bags washed and the residues analysed. Fresh bags are introduced for the next time period and so on, until the complete sequence of incubation times has been achieved; the process is then repeated in reverse order. Degradation profiles were shown to be sensitive to incubation sequence in contrast to the findings of Huntington and Givens (1997), who showed no effect of incubation sequence on the degradability of hay, soya or fishmeal in cattle and sheep.

The use of mobile nylon bags to determine partial and total tract apparent digestibility of food components

Independently, Macheboeuf *et al.* (1996) and Hyslop and Cuddeford (1996) used mobile nylon bags to study nutrient disappearance throughout the digestive tract of horses and ponies respectively. The latter authors tested a range of bag sizes and showed that large bag sizes (19 x 110, or 19 x 55, or 45 x 45 mm) resulted in transit times in excess of 100 h and, as a result, there were large feed constituent disappearances. Bags which gave transit times and feed disappearances in accordance with expectation measured 10 x 60 mm; the pore size was 41 μm. This was the size of bag used by Macheboeuf *et al.* (1996), Moore–Colyer *et al.* (1997a), Hyslop *et al.* (1998) and McLean *et al.* (1999b). Moore–Colyer *et al.* (1997a) used the mobile nylon bag technique to partition fibre degradation in the digestive tract of caecally–fistulated ponies. Bags were filled with 350 mg of a ground, dietary fibre source (unmolassed sugar beet pulp, or hay cubes, or soya hulls, or a 50:50 oat hull:naked oat mixture) ground to pass through a 1 mm screen. On two consecutive mornings, 20 bags were administered directly into the stomach of each pony, using a naso–gastric tube. A magnetic capture device was placed in the cannula just posterior to the ileo–caecal valve. Each mobile bag contained 2 x 100 mg steel washers so that as the bags entered the caecum, they were captured. Ten to 16 bags were captured in this manner; the remainder were allowed to continue through the gut and were collected in the faeces.

Bags that were recovered entering the caecum, 1 to 8 h after dosing, provided data on disappearance following a range of incubation times in the pre–caecal part of the gastrointestinal tract. Degradation profiles were fitted to the losses from the mobile bags using the same models that have been applied to *in situ* disappearances (Øskov and McDonald 1979; Dhanoa *et al.*1985). This experiment also allowed the calculation of both pre–caecal and total tract losses of non–starch polysaccharide (NSP).The results of this study contradicted the widely held view that dietary fibre is degraded only in the large intestine of the horse. Pre–caecal losses of NSP were 84, 111, 127 and 164 g/kg of the total tract NSP disappearance for the mixture of oat products, hay cubes, soya hulls and beet pulp respectively. Allowing mobile nylon bags to pass through the entire length of the digestive tract of the horse and then recovering them from the faeces over an extended period of time, yields data that reflect a range of incubation times in the whole tract (Hyslop *et al.* 1998).

The use of a marker to measure caecal outflow

To reliably determine passage rate through sub–segments of the gastrointestinal tract requires that the region be cannulated so that markers can be introduced directly. Hyslop *et al*. (1999b) pulse dosed chromium–mordanted feeds into the caecum of caecally–fistulated ponies and withdrew caecal digesta samples by suction at regular intervals over a 10 h period. The chromium concentration in caecal digesta samples was measured and caecal outflow rate, k, was determined by fitting to the chromium concentration data a simple exponential relationship of the form:

$$[Cr] = A\,e^{-kt} \qquad (1)$$

where A represents chromium concentration [Cr] at time t = 0. Caecal outflow rate, k, varied between 24 and 38.7% per hour depending on the type of feed marked whilst the R^2 of the exponential relationship, ranged from 0.717 to 0.948.

The use of models to describe the digestive process in the horse

Time–independent passage is the paradigm where there is complete and instantaneous mixing of influxing particles with those resident in the compartment, there is an equal opportunity for escape of all particles from within the compartment, and there is constant inflow, outflow and compartmental mass. This is best illustrated by the outflow of chromium–mordanted particles from the caecum which follow an exponential distribution (Hyslop *et al*. 1999b). Excretion of ytterbium–labelled particles in the faeces of horses followed a unimodal distribution when the animals were given an oral, pulse dose of marked feed (Hyslop, 1998); the data were fitted using the models of Grovum and Williams (1973) and Dhanoa *et al*. (1985), which rely on an exponential relationship. Hyslop (1998) has proposed that passage rate through the small intestine of the horse is time–dependent (this paradigm is where laminar flow occurs, there is little mixing of particles, and the probability of passage is greater the longer the particles are resident in the compartment). To this end, McLean *et al*. (1999b) have modelled mobile bag data assuming a Gamma 2 time dependency (Ellis *et al*. 1994) which allows the modelling of data that do not follow an exponential relationship. Some would argue that this is unnecessary and that the data can be modelled using a time–independent paradigm (J. France, pers. comm.). Hyslop (1998) has suggested that degradation profiles obtained from *in situ* studies can be combined with those from mobile nylon bag studies to provide an overall impression of feed degradation in the horse. Data from marker experiments can be fitted, using time–independent models, which enable the calculation of, k, the rate constant for the exponential rate of digesta passage. With this information, the Effective Degradability (ED) can be measured as follows (Ørskov and McDonald 1979):

