Models for estimating digesta passage kinetics in the gastrointestinal tract of the horse

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ABSTRACT: Fecal samples were collected to evaluate mathematical models to describe the kinetics of digesta passage in the segments of the equine gastrointestinal tract and to compare the passage kinetics of hay and oats. Four Norwegian Cold-blooded trotters (cecally cannulated, approximately 500 kg of BW) were fed Cr-mordanted hay and Yb-marked oats with their morning meal. The meal consisted of 2 kg of hay and 1 kg of oats processed as ground, pelleted, extruded, or micronized. Each horse was fed each type of oats on different days of collection, after a 5-d adaptation period, in a 4 × 4 Latin square design. Fecal samples were collected 5, 6, 7, 8, 9, 10, 11, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, 36, 38, 48, and 52 h after administration of the marker dose. The samples were analyzed for Cr and Yb, and values were plotted using 1- and 2-compartment nonlinear passage models and an algebraic model. The 1-compartment G4 model and the 2-compartment G4G1 model showed an equally good fit to the observed excretion curves, based on low mean square error and SE. The excretion curves for hay (Cr) and oats (Yb) showed a striking similarity, and there seemed to be no difference in retention time between hay and oats in the horse. The mixing compartments in the horse are believed to be the cecum or both the cecum and the right ventral and dorsal segments of the colon, but further research in this area is needed to make a final conclusion.

Key words: compartmental model, hay, horse, oat, passage kinetics, retention time

J. Anim. Sci. 2006. 84:3321–3328
doi:10.2527/jas.2006-039

INTRODUCTION

Several investigators have modeled passage kinetics of the ruminant gastrointestinal (**GI**) tract. Little has been published on the modeling of GI digesta kinetics in the horse. It has been suggested that the main mixing compartments of the equine GI tract are represented by the cecum and the right ventral and right dorsal colon (Moore-Colyer et al., 2003). It has not been determined whether these GI segments should be considered one or several separate mixing compartments, and no consensus values are available on the residence times of digesta in these parts of the GI tract.

To estimate hindgut fractional passage rate and total tract retention time, various models can be fitted to marker excretion data. The simplest is the 1-compartment model with first order kinetics (time-independent). Grovum and Williams (1973) described a model with 2 time-independent compartments and a time delay to estimate rate of passage in sheep. Matis (1972) suggested a model assuming that marked feed particles have gamma-distributed residence times. In this model, the probability of a particle escaping the GI segment increases with its residence time in the compartment (time dependency). Time dependency has also been introduced into a 2-compartment model with assumed gamma distribution of residence time in the first compartment, and an exponential distribution in the second.

It has been suggested that the hindgut passage kinetics are a time-dependent process in horses and that feed particle size does not influence the retention time in the hindgut (Moore-Colyer et al., 2003). Thus, it can be hypothesized that hay and oats have compatible passage rates, in spite of having different mean particle sizes, and that digesta passage in the equine hindgut is a time-dependent process.

The main objectives of this study were to 1) evaluate different mathematical models to describe digesta passage kinetics in segments of the equine GI tract, and 2) compare the passage kinetics of hay and oats.

MATERIALS AND METHODS

Animals, Management, Experimental Feeds, and Diets

All horses were cared for according to the laws and regulations controlling experiments on live animals in

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Received January 20, 2006.
Accepted July 14, 2006.

Table 1. Chemical composition of the feeds fed to the horses

Item	Feed				
	Ground oats	Pelleted oats	Extruded oats	Micronized oats	Hay
DM, g/kg	927	927	928	930	955
CP, g/kg of DM	115	109	117	104	74
Crude fat, g/kg of DM	39	39	24	48	—
Starch, g/kg of DM	355	381	409	375	—
NDF, g/kg of DM	277	230	253	302	621
ADF, g/kg of DM	116	95	93	127	339
Ash, g/kg of DM	25	24	24	26	59

Norway (i.e., the Animal Protection Act of December 20, 1974, and the Animal Protection Ordinance concerning Experiments on Animals of January 15, 1996). All horses remained healthy during the experiment.

