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FIBRE DIGESTION AND DIGESTA RETENTION FROM DIFFERENT PHYSICAL FORMS OF THE FEED IN THE RABBIT

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Abstract—1. Digestibility of fibre was higher in guinea-pigs than in rabbits, however, the digestibility of hemicellulose fraction containing agar was similar in both animals.

2. The digestibility of fibre of a fine particle diet was higher than that of a large particle diet in the rabbit permitted coprophagy, whereas it was lower in the rabbit prevented from coprophagy.

3. The fine particle diet tended to cause shorter retention time of digesta in the rabbit prevented from coprophagy.

4. These suggest that the digestibility of fine components relates to their physical properties which affect the retention time of digesta in the rabbit.

INTRODUCTION

The rabbit is a typical caecum fermenter which has a well-developed caecum having an important nutritional function with a mechanism for selective retention of fine particle and solutes. Rabbits are herbivorous animals, consuming a high roughage diet. However, as reviewed by Cheeke *et al.* (1986), the digestibility of the crude fibre fraction of roughage is remarkably low and varies considerably depending upon the diet. Rabbits have a digesta separation mechanism in the colon (Hörnicke and Björnhag, 1980) which results in selective retention of fluid and fine particles in the caecum (Pickard and Stevens, 1972). The low digestibility of fibre in the rabbit seems to be related to the digestive strategy which results in the relatively rapid elimination of large, hard-to-digest particles from the hindgut, enabling the animal to maintain a higher level of feed intake than it would otherwise be able to.

In relation to the digestive strategy of the rabbit, it can be predicted that the digestibility of fibre varies according to physical property, particle size, fluidity and solubility of dietary fibre, because long retention time causes higher capacity of microbial degradation of fibre.

The guinea-pig is a strictly herbivorous, non-ruminant animal with a voluminous caecum which can retain digesta for a considerable time (Sakaguchi *et al.*, 1986) and is more efficient in the digestion of fibre and its components than rabbits, hamsters and rats (Sakaguchi *et al.*, 1987). It has been reported that guinea-pigs digest organic matter and crude fibre as efficiently as horses and ponies (Slade and Hintz, 1969). No selective retention of digesta is observed in the guinea-pig. Liquid and particle digesta move together through the gastrointestinal tract. This movement of digesta can be considered to be advantageous in the digestion of fibre (Hume and Sakaguchi, 1991).

The objective of the present study was to test this hypothesis by comparing fibre digestibility and mean retention times of digesta markers in rabbits and guinea-pigs fed an agar-containing diet and in rabbits fed diets having different sizes of fibre particles.

MATERIALS AND METHODS

Animals and feeding

Eighteen rabbits (mean body mass 1.45 kg), with or without neck collars to prevent caecotrophy, and four guinea pigs (mean body mass 646 g) were used. All animals were housed individually in stainless steel mesh metabolism cages (0.36 m diameter × 0.3 m high) and fed freely in an air conditioned room (24 ± 1°C). In experiment 1, diet 1 (alfalfa meal 44%, rolled barley 33%, agar 13.2%, sucrose 8.8% and vitamin mix 1.0%) was fed to eight rabbits and four guinea-pigs. In experiment 2, diet 2 (alfalfa meal 40%, sucrose 20%, corn starch 9.8%, corn oil 8.0%, mineral mix 8.0% and vitamin mix 2.0%) was fed to 10 rabbits. Diet 2 was divided into two categories according to the particle size of alfalfa meal (large: 0.25–2.0 mm mesh; fine: under 0.15 mm mesh). The composition of the experimental diet is shown in Table 1. Each diet was pelletted.

Markers of liquid and solid digesta were mixed with a small amount of the experimental diet and given 2 hr after the digestion trials. The animals were starved for 2 hr before the administration of the markers.

Feed and water were available freely in both periods and coprophagy was not prevented in the guinea-pig so that feeding habits were as normal as possible.

Preparation of particles

In experiment 2, lucerne meal milled through a 2 mm screen was sieved on to a 0.25 mm screen. The residual lucerne meal was divided into two equal portions. One was used as large particle (0.25–2.0 mm mesh), the other was milled completely through a 0.15 mm screen then used as fine particle (under 0.15 mm mesh).