$$ED = a + \frac{(bc)}{c+k} \qquad (2)$$

where a is the rapidly degradable (soluble) fraction; b, the slowly degraded fraction; c, the rate at which b is degraded.

Time–dependent rates of passage can be accounted for in the calculation of ED by using λ values or rate constants appropriate to this type of passage. Ellis *et al.* (1994) describe these time–dependent, Gamma functions which vary from Gamma 2 to Gamma 6, the Gamma 1 function representing the time–independent, exponential relationship. ED can be calculated using the Gamma 2 function as follows:

$$ED = a + (bc)/[c + (2/MRT)0.59635] \qquad (3)$$

where MRT is the mean retention time of food particles in the tract or in parts of it.

Hyslop (1998) has combined knowledge of degradation profiles with estimates of digesta passage rate using different models, to partition digestion throughout the digestive tract of the horse. Assuming MRTs of 3, 4 and 41 h in the small intestine, caecum and colon respectively, he calculated the loss of dry matter from sugar beet pulp (SBP) and hay cubes in different parts of the gastrointestinal tract by using equations (2) and (3) above. The results (Table 1) give estimates for total DM loss from SBP and hay cubes as 70 and 52% respectively.

Table 1 Proposed partition of dry matter degradation (%) of two feeds throughout the digestive tract of ponies.

		Sugar beet pulp	Hay cubes
Effective Degradability in:	Small intestine[1]	17	31
	Caecum[2]	41	13
	Colon[2]	12	8

[1] time–dependent passage; [2] time–independent passage.

Starch digestion

Effect of processing on cereal starch digestibility

Processing can affect starch digestibility although the magnitude of the effect depends on the nature of the process used. Crude physical treatments, such as rolling, crushing or coarse grinding, do not significantly improve oat starch digestibility (Kienzle *et al*. 1992) or that of corn (Meyer *et al.* 1993). In contrast, fine grinding (<2mm) can improve small intestinal corn starch digestibility (Kienzle *et al.* 1992; Meyer *et al.* 1993). Cooking, either by micronising or popping (Householder 1978; Meyer *et al.* 1993) can lead to significant improvements in pre–caecal starch digestibility, particularly with respect to corn (Meyer *et al*. 1993). Potter *et al.* (1992) noted that the effects of processing on cereals could be masked by differences between sources of starch. In view of this, some experiments were planned to examine the effects of processing barley on its digestion by the horse, a cereal previously shown to have a low pre–caecal digestibility (Meyer *et al.* 1993).

Effect of processing technique on apparent digestibility of barley components

Barley of one variety, from one field, was harvested, dried and then subsequently rolled, micronised or extruded for use in a series of experiments. Animals used were mature, Welsh–cross, pony geldings (body weight 280 kg) and each was fitted with a caecal cannula.

This work has recently been reported (McLean *et al.* 1999a) and involved offering ponies 4 kg DM per day (in two equal meals at 09.00 and 17.00 h) of either 100% hay cubes or one of three diets (different forms of barley) consisting of a 50:50 barley:hay cube mix. The results from this incomplete Latin square changeover design experiment were in accordance with expectation in that it has been found different physical processing methods do not alter total tract apparent digestibilities (Potter *et al.* 1992). The apparent digestibilities of the energy (DE) and crude protein of the barley were unaffected by processing; the DE contents of the rolled, micronised and extruded barley were 14.5, 14.8 and 15.0 MJ/kg DM respectively, similar to the NRC (1989) value of 15 MJ/kgDM. Apparent organic matter and starch digestibilities were respectively 0.84 and 0.97 for the rolled barley, 0.85 and 0.97 for the micronised barley, and 0.84 and 0.97 for the extruded barley. *In vivo* total tract apparent digestibility studies give no indication of whether the starch was degraded by mammalian enzymes in the small intestine or by microbial enzymes in the large intestine. These ponies were fed approximately 2.4 g starch/kg body weight per meal and the apparent digestibility of the starch was uniformly high.