Four Norwegian Cold-blooded trotter geldings (age, 5 to 8 yr; initial BW 486 to 532 kg) were used in the study. They were individually stabled in tie stalls bedded with rubber mats and wood shavings. The horses were fitted with a permanent cecal cannula close to the ileo-cecal junction, but the cannula was not used during the experiment. The horses were exercised daily in an outdoor rotary exerciser (walk and trot) for 60 to 90 min. The surgical procedure of fistulation was completed for all horses more than 1 yr before this experiment.

Oats were chosen to represent cereals, and the same batch of oats was processed in 4 ways: ground, pelleted, extruded, and micronized (Table 1). The horses were fed a diet consisting of 7 kg of long hay/d (mainly timothy, Table 2), and 3 kg of one of the types of oats/d. The diet corresponded to 12.6 to 14.3 g of hay/kg of BW and 5.2 to 5.7 g of oats/kg of BW. The daily ration was divided into 3 meals, offered at 0800, 1400, and 2000. Each meal consisted of 1 kg of oats and 2 kg of hay (morning and midday meals) or 1 kg of oats and 3 kg of hay (evening meal), simulating a normal feeding situation. Water was available for ad libitum consumption from individual water bowls.

Marker Preparation and Dosing

The same long unchopped hay fed to the horses was Cr-mordanted according to the method described by Udén et al. (1980). The oats were marked with Yb by an immersion technique, as described by Austbø and Volden (2006). Oats samples (ground to pass a 3-mm screen) were placed into 37-μm nylon bags (approximately 20 × 40 cm; 2,000 g) and soaked (200 g/L, as-is basis) for 24 h in a 2.5 g/L solution of Yb acetate. Next, the oats rinsed in tap water for 1 h and then soaked in 0.01 *M* acetic acid solution at pH 4 for 1.5 h to remove loosely bound Yb. The labeled feed was rinsed in tap water once more for 0.5 h and dried at 45°C for 24 h. Mean Cr concentration in the mordanted hay was 7.62 mg/g (6.04 to 8.25 mg/g), and the mean Yb concentration in the labeled oats was 8.66 mg/g (5.76 to 10.98 mg/g). After 5 d of diet adaptation, Cr-mordanted hay (0.5 kg) and Yb-labeled oats (0.2 kg) were included in the morning meal. Hay and oats were given separately and

Table 2. Evaluation of different passage models for oats in the gastrointestinal tract of horses[1]

Model[2]	TT, h	K_1, %/h	K_2, %/h	$CMRT_1$, h	$CMRT_2$, h	CMRT, h	TMRT, h	MSE	SEP
G2	14.34	0.082	—	14.67	—	14.67	29.01	0.00718	0.0560
G3	12.29	0.096	—	14.92	—	14.92	27.21	0.00240	0.0423
G4	10.60	0.103	—	16.02	—	16.02	26.62	0.00202	0.0395
G1G1	14.47	0.086	0.144	7.00	7.00	14.00	28.48	0.00731	0.0578
G2G1	12.32	0.123	0.202	9.89	4.99	14.88	27.20	0.00253	0.0422
G3G1	11.20	0.181	0.116	8.03	9.28	17.31	28.51	0.00305	0.0409
G4G1	9.50	0.143	0.218	11.89	5.30	17.19	26.69	0.00191	0.0375
Thielmans[3]	—	—	—	—	—	—	26.17	—	—

[1]TT = Transit time; K_1 = mean fractional passage rate from the time-dependent compartment; K_2 = mean fractional passage rate from the time-independent compartment; $CMRT_1$ = mean retention time in the time-dependent compartment; $CMRT_2$ = mean retention time in the time-independent compartment; CMRT = compartment mean retention time (for the 2-compartment models CMRT = $CMRT_1$ + $CMRT_2$); TMRT = total mean retention time (TT + CMRT); MSE = mean square error; SEP = SE predicted (calculated 5 to 26 h postfeeding).

[2]Compartment models by Pond et al. (1988).

[3]Based on the algebraic model by Thielmans et al. (1978).

offered immediately after the markers had been consumed.