Collection procedure

A 7-day precollection period was followed by a 12-day collection period. The first 5 days of the collection period

Table 1. Composition of experimental diet (g/kg)

Experiment	1	2
Ingredients		
Lucerne (*Medicago sativa*) meal	440	400
Casein	—	122
Rolled barley	330	—
Agar	132	—
Sucrose	88	200
Wheaten starch	—	98
Soybean oil	—	80
Mineral mix*	—	80
Vitamin mix†	10	20
Analysis		
Moisture	89	107
Organic matter	865	819
Crude protein (nitrogen × 6.25)	119	183
NDF	463	207
ADF	124	144
Crude ash	47	74

*Composition (mg/kg mixture): 145.6 $CaHPO_4 \cdot 2H_2O$, 257.2 KH_2PO_4, 93.5 $NaH_2PO_4 \cdot H_2O$, 46.6 NaCl, 350.9 Ca-lactate, 31.4 Fe-citrate, 71.7 $MgSO_4$, 1.1 $ZnCO_3$, 1.2 $MnSO_4 \cdot 6H_2O$, 0.3 $CuSO_4 \cdot 5H_2O$, 0.1 KI.

†Composition (mg/kg mixture): 1000 retinol acetate, 2.5 cholecalciferol, 1200 thiamin hydrochloride, 4000 riboflavin, 800 pyridoxine hydrochloride, 0.5 cyanocobalamin, 30000 ascorbic acid, 5000 tocopherol acetate, 5200 menadione, 20 biotin, 200 pteroylmonoglutamic acid, 5000 calcium pantothenate, 50,000 *p*-aminobenzoic acid, 6000 nicotinic acid, 6000 inositol, 200,000 choline chloride, 730,577 cellulose powder.

NDF, neutral detergent fibre (Van Soest and Wine, 1967).

ADF, acid detergent fibre (Van Soest, 1963).

were to estimate the digestibility of feed. The next 7-day period was to estimate digesta retention time. Feed consumption of each animal was recorded daily.

Faeces were collected daily during the 5-day collection period in digestion trials. During the last 7-day collection period, faecal samples were taken every 2 hr for the first 24 hr, every 4 hr for the next 12 hr, every 6 hr for the next 48 hr and every 8 hr for a further 96 hr after dosing.

Digesta markers

Cr-mordanted Italian ryegrass (*Lolium multiflorum* L.) cell wall constituents (Cr-CWC) as a particle marker and Co-EDTA as a liquid digesta marker were used to estimate retention time. Cr-CWC were prepared by the method of Udén *et al.* (1980). The Cr-CWC prepared was ground to coarse particle size and passed through a 40 mm mesh screen. The resulting particles were then passed through a 20 mm mesh screen and those which remained on the screen were used in the experiment. The diameter of the particles was in the range 0.381–0.840 mm and the length was shorter than 5 mm.

Analytical methods

The pooled faecal samples from the digestion trials were oven-dried at 60°C, then ground and analysed for dry matter, crude ash and total nitrogen (AOAC, 1975) and for neutral-detergent fibre (NDF) and acid-detergent fibre (ADF) by the methods described by Van Soest and Wine (1967) and Van Soest (1963), respectively. Organic matter was determined by subtracting ash from dry matter.

To determine concentrations of Cr and Co, faecal samples were oven-dried at 60°C and ashed at 550°C for 5 hr. The ashed samples were treated according to the method described by Williams *et al.* (1962). Analysis of Cr and Co in the treated sample was made by atomic absorption spectroscopy (Atomic absorption spectrophotometer AA-80; Nippon Jarrell-Ash, Kyoto).

