British Journal of Nutrition (2003), **90**, 373–383
DOI: 10.1079/BJN2003920

The rat as a model for pigs: comparative values for the digestibility of NSP and other macronutrients

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(Received 5 August 2002 – Revised 5 March 2003 – Accepted 17 April 2003)

The present investigation was undertaken to study whether conventional male Wistar rats could be used as a model for pigs with regard to total tract digestibilities of NSP and macronutrients and whether nebacitin-treated rats could be used as a model for small intestinal digestibility in pigs. Nineteen experimental diets prepared from different fractions of wheat and oats, and which all had been evaluated in experiments with ileal cannulated pigs, were used for the present study. There was a close relationship between the total tract digestibilities of organic matter in the two species. The same was the case with regard to the digestibility of total NSP and arabinoxylans, but the values were on average 6 % lower in rats than in pigs. On average, there were no significant differences between rats and pigs with regard to faecal protein digestibility. However, protein in oat-based diets was significantly better digested in the rat than the pig. The digestibility of fat was consistently higher in rats than in pigs, with the biggest difference being found in oat-based diets, in which most of the fat was locked in cell structures. For the wheat-based diets, in which a large proportion of the fat was present as added fat, there was a greater similarity between the two species. In nebacitin-treated rats the digestibility of organic matter, starch, protein and fat was negatively related to the dietary level of NSP, but this model could not be used to predict the small intestinal digestibility of NSP and macronutrients in ileal-cannulated pigs.

Digestibility: Non-starch polysaccharides: Protein: Fat: Pigs: Rats

The laboratory rat has been widely used to investigate basic principles of nutrition in single-stomached animals. In contrast to human nutrition, however, the use of rats as models in pig nutrition is less well accepted, because it is relatively easy to obtain results from the pig itself. The great value of the rat as a model lies in the economic factors associated with facilities and time, which allows the use of large numbers of animals and a rapid production of results.

The digestibility of energy and protein in the pig and rat is highly correlated for several diets (Eggum, 1973; Eggum *et al.* 1982), indicating that the rat may be a good model for pigs for these variables. However, it is less clear whether rats are also suitable models for pigs with regard to the digestibility of other nutrients and the fermentation of non-digestible carbohydrates, primarily as NSP, by the gut microflora. Like the pig, rats harbour a permanent bacterial flora in the stomach and small intestine, and similar groups of bacteria were found in the large intestine of both species (Jensen, 1992). However, there are obvious differences between rats and pigs that may be of importance for the microbial fermentation. The relative size of the caecum in rats is bigger than in pigs and the rat may practise coprophagy. Further, the rat is a small animal with a faster transit through the gut, and this can reduce bacterial polysaccharide breakdown compared with the pig (van Soest *et al.* 1983). Accordingly, van Soest *et al.* (1983) concluded from the results of comparative studies in rat, pig and human subjects that the degree of fermentation was lower in rats than in human subjects and pigs (rats < human subjects < pigs). It is not known, however, whether this will be valid for all types of NSP.

Cannulation of pigs with various types of fistulas at the terminal ileum is commonly used in pig nutrition to separate the enzymatic digestion in the small intestine from the bacterial fermentation in the large intestine. However, the escalating costs for performing experiments with surgically manipulated pigs and the growing public concern against the use of this type of animal model in nutrition research are two weighty arguments for consideration of the use of rats as models for pigs (Bach Knudsen, 1991). One option is the use of rats in which the intestinal flora is reduced by treatment with antibiotics. Because in these rats bacterial fermentation, as measured by the concentration of ATP, is largely suppressed, excretion of dietary constituents in the faeces reflects material not digested by

Abbreviations: AX, arabinoxylans; MTT, mean transit time.

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the rats' endogenous enzymes. Nebacitin-treated rats were used in investigations where the role of bacterial fermentation on N and energy metabolism (Eggum *et al.* 1979) and the digestibility of starch (Björck *et al.* 1986) have been studied. However, the reliability of the nebacitin-treated rat as a model for the small intestinal digestibility in the pig remains to be evaluated.