Sampling and Marker Analysis

Fecal samples (approximately 100 g) were collected by rectal sampling at 5, 6, 7, 8, 9, 10, 11, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, 32, 34, 36, 38, 48, and 52 h after administration of the marker dose. The samples were dried at 60°C for 48 h and ground to pass a 1-mm screen. Before marker analysis, samples of 500 mg were ashed at 550°C for 16 h. Chromium was analyzed using the method described by Williams et al. (1962), and Yb was analyzed with the procedure described by Siddons et al. (1985).

Passage Models and Calculations

To evaluate different passage models, the fecal marker distribution curves of Cr and Yb were analyzed using the NLIN procedure (SAS Inst. Inc., Cary, NC), in a modified version of the procedure described by Moore et al. (1992). One-compartment models with gamma time-dependency (Gn, n = 2 to 4) and 2-compartment models with gamma time-dependency in the first compartment and time-independency in the second compartment (GnG1, n = 2 to 4; Pond et al., 1988) were tested. In the time-dependent compartment, it was assumed that the fractional passage rate was initially zero and increased with time until it reached a constant asymptote (λ), which was the maximum fractional passage rate (Pond et al., 1988).

Mean retention times (**CMRT**) in 1-compartment, time-dependent models and in the first time-dependent compartment ($\mathbf{CMRT_1}$) in the 2-compartment models were calculated as n/λ and n/λ_1, respectively. Mean retention time in the second time-independent compartment ($\mathbf{CMRT_2}$) was calculated as $1/K_2$, where K_2 is the fractional passage rate out of the time-independent compartment. The CMRT in the 2-compartment model was calculated as $CMRT_1 + CMRT_2$. In the model calculations, it is assumed that a transit time (**TT**) represented the time spent outside the compartments: the stomach, small intestine, and the caudal part of the large intestine. The TT is similar to time delay, described by Moore-Colyer et al. (2003) as the time postdose to first appearance of marker in feces. The CMRT represented the mean retention time in the hindgut.

Total mean GI retention time (**TMRT**) was calculated as TT + CMRT. Mean fractional passage rate from the time-dependent compartment (K_1), was calculated as the asymptotic fractional rate of passage (λ or λ_1) multiplied by a constant given for each Gn model, as described by Pond et al. (1988); i.e., 0.59635 for G2G1, 0.47454 for G3G1, and 0.40857 for G4G1. Mean square error (**MSE**) was used to evaluate the goodness of fit for the nonlinear models, as recommended by Pond et al. (1988). To further evaluate the fit of the ascending part of the marker distribution curve, illustrating the gamma time-dependency in the Gn (n = 2 to 4) part of the model, the SE predicted (**SEP**) was evaluated. The mean SEP between predicted and measured values in the ascending part of the curve (5 to 26 h postfeeding) was calculated for each model.

Total tract mean retention time was also estimated algebraically ($\mathbf{TMRT_{alg}}$), according to the equation described by Thielmans et al. (1978):

$$TMRT_{alg} = \frac{\sum_{n-1}^{i} t_i \, C_i \Delta_i}{\sum_{n-1}^{i} t_i \, C_i \Delta_i},$$

where t_i is the time (h) from the dosage of markers to the midpoint of the *i*th collection interval, C_i is the concentration of the marker in the *i*th sample, Δ_i is the interval (h) between the 2 samplings, and n is the number of samplings.

Statistical Analysis

Data were analyzed as a Latin square, split-plot design, in which the different grain processing methods represented the 4×4 Latin square. Data were evaluated using the MIXED procedure of SAS, as described previously by Littell et al. (1998), and model sums of squares were separated into overall mean, horse, period, grain processing, whole-plot error, passage model, passage model × grain processing interaction, feed (within passage model), and subplot error. All variables were considered fixed, except horse, whole-plot error, and subplot error, which were considered random. The PDIFF statement was used to separate means. The significance level was set to $P < 0.05$, and values between 0.05 and 0.10 were considered to reflect trends.