The use of *in situ* studies to indicate the likely site of barley digestion

The three different forms of barley were incubated in the caeca of fistulated ponies to provide time–based, degradation data utilising microbial enzymes (McLean *et al.* 1998b). Degradation profiles were fitted to the dry matter and starch disappearance data according to Ørskov and McDonald (1979). The degradation coefficient, a, was greatest for the micronised barley, and significantly so ($P < 0.05$) for dry matter loss. As expected, no differences existed between the different forms of barley after 40 h of incubation, although extrusion reduced the effective degradability of dry matter to a small, but significant ($P < 0.05$) extent, when compared to the rolled barley. This negative effect may have been because the extrusion process caused the formation of indigestible Maillard products. More importantly, at outflow rates $k = 0.50$, 0.33 and 0.20, which reflected MRTs of 2, 3 or 5 h in the pre–caecal segment of the digestive tract, the DM degradability was greatest for the micronised cereal. This was followed by the extruded barley; the rolled barley had the lowest effective degradabilities (B.M.L. McLean, unpublished data). However, the only significant ($P<0.05$) difference was at $k = 0.50$ when the effective DM degradability of micronised barley was 0.69 compared to that of 0.63 for the rolled barley. When considering starch degradation, there were no significant differences between degradation parameters although, again, the coefficient, a, for micronised barley was the highest. In contrast, comparison of the ED values of starch at $k = 0.50$, 0.33 and 0.20 produced significant differences between the differently processed barleys. At $k = 0.50$, micronised barley was degraded more than the other barleys and significantly so ($P < 0.05$) in respect of extruded barley. This was also the case at $k = 0.33$, and at $k = 0.20$ the starch of micronised barley was signficantly ($P < 0.05$) more degraded than that of the other two barleys: 0.93 compared to 0.85 for extruded and 0.86 for rolled barley. These important differences between barley sources in terms of starch degradability will affect the nature of the feed residues from a meal that enter the caecum. If we assume a transit time from the oesophagus to the ileo–caecal valve of 3 to 4 h, then the provision of micronised barley should result in less undigested starch entering the large intestine compared to when rolled barley is fed. If undigested starch were made available to the microflora within the large intestine of the horse, then changes in the caecal environment would be expected that would be analogous to those measured in the rumen of cows or sheep overfed on cereal. There would be a reduction in pH together with a change in the molar proportions of the volatile fatty acids: increased propionate and decreased acetate.

Effect of processing technique on caecal parameters in barley–fed ponies

The effects of physical processing of barley on intra–caecal pH and volatile fatty acid parameters have recently been reported (McLean *et al.* 1998a). The provision of a meal supplying 2.4 g starch/kg body weight in the form of rolled, micronised or extruded barley, together with hay cubes, significantly reduced ($P < 0.05$) caecal pH and acetate, and increased propionate, compared to a 100% hay cube diet, when measured 5 h post–feeding. Feeding rolled barley with the hay cubes caused lower ($P < 0.05$) acetate and higher ($P < 0.05$) propionate compared to when micronised barley was fed with the hay; these changes were apparent through most of the day following the 09.00 h meal. The micronised barley increased ($P < 0.05$) acetate and lowered ($P < 0.05$) propionate compared to extruded barley at most hourly samplings throughout the day. At 5 h post–feeding, caecal pH values were 6.24, 6.33, 6.38 and 6.48 respectively for rations containing rolled, micronised and extruded barleys with hay cubes, and hay cubes alone. Acetate values (mmol/mol) in the caecum were 627, 716, 685, and 764, whereas propionate levels were 302, 221, 250 and 174 respectively. As expected, the hay cubes ration resulted in the highest acetate (764) and the lowest propionate (174) values; the ration containing the micronised barley had the closest values, 716 and 221 respectively.

The use of mobile nylon bags to measure pre–caecal starch digestion

The mobile nylon bag technique has been used to study the degradation dynamics of forages over the whole length of the digestive tract of equids (Hyslop *et al.* 1998) and in the pre–caecal segment (Moore–Colyer *et al.* 1997b). Recently (McLean *et al.* 1999b) has used the technique to investigate the degradation of purified wheat starch, chemically modified wheat starches and a purified pea starch. Bag transit times to the caecum following introduction by naso–gastric tube into the stomach varied between 1 and 7.5 h. Pea starch was the least well degraded (probably due to the presence of resistant starch RS_3) in the small intestine whereas wheat starch required extensive chemical modification (cross–linking) before pre–caecal degradation was significantly ($P < 0.5$) reduced. It was concluded that the mobile nylon bag technique could be used to successfully model feed degradation dynamics over time in the pre–caecal segment of the equine digestive tract. Thus, the technique was used to measure pre–caecal losses of dry matter and starch from the differently processed barleys. Initial results for the effective degradabilities of the dry matter of rolled, micronised and extruded barleys at $k = 0.50$, 0.33 and 0.25 showed that extruded barley had a significantly ($P < 0.05$) lower Effective Degradability at all assumed MRTs. There were no differences between rolled or micronised barleys (B.M.L. McLean, unpublished data). The starch data have yet to be modelled.