The aim of the present investigation was to study whether the conventional rat could be used as a model for the pig with regard to the faecal (i.e. total tract) digestibility of NSP and other macronutrients derived from diets based on different fractions of wheat and oats. Further, we investigated whether nebacitin-treated rats could predict the small intestinal digestibility of NSP and nutrients in the pig. The results obtained on digestibilities in pigs have been published previously (Bach Knudsen & Hansen, 1991; Bach Knudsen *et al.* 1993*a*,*b*; Bach Knudsen & Canibe, 2000).

Material and methods

Diets

Nineteen experimental diets were prepared from different fractions of wheat and oats as described previously (Bach Knudsen & Hansen, 1991; Bach Knudsen *et al.* 1993*a*,*b*; Bach Knudsen & Canibe, 2000). The corresponding pig and rat diets were prepared from the same batches of cereal components. Because during each experiment the rat studies were performed after the pig studies, cereal components were kept frozen until used for the rats. Additional protein (casein, egg powder) and fat sources (soyabean oil, lard) were taken from different batches for pigs and rats. In Expt 3, whey protein contained in the pig diets was replaced by casein in the rat diets. Ingredients and the chemical composition of the diets are given in Tables 1 and 2 respectively. Total NSP contents of the diets (28–108 g/kg DM) were rather low compared with normal pig diets, because the pig studies were planned to investigate the physiological effects of different fractions of cereal grains. Cr_2O_3 marker was added to the diets for the pigs (1–4 g marker/kg DM); balances in the rats were performed without marker. For the pigs, diets were thoroughly mixed with water before feeding, while the rats were fed the diets in dry form.

Animals and feeding

The protocol for the experiments was approved by the Danish Animal Experiments Inspectorate, Copenhagen, Denmark.

Pig studies. The general experimental procedure has been described elsewhere (Bach Knudsen & Hansen, 1991; Bach Knudsen *et al.* 1993*a*,*b*; Bach Knudsen & Canibe, 2000). In brief, a total of seventy-six pigs (40–50 kg), cannulated at the end of the small intestine, were used in the five experiments. Surgery was performed at 30–35 kg and a T-cannula was placed in the ileum 150 mm anterior to the ileo–caecal junction. In each experiment, pigs were divided into groups of four animals per diet. They were fed three times per d at 07.00, 15.00 and 23.00 (or 22.00) hours, with an amount of diet adjusted to give the same amount of net energy per d. After an adaptation period of 7 d, faeces were collected quantitatively on days 7–11 and ileal digesta on days 12–14. Ileal digesta were collected for a total period of 12 h: on day 12 at 09.00–11.00 and 13.00–15.00 hours, on day 13 at 08.00–10.00 and 12.00–14.00 hours, and on day 14 at 07.00–09.00 and 11.00–13.00 hours. In Expts 1 to 3, faecal collections were repeated on days 21–25 and ileal collections from days 26–28.

Faeces were collected two times per d, frozen and stored at −20°C. At the end of each experiment, faeces were mixed before sampling for analysis. The ileal digesta were collected on ice, frozen immediately after collection, stored at −20°C and mixed thoroughly before samples were taken for analysis.

Rat studies. The general experimental procedure has been described by Eggum (1973). For all experiments, male Wistar rats with an initial weight of approximately 70 g were used. The rats were kept individually in metabolism cages, and were fed a fixed amount of feed (10 g DM/d) and had free access to water. Two groups of five rats each were used per diet. One group received no antibiotic, for the second group nebacitin (bacitracin-neomycin sulfate (2:1 w/w); Løve Apotek, Viborg, Denmark) was added to the diets (7 g/kg DM). After an adaptation period of 5 d, faeces were collected quantitatively on days 6–10. Faeces were collected two times per d, frozen and stored at −20°C. At the end of each experiment, freeze-dried faeces obtained from each rat were mixed before sampling for analysis.