RESULTS AND DISCUSSION

Modeling the GI Tract of the Horse

In order to fully understand the equine digestive processes, the rate of passage through the different segments of the GI tract must be known. The passage rate is relevant to digestibility, water balance, exercise performance, and digestive disorders. Knowledge about how different feeds and feed processing will affect the transit parameters is also of great interest in the processing of feeds. Moreover, it is important to know what normal passage times are before trying to understand pathological conditions that affect the digestive tract in horses.

Earlier studies (Moore-Colyer et al., 2003, Austbø and Volden, 2006) have concluded that the digesta passage in horses is time-dependent, which means that particles that have spent the longest time in the mixing compartment(s) have a higher possibility of escaping the compartment(s). The integer gamma functions were chosen by Matis (1972) to model such a time-dependent

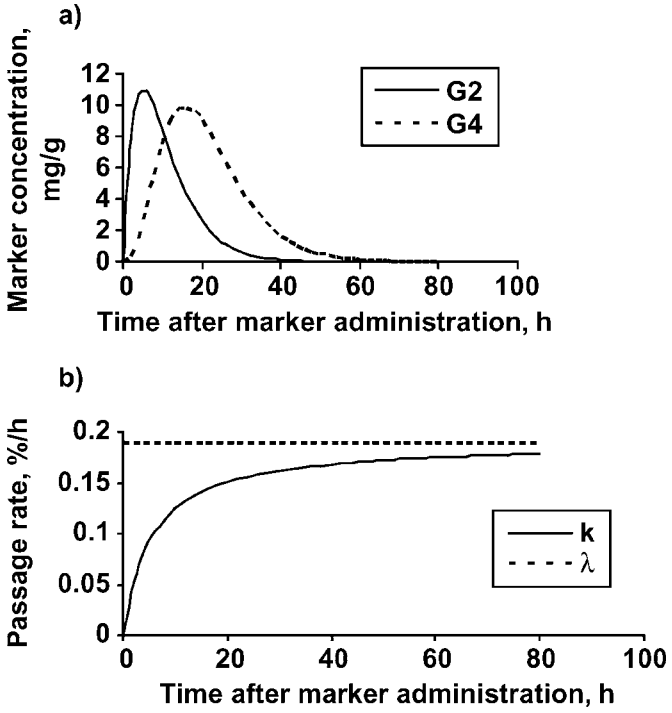

Figure 1. Illustration of 1-compartment passage models. a) Comparison of 2 of the integer gamma functions used by Pond et al. (1988) to model gastrointestinal passage rate; b) illustration of the passage rate k out of the mixing compartment, showing the approach to the maximum rate λ.

process. The functions are denoted as Gn, with n corresponding to the integer of the gamma function. The G1 represents an exponential distribution of residence times and is time-independent. Functions of G2 or higher represent time-dependent distribution of residence times. The order of the integer in the function alters the shape of the retention time distribution curve of feed particles, as shown in Figure 1. The rate at which the particles escape the mixing compartment(s) is denoted k and reaches toward a maximum denoted λ. The λ-value is used to calculate mean passage rate out of the time-dependent compartment.

Other studies have proposed a model describing 2 mixing compartments of a time-dependent or time-independent nature (Grovum and Williams, 1973), and this type of model has been successfully adapted to ruminant fecal excretion data (Pond et al., 1988). These models are denoted as GnG1 and hence include 1 time-dependent and 1 time-independent compartment. In the current study, these passage models were used to evaluate passage kinetics in horses. To evaluate the model estimation of TMRT, the nonlinear models were compared with the algebraic method described by Thielmans et al. (1978).

Influence of Passage Model on Estimated Passage Parameters

Key passage parameters of different passage models in oats are presented in Table 2, and corresponding parameters for hay are presented in Table 3. The estimated transit and retention times differed according to the model used, although there was little variation in TMRT between the different models in both feeds. Nevertheless, the TMRT was reduced with increased Gn factor for the 1-compartment models (P = 0.04) and became more similar to the results obtained from the algebraic model. The same tendency was not consistent for the 2-compartment models.