Calculations

Single exponential regression equations were fitted statistically to the time-course decline of the faecal concentrations of Cr and Co in rabbits and guinea-pigs. A turnover time of each marker was estimated from the decline in faecal concentration of marker by the function (Brandt and Thacker, 1958):

$$Y = Y_0 \times e^{-kt}$$

where Y is the concentration of Cr or Co in faeces at time t, Y_0 is the constant depending on the level of Cr or Co fed, k is the rate constant and t is the time interval after feeding of the markers (hr). Turnover time was calculated as the reciprocal of the rate constant (k) if the exponential curve fitted to the time-course excretion values of the markers after faecal marker concentration reached a maximum. Total mean retention time (MRT) in the gastrointestinal tract was calculated as the sum of the reciprocal of k and transit time (TT) equal to the first appearance of the marker after a dose.

Differences between mean values obtained in experiment 1 were evaluated statistically by Student's t-test (Snedecor and Cochran, 1967). The results in Experiment 2 were analysed as a 2 × 2 factorial design and tested for statistical difference by Duncan's multiple range test (Duncan, 1955).

RESULTS

Experiment 1

Feed intake and digestibility (*Table* 2). The rabbits without collar and the guinea-pigs gained slightly in weight (mean 10.7 g/day, 4.4 g/day, respectively) during the experimental period, but the rabbits with collar lost weight slightly (mean 4.2 g/day). Daily feed intake on a metabolic body size (per kg body weight$^{0.75}$) basis was similar in the rabbit without collar, the rabbit with collar and the guinea-pig.

Apparent digestibilities of dry matter, organic matter, crude protein, NDF and ADF were significantly higher in the rabbit without collar than in the rabbit with collar, however, there was no statistical significant difference in the hemicellulose fraction between the rabbits with and without collar. The guinea-pigs digested dry matter, organic matter, ADF and crude ash more efficiently than the rabbits without collar. However, there was no significant difference in the digestibilities of crude protein and hemicellulose fraction between the rabbits without collar and the guinea-pigs.

Retention of digesta markers (*Table* 3). In the rabbits with and without collar, calculations of digesta retention time of liquid marker were significantly larger than those of particle marker. Prevention of coprophagy decreased the retention time of liquid and particle digesta marker.

In the guinea-pig there were no differences in the values of $1/k$, TT and MRT ($1/k$ + TT) between particle marker and liquid marker.

Experiment 2

Feed intake and digestibility (*Table* 4). Apparent digestibilities of dry matter, organic matter, crude protein and crude ash were higher in the rabbit without collar than in the rabbit with collar with both sizes of dietary particles. Fibre components (NDF and ADF) were not statistically different between the rabbits with and without collar on the large size of dietary particle diet, however, they were lower in the rabbit with collar than in the rabbit without collar on fine size of dietary particle diet. In the rabbit without collar, ADF and NDF were digested effectively on

Table 2. Experiment 1. Feed intake and apparent digestibilities of feed in the rabbit and guinea-pig fed agar-containing diet

	Rabbit ($N = 8$)					
	Without collar‡		With collar§		Guinea-pig ($N = 4$)	
	Mean	SE	Mean	SE	Mean	SE
Initial BW	1756	61	1766	47	646	68
Weight gain (g/5 day)	53.6	15.1	−21.0**	14.2	22.0	3.6
Feed intake ($g/kg^{0.75}$/day)	48.1	2.5	48.8	2.8	47.6	1.6
Digestibility (%)						
Dry matter	61.8	0.4	56.6**	1.0	66.9†	1.7
Organic matter	62.0	0.3	56.9**	0.9	67.8††	1.4
Crude protein	58.4	1.5	40.5**	2.4	65.9	1.9
NDF	47.4	0.8	43.9*	1.4	53.7†	2.1
ADF	18.3	1.3	11.3*	2.0	31.5†	3.9
Hemicellulose	57.9	1.2	55.8	1.5	61.8	1.5
Crude ash	55.9	2.2	48.9*	2.2	72.6†	3.0

‡Animals without collar were permitted coprophagy.
§Animals with collar were prevented coprophagy.
||Animals were permitted coprophagy.
*,**Mean values are significantly different from the rabbit without collar ($P < 0.05$, $P < 0.01$ respectively).
†,††Mean values are significantly different from the rabbit without collar ($P < 0.05$, $P < 0.01$ respectively).
Hemicellulose fraction is calculated by substracting ADF from NDF.

fine size of dietary particle diet compared with on large size of dietary particle diet.