The effect of level of starch intake, starch source and cereal processing on caecal function

Willard *et al.* (1977) showed that caecal pH was affected by diet; pH was significantly ($P<0.05$) lower 4, 5 and 6 h after feeding 6 kg concentrate to horses compared to when hay was fed. Furthermore, the molar proportions of acetate and propionate were altered; there was more propionate *pro rata* when concentrate was fed and lactic acid levels were higher. An interesting observation by these authors was that horses fed the concentrate–only diet chewed wood and practised coprophagy. The lowest mean caecal pH, 6.12, was recorded by Willard *et al.* (1977) 6 h after the concentrate was fed.

Essentially, the results obtained by Willard *et al.* (1977) showed that feeding large amounts of starch–rich feed affects the caecal environment in terms of pH and the proportions of volatile fatty acids formed therein. This latter effect had already been recorded by Hintz *et al*. (1971) when they examined the effects of feeding different forage: concentrate ratios.

Garner *et al*. (1975) developed an experimental model for the induction of laminitis in horses. A gruel of 85% corn starch and 15% wood cellulose was introduced via a stomach tube at the rate of 17.6 g/kg body weight in order to create a 'grain overload'. Assuming a dry matter (values not given) for the gruel of 200 g/kg, then the starch supplied would have been about 3 g starch/kg body weight. Grain overload together with gastrointestinal disease are the most common predisposing factors to laminitis in horses (Slater *et al*. 1995). Prior to grain overload, mean caecal pH was 7.18, and 8 h after the overload fell to 5.72. At this pH and by this time, *Lactobacillus* spp had significantly ($P<0.05$) increased in number (Garner *et al*. 1978). These authors concluded that low caecal pH causes the death of favourable microorganisms, releasing endotoxins, and that lactic acid accumulates and causes a generalised lactic acidosis. Radicke *et al.* (1991) measured the effect of feeding, 1 to 2, 2 to 3, or 3 to 4 g of starch/kg body weight per meal using either oats or corn as a source of the starch. As expected, at all levels of intake, caecal pH was lower when corn was fed and the differential between the two cereals increased in proportion to starch intake. Increasing oat starch intakes to the levels regarded as 'safe' by Potter *et al*. (1992) did not significantly reduce caecal pH. However, feeding the same level of corn starch caused a marked reduction in caecal pH to values close to 6. Radicke *et al*. (1991) considered that a caecal pH of 6 represented sub–clinical acidosis, and below 6 there was considerable risk of development of clinical conditions and of imbalancing caecal fermentation. This was in accord with the results obtained earlier by Garner *et al*. (1978). Recently, Johnson *et al*. (1998) fed a changing ration over a four week period to 400–500 kg horses. Initially, they were fed 8 kg hay, then 6 kg hay and 2 kg concentrate, then 4 kg hay and 4 kg concentrate, and in the fourth week, 2 kg hay and 6 kg concentrate. The daily ration was fed in two equal parts so ultimately the horses received meals of 3 kg concentrate and 1kg of hay. If the concentrate contained 550 g starch/kg, then the starch supplied would have been between 3.3 and 4.1 g/kg body weight, within the Potter *et al*. (1992) recommendations. However, the authors measured a declining faecal pH from about 6.6 to below 6 and noted abnormal behaviours similar to those recorded by Willard *et al*. (1977). Unfortunately, Johnson *et al.* (1998) failed to confirm the relevance of faecal pH to caecal pH at post mortem. A recent survey (L. Paul, unpublished data) of faeces from horses fed different diets confirmed that the nature of the diet can affect the faecal pH. Horses at grass produced faeces with a pH (± SD) of 6.74 ± 0.003 (n = 34), racehorses fed 70% oats had an average faecal pH of 6.38 ± 0.049 (n = 18) and forage–fed ponies had a value of 6.49 ± 0.035 (n = 6). Johnson *et al*. (1998) showed that the daily feeding of 225 mg of virginiamycin (as 'Founderguard') prevented the extreme fall in faecal pH associated with the increased level of concentrate feeding although at the highest level, faecal pH was still significantly ($P< 0.05$) reduced compared to horses fed only hay. The starch was mostly cereal in origin, supplied by wheat and barley, so that there would be no expectation of low pre–caecal starch digestion; unfortunately, the authors did not describe the form of the concentrate. The fact that virginiamycin appeared to have some 'protective' effect, possibly through suppressing lactic acid production (Rowe *et al*. 1994), suggests that, even with relatively low starch intakes, horses may suffer caecal dysfunction without enduring very low caecal pH. This is in accordance with the views of Radicke *et al*. (1991).

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