In the 1-compartment models, the estimated time spent in the time-dependent compartment increased as the gamma-dependency increased. Consequently, the estimated TT decreased. For the 2-compartment models, there was a large variation in the estimated time spent in each of the 2 compartments, and the ratio between the retention times in compartments 1 and 2 was largely affected by the model. The estimated time in the first, time-dependent compartment showed a tendency to rise as the gamma-dependency increased. The estimated time in this compartment rose to almost 12 h in the G4G1 model. Consequently, the TT decreased as the gamma dependency increased.

Evaluation of the Models

Information on the use of nonlinear models for estimating attributes of digesta flow in horses is limited. In cattle, the G3G1 model has been proposed as the model that best describes the GI passage (Huhtanen and Kukkonen, 1995). In sheep, Moore et al. (1992) proposed the G4G1 model as the model with the best fit to the observed marker distribution curves. Holland et al. (1998) concluded that a 1-compartment model can be used to represent fecal kinetics in horses. Moore-Colyer et al. (2003) proposed the 2-compartment G3G1 model as the best model but noted that the G4G1 model had only a slightly poorer fit evaluated by R^2. However, Holland et al. (1998) and Moore-Colyer et al. (2003) investigated only 1-compartment or 2-compartment models, and their studies did not compare the 2 types.

The MSE was used to evaluate the goodness of fit for the nonlinear models, as recommended by Pond et al. (1988). In addition, SEP was calculated for the ascending part of each excretion curve to evaluate the difference between the concentration of marker predicted by the model and the actually observed values (Tables 2 and 3). The G4 and G4G1 models must be considered equally suited to describe the equine intestinal passage. The G3 model was ranked third best model overall, differing about 0.5 h in TMRT because of a longer calculated TT. The G2 model and the G1G1 model showed the largest variation and were therefore considered the least suitable of the investigated models. The models that estimated the lowest TMRT also showed the lowest MSE and SEP. The same models were in the middle range of estimated time spent outside the mixing compartments (TT).

The algebraic model used by Thielmans et al. (1978) calculated the TMRT using the actual amount of

Table 3. Evaluation of different passage models for hay in the gastrointestinal tract of horses[1]

Model[2]	TT, h	K_1, %/h	K_2, %/h	$CMRT_1$, h	$CMRT_2$, h	CMRT, h	TMRT, h	MSE	SEP
G2	14.21	0.090	—	13.55	—	13.55	27.76	0.00169	0.0384
G3	12.03	0.125	—	14.54	—	14.54	26.57	0.00101	0.0294
G4	10.40	0.106	—	15.61	—	15.61	26.01	0.00089	0.0274
G1G1	14.08	0.091	0.152	6.82	6.82	13.64	27.72	0.00200	0.0397
G2G1	12.06	0.132	0.200	9.40	5.19	14.58	26.65	0.00106	0.0290
G3G1	11.03	0.195	0.109	7.55	9.36	16.91	27.94	0.00125	0.0282
G4G1	9.22	0.147	0.315	11.95	4.83	16.78	26.00	0.00097	0.0253
Thielmans[3]	—	—	—	—	—	—	25.50	—	—

[1]TT = Transit time; K_1 = mean fractional passage rate from the time-dependent compartment; K_2 = mean fractional passage rate from the time-independent compartment; $CMRT_1$ = mean retention time in the time-dependent compartment; $CMRT_2$ = mean retention time in the time-independent compartment; CMRT = compartment mean retention time (for the 2-compartment models CMRT = $CMRT_1$ + $CMRT_2$); TMRT = total mean retention time (TT + CMRT); MSE = mean square error; SEP = SE predicted (calculated 5 to 26 h postfeeding).
[2]Compartment models by Pond et al. (1988).
[3]Based on the algebraic model by Thielmans et al. (1978).

marker recovered from feces and estimated a TMRT close to the G4 and G4G1 models. This further supports the conclusion that these models give the best estimate of the equine GI passage. Austbø and Volden (2006) reached the same conclusion as in the present experiment, i.e., G4 and G4G1 must be considered equally good models for the equine intestinal passage when evaluated by MSE.