Interaction between particle size of diet and prevention of coprophagy (with or without collar) was not present in analysing the results of 2 × 2 factorial in each digestibility of component.

Retention of digesta markers (*Table* 5). In the rabbit with collar there were no statistical differences in the values of $1/k$, TT and MRT ($1/k$ + TT) between particle marker and liquid marker with the large particle diet, however, significantly larger differences in $1/k$ and MRT with the fine particle of diet. These differences are smaller than those in Experiment 1. The retention times of both digestible markers were slightly higher with the large particle diet than the fine particle diet (no statistical difference).

Table 3. Experiment 1. Measures of retention of digesta markers in the rabbit and guinea pig fed agar-containing diet

	Rabbit ($N = 8$)					
	Without collar§		With collar‖		Guinea-pig ($N = 4$)	
	Mean	SE	Mean	SE	Mean	SE
Particle						
$1/k$	11.7	1.8	5.5**	0.9	10.6	0.5
TT	5.0	0.8	6.5	0.6	4.5	0.5
MRT	16.7	1.7	12.0*	1.1	15.1	0.6
Liquid						
$1/k$	75.0†	9.4	36.9**†	4.2	10.8‡	1.0
TT	5.0	0.8	6.8	0.7	4.5	0.5
MRT	80.0†	9.3	43.6**†	4.4	15.3‡	0.8

§Animals without collar were permitted coprophagy.
‖Animals with collar were prevented coprophagy.
k, Rate constant which is the dilution rate (per hr) of the marker in the digestive tract. TT, Time interval between feeding and first appearance of the marker in the faeces (transit time). MRT, Sum of $1/k$ and TT.
*,**Mean values are significantly different from the rabbit without collar ($P < 0.05$, $P < 0.01$ respectively).
†Mean values are significantly different from particle marker ($P < 0.01$).
‡Mean values are significantly different from the rabbit without collar ($P < 0.01$).

DISCUSSION

In the guinea-pig, digesta are retained mainly in the caecum and the upper proximal colon (Sakaguchi *et al.*, 1985). When markers are injected into the caecum, the rate constant of marker dilution in caecal contents agrees with that in the faeces. Furthermore, the rate constant of marker dilution in the faeces after oral application agrees closely with that in the caecum and in the faeces after caecal injection (Sakaguchi *et al.*, 1986). These findings suggest that the dilution rate of marker in the faeces can be regarded as a reflection of marker dilution in the caecum after oral application. The retention time of digesta in the large intestine (mainly caecum) can, therefore, be calculated from the faecal values for marker excretion in the guinea-pig.

In this experiment, apparent digestibilities of dry matter, neutral detergent fibre (NDF) and acid detergent fibre (ADF) were higher in the guinea-pig than in the rabbit. As mentioned above, guinea-pigs digest organic matter and crude fibre as efficiently as horses and ponies (Slade and Hintz, 1969). No selective retention of digesta also observed in this experiment in the guinea-pig might be considered to be advantageous in digestion of fibre. The large intestine of the brushtail possum functions much like the caecum of the guinea-pig, with no selective retention of digesta; brushtail possums digest more fibre (both ADF and NDF) than rabbits which retain fluid and fine particle digesta selectively on a 44.4% alfalfa diet (Sakaguchi and Hume, 1990).

In Experiment 1, prevention of coprophagy lowered the digestibilities of crude protein and ADF, but had little effect on the digestibility of NDF and hemicellulose fraction. It was suggested that the hemicellulose fraction of the diet containing agar moved mostly as fluid digesta in the gastro-intestinal tract, because the digestibility of NDF which contained hemicellulose fraction was much higher than that of ADF connecting with long retention time of

Table 4. Experiment 2. Feed intake and apparent digestibilities of feed in the rabbit fed large or fine particle diet