Considering the anatomy of the equine GI tract, the large blind sac of the cecum is a natural site for mixing and probably selective retention of feed particles. The cecum, with its blind end at the lowest point of the abdominal cavity, is optimally situated for gravity-assisted segregation and retention of dense, lignified particles. However, it is uncertain whether this mixing should be considered time-dependent or time-independent. The unique shape of the equine colon also facilitates retention at several positions, the right dorsal segment as the most probable site for retention. In this segment, the digesta, which is still quite fluid, passes from a narrow part of the intestine into the large-diameter sac, naturally slowing the speed and possibly creating a turbulent-like mixing. However, it is less likely that the retention at this stage is age-dependent. Meyer and Coenen (2002) assumed that in the first part of the large colon (left ventral), larger particles are retained, whereas the opposite occurs in the right dorsal to the ascending colon. However, it is unclear whether this applies to mixed diets (hay and cereals) or only to all-forage diets. Argenzio et al. (1974) found that the passage of digesta was particularly slow through the pelvic flexure and from the dorsal to the small colon, which could favor these sites as sites for retention of larger particles. More research in this area is needed to make final conclusions on the subject.

The TT represents the time spent outside the mixing compartments: the stomach, small intestine, and the caudal part of the large intestine. There was a 1.1 to 1.2 h difference ($P < 0.001$) in calculated TT between the G4 and G4G1 models, eliminating the difference resulting from the higher calculated retention time in the 2 compartments (CMRT) of the G4G1 model. For the models with a poorer fit, TT-values were higher than for models with a better fit.

The current study showed that the estimates of the passage parameters were dependent on the model used. Although the difference in total tract retention times did not vary much between the models, the estimated times in the different compartments differed. In the 1-compartment models, the estimated time spent in the mixing compartment increased as the gamma-dependency increased. Consequently, the estimated TT decreased. For the 2-compartment models, there was a large variance in the estimated time in each of the 2 compartments. The estimated time in the first, time-dependent compartment showed a tendency to rise as the gamma-dependency increased. The estimated time in this compartment reached almost 12 h in the G4G1 model. Consequently, TT decreased as the gamma dependency increased.

Comparison of Passage Parameters for Oats and Hay

Composite marker excretion curves describing the effect of different feed types are presented in Figure 2. The excretion curves for Yb (oats) and Cr (hay) were surprisingly similar, and for both markers, the peak values were achieved after 26 h. The cumulative distribution plot (Figure 3) showed that more than 95% of the markers were already excreted from the animal after 35 h.

Using the G4G1 model, the TMRT was 26.7 h for the oats and 26.0 h for the hay ($P = 0.03$). This experiment indicated that there was little specific retention of the fibrous hay particles compared with the oat particles.

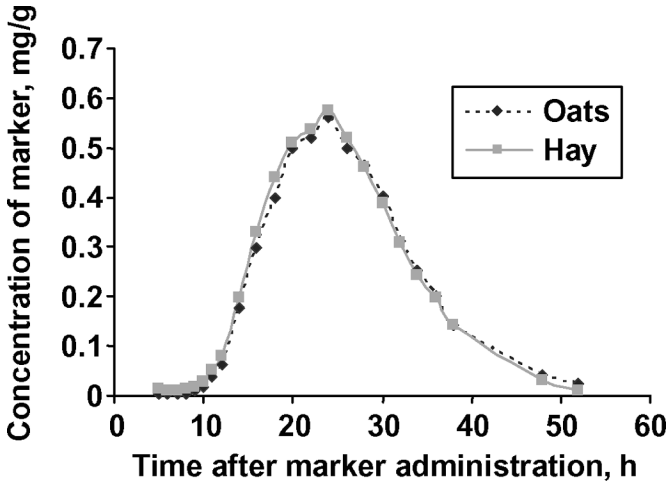

Figure 2. Comparisons of fecal marker distributions of Yb-labeled oats and Cr-mordanted hay in horses.

The hay was fed unchopped and should reflect the traditional regimen of horse feeding. A study by Holland et al. (1998) showed that TMRT was considerably longer for diets consisting of hay only than for mixed diets (hay and cereals), whereas Pagan et al. (1998) reached the opposite conclusion. They explained the difference with a difference in DM for the 2 diets and an increased salivation and water intake for the horses on a hay diet, both factors favoring a faster passage rate. In the experiment by Holland et al. (1998), the total tract retention time was only 20 h for horses on a diet consisting of both hay and cereals, which differs considerably from other studies. In their experiment, the horses were fed 20 g/kg of BW of hay plus 3.0 kg of cereals/d for the horses in the hay and concentrate group, which is considerably higher than the amount fed in the current study. Cuddeford et al. (1995) found a higher mean retention time, varying from 47.6 to 59.6 h (measured with Cr), which is 2-fold the retention time found in the current study. In the experiment of Cuddeford et al. (1995), the horses were fed alfalfa hay and oat straw 16.1 to 20.7 g/kg of BW, which is higher than in the current study and might have influenced the passage rate. The horses had a faster passage rate when fed large proportions of oat straw than when fed only alfalfa. Udén et al. (1982) found MRT in equines to be 23 h and the TT (time of first appearance of marker) to be 9 h. This resulted in a TMRT of 32 h, which is similar to the current study. The horses in the experiment of Udén et al. (1982) were fed 13 g/kg of BW, similar to the current study. Austbø and Volden (2006) found a TMRT of 26.8 h in horses fed the same diet as the current study.

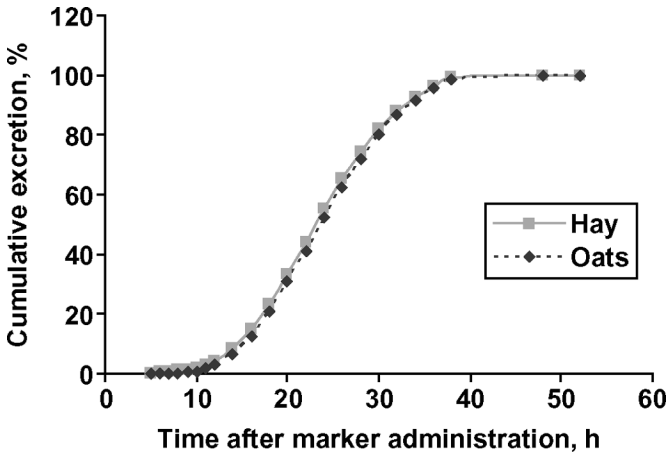

Figure 3. Cumulative excretion of Yb (oats) and Cr (hay) in horses.

Table 4. Comparison of retention times (h) for oats and hay in compartments of the equine gastrointestinal tract, calculated by the 2-compartment G4G1 model[1]

Item	Oats	Hay	SEM	*P*-value[2]
TT	9.50	9.22	0.19	0.27
$CMRT_1$	11.89	11.95	0.31	0.49
$CMRT_2$	5.30	4.83	0.27	0.06
TMRT	26.69	26.00	0.24	0.03

[1]TT = Transit time, time spent outside the mixing compartments; $CMRT_1$ = mean retention time in the time-dependent compartment; $CMRT_2$ = mean retention time in the time-independent compartment; TMRT = total mean retention time (TT + $CMRT_1$ + $CMRT_2$).
[2]*P*-values > 0.05 represent nonsignificant differences.

When excretion data were fitted to the G4G1 model, there was a tendency for hay to pass more rapidly than oats through the second compartment ($CMRT_2$; P = 0.06; Table 4). The differences between oats and hay were not significant for the other individual compartments, but for the total TMRT, there was a somewhat longer retention time for the oats than for the hay (P = 0.03; Table 4).

Comparison of Feed Processing

A comparison of the passage parameters of the 4 different feed processing methods showed no significant differences (Table 5), and data were therefore combined for further statistical analysis. However, this result is only based on different processing of oats, and should be further investigated with other types of grain.