Collar	Large particle Without*	With†	Fine particle Without*	With†	SEM
Feed intake					
(g/kg$^{0.75}$/day)	60.9	55.6	66.4	54.2	4.3
Digestibility (%)					
Dry matter	75.0‡	71.0§	76.0‡	70.4§	1.4
Organic matter	76.9‡§	73.0§	78.3‡	72.4§	1.3
Crude protein	85.4‡	77.0§	85.7‡	77.9§	1.2
NDF	34.6‡§	31.2§	38.8‡	24.8‖	3.2
ADF	26.5‡	25.9‡	32.5§	17.2‖	2.7
Crude ash	53.6‡	47.6§	57.5‡	48.9§	2.8

*Animals without collar were permitted coprophagy.
†Animals with collar were prevented coprophagy.
‡,§,‖Mean values in the same horizontal row with different superscripts are significantly different ($P < 0.05$).

fluid digesta. Sakaguchi and Hume (1990) have suggested that agar behaves as soluble fibre in the gastrointestinal tracts and it may be expected to be selectively retained in the rabbit caecum along with liquid and fine particles and consequently be extensively degraded by microbial enzymes.

According to several reports on digestion in the rabbit, prevention of coprophagy results in lowering of digestibilities of dry matter and protein and retention of nitrogen (Thacker and Brandt, 1955; Yoshida *et al.*, 1966; Stephens, 1977; Gioffré *et al.*, 1981; Teleki *et al.*, 1985), but has no effect on the digestibility of fibre (Gioffré *et al.*, 1981; Udén and Van Soest, 1982). The results of this experiment are different from those reported so far. If particle size of fibre component in the diet is small, this component is expected to be selectively retained in the caecum. This may result in a higher digestibility of fibre on the diet containing small particles of fibre. If there is any difference in particle size of fibre component in the diet between previous reports and this study, the different effect of prevention of coprophagy on the digestibility of fibre may be expected.

The prevention of coprophagy caused shorter retention time of fluid and particle digesta in these experiments. This suggests that some amount of particle digesta is retained in the caecum and is recycled through the digestive tracts by caecotrophy, as well as the large amount of liquid digesta.

In Experiment 2, the digestibilities of fibres (NDF and ADF) of the fine particle diet were higher than those of the large particle diet in the rabbit without collar, whereas they were lower in the rabbit with collar, suggesting that the digestibility of fibre of the large particle diet was little affected by the presence of caecotrophy. MRTs of the digesta markers in the rabbits fed the small particle diet were somewhat shorter (no statistical significance) than in the rabbits fed the large particle diet, connecting lower digestibility of fibre. These suggest that physical properties affect the digestibility of fibre and large particle size lowered the role of the caecum in the digestion of fibre in the rabbit.

It has been reported that fine grinding of feed ingredients led to an increase in retention time (Laplace and Lebas, 1977). Gidenne *et al.* (1991) reported grinding of lucerne meal did not improve cell wall digestibility and caeco–colic MRT was higher with fine particle diet than with non-grinding lucerne meal. These results of the retention of digesta are in contrast with our results. The contrast could be caused by the different condition of sampling between the experiments and ours. The rabbits in this experiment wore neck collars to prevent coprophagy. Increasing the retrograde motility of the colon with a finely ground diet (Bouyssou *et al.*, 1988) may result in larger amounts of digesta being retained in the caecum. This should mean increased digesta recycling by caecotrophy, contributing to a longer retention time of digesta in the rabbit permitted coprophagy.

Table 5. Experiment 2. Measures of retention of digesta markers in the rabbit with collar fed large or fine particle diet†

	Large particle ($N = 4$) Mean	SE	Fine particle ($N = 5$) Mean	SE
Particle				
$1/k$	36.9	11.0	16.2**	2.9
TT	6.5	1.0	10.2	2.0
MRT	43.4	11.3	26.2*	4.8
Liquid				
$1/k$	54.1	11.7	33.3	2.5
TT	4.0	0.5	7.5	0.7
MRT	58.1	12.2	40.8	2.9

†Animals with collar were prevented coprophagy.
k, Rate constant which is the dilution rate (per hr) of the marker in the digestive tract. TT, Time interval between feeding and first appearance of the marker in the faeces (transit time). MRT, Sum of $1/k$ and TT.
*,**Significantly different from liquid marker ($P < 0.05$, $P < 0.01$, respectively).

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