Other Factors Influencing Gastrointestinal Retention Time

Pagan et al. (1998) found a reduced TMRT in exercised horses. The horses in the current experiment were exercised daily for 60 to 90 min in walk and trot in an outdoor rotary exerciser, which can be considered a medium level of exercise. Several of the previous experiments mentioned have been on horses on a low exercise level, which may interfere with the intestinal passage time. Drogoul et al. (2000) found a TMRT of the particulate matter of 37.2 to 46.7 h (fistulated and nonfistu-

Table 5. Comparison of retention times (h) between feed processing methods of oats, calculated by the 2-compartment G4G1 model[1]

Processing	Ground	Pelleted	Extruded	Micronized	*P*-value[2]
TT	8.72	10.27	9.97	9.04	0.16
$CMRT_1$	12.41	11.65	11.89	11.60	0.88
$CMRT_2$	5.36	4.99	5.31	5.55	0.98
TMRT	26.49	26.90	27.16	26.19	0.85

[1]TT = Transit time, time spent outside the mixing compartments; $CMRT_1$ = mean retention time in the time-dependent compartment; $CMRT_2$ = mean retention time in the time-independent compartment; TMRT = total mean retention time (TT + $CMRT_1$ + $CMRT_2$).
[2]*P*-values > 0.05 represent nonsignificant differences.

lated, respectively) in ponies. These ponies were not exercised during the experiment and were fed a forage-only diet.

The current experiment was performed using cannulated horses. This has been shown to affect the passage kinetics. Pulse et al. (1973) and Austbø and Volden (2006) found increased TMRT after cecal cannulation.

In cows, it has been observed that feeding level and feed particle size may affect the passage kinetics (Poore et al., 1991). As the ruminant regurgitates and rechews the ingesta, the initial particle size is of importance to the retention time. The horse is known to chew the feed more thoroughly than the ruminant does, and the horse does not regurgitate. Moore-Colyer et al. (2003) concluded that chop length of forages did not seem to influence digesta TMRT. In the experiment conducted by Drogoul et al. (2000) using fistulated horses, there was a difference in TMRT between chopped (3 cm) and ground/pelleted (0.8 mm) hay, ranging from 37.2 to 47.2 h, respectively. It is believed that the difference between unchopped and chopped hay would not greatly influence the retention time in horses, given the ability to chew the hay particles thoroughly. However, ground and pelleted hay consists of much smaller particles and consequently could be expected to have passage kinetics more similar to concentrates. All together, the aforementioned studies have major differences in diet composition, feeding practice, exercise, body size, and breed and are difficult to compare in all aspects.

Use of Markers

Use of different markers to label feedstuffs allows simultaneous estimation of passage measurements of different types of feeds (Poore et al., 1991; Moore et al., 1992). Criticism of the use of markers (Erdman and Smith, 1985; Faichney, 1986; Combs et al., 1992) has been mainly for experiments using markers loosely added to the feed. Experiments have been conducted on feed sprayed with marker or marker added to the feed as powder. This procedure gives little evidence that the markers found in feces are representative of the hay or cereal particles, as opposed to the liquid phase. The current experiment used markers strongly bound to the feed particles, which would ensure a much smaller error than using loosely bound markers (Poore et al., 1991). The same procedure was used by Drogoul et al. (2000) and Austbø and Volden (2006), who also investigated the TMRT of a liquid marker, which was significantly shorter than the TMRT for the particulate matter. This ensures that the measured values are from the fed particles rather than from the liquids. In this experiment, the marked feed was fed immediately before the rest of the ration. The effect of this feeding regimen should not influence the passage parameters significantly, according to Poore et al. (1991). Moore-Colyer et al. (2003) also concluded that Yb is a successful external marker for determining TMRT of fiber-based diets in ponies.

IMPLICATIONS

This study showed that both 1- and 2-compartment time-dependent models can be fitted to describe the gastrointestinal passage kinetics of the horse. The G4 model and the G4G1 model gave the best fit to the observed excretion curves, as determined by the smallest variation, and are thereby proposed as the models that best describe the equine gastrointestinal passage. The results indicate that particulate mixing and selective retention takes place during the passage process in the equine hindgut, although mixing and selective retention is of less importance compared with ruminants. There is little difference in total mean retention time between particles of hay and oats. The passage rate of the hay also seems to be related to the passage rate of the oats. Knowledge on passage kinetics is important to understand the process of digestion in the equine gastrointestinal tract and will be important in optimizing the feeding of the horse.

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