Analytical methods

DM contents of feed, ileal digesta and faeces were determined by drying at 105°C for 5 h. All the following analyses were made in duplicate. Protein (N × 6·25) was determined by the Kjeldahl method using a Kjell-Foss 16200 autoanalyser (Foss A/S, Hillerød, Denmark) and fat (HCl-fat) was extracted with diethyl ether after acid hydrolysis (Stoldt, 1952). Total ß-glucan was determined by the fluorometric method of Jørgensen & Aastrup (1987) (Expts 1 and 2) and by the enzymatic methods of McCleary & Glennie-Holmes (1985) (Expts 3–5). Starch was analysed by the enzymatic method described by Bach Knudsen *et al.* (1987) (Expts 1–4) and Bach Knudsen (1997) (Expt 5) and total NSP and their constituent sugars as alditol acetates by GLC for neutral sugars, and by a colorimetric method for uronic acids using a modification of the Uppsala procedure (Theander & Westerlund, 1986) and the procedure of Englyst *et al.* (1982) (Bach Knudsen, 1997). Starch was quantitatively removed by incubation (100°C, 60 min; 60°C, 16 h) with a thermostable α-amylase (Termamyl; Novo A/S, Bagsvaerd, Denmark) and with a ß-glucanase-free amyloglucosidase (Boehringer Mannheim GmbH, Mannheim, Germany). The polysaccharides in the starch-free residues were allowed to swell in the presence of H_2SO_4 (12 M, 30°C, 60 min), hydrolysed with 1 M-H_2SO_4 (100°C, 2 h), reduced with potassium borohydride to alcohols and acetylated with 1-methylimidazole to catalyse the reaction; allose was used as internal standard.

Table 1. Ingredients of the experimental diets fed to the rats (g/kg DM)

Expt	Diet*	No.	Group	Wheat flour	Wheat aleurone testa	Wheat pericarp	Wheat bran	Rolled oats	Oat flour 1	Oat flour 2	Oat groats	Oat bran	ß-Glucan-enriched fraction	Insoluble residues	Casein	Egg powder	Soyabean oil	Lard
1	WFI	1	W	787	–	–	–	–	–	–	–	–	–	–	82	–	75	–
	WFA	2	W	637	158	–	–	–	–	–	–	–	–	–	80	–	69	–
	WFPT	3	W	715	–	70	–	–	–	–	–	–	–	–	86	–	73	–
	WFWB	4	W	713	–	–	79	–	–	–	–	–	–	–	81	–	71	–
2	WFII	5	W	787	–	–	–	–	–	–	–	–	–	–	82	–	75	–
	WFOBI	6	W + O	676	–	–	–	–	–	–	–	148	–	–	59	–	61	–
	RO	7	O	–	–	–	–	857	–	–	–		–	–	67	–	20	–
	ROOB	8	O	–	–	–	–	726	–	–	–	138	–	–	62	–	18	–
3	OG	9	O	–	–	–	–	–	–	–	876	–	–	–	68	–	–	–
	OFI	10	O	–	–	–	–	–	851	–	–	–	–	–	93	–	–	–
	OFII	11	O	–	–	–	–	–	–	880	–	–	–	–	64	–	–	–
	OB	12	O	–	–	–	–	–	–	–	–	900	–	–	44	–	–	–
4	WFIII	13	W	771	–	–	–	–	–	–	–	–	–	–	83	–	45	45
	WFßGlc	14	W + O	709	–	–	–	–	–	–	–	–	60	–	85	–	45	45
	WFIR	15	W + O	473	–	–	–	–	–	–	–	–	–	385	30	–	28	28
	WFOBII	16	W + O	625	–	–	–	–	–	–	–	169	–	–	69	–	33	48
5	LF	17	W	652	–	–	70	–	–	–	–	–	–	–	20	150	20	50
	HFWB	18	W	551	–	–	200	–	–	–	–	–	–	–	11	150	–	50
	HFOB	19	W + O	292	–	–	–	–	–	–	–	470	–	–		150	–	50

O, diets based on oats; W + O, diets based on wheat plus oats; W, diets based on wheat.
*For details of ingredients and procedures, see p. 374 and Bach Knudsen & Hansen (1991), Bach Knudsen *et al.* (1993*a*,*b*) and Bach Knudsen & Canibe (2000).

Table 2. Chemical composition of the experimental diets*

Expt	Diet	No.	Group	Protein (g/kg DM)	HCl-fat (g/kg DM)	Starch (g/kg DM)	Total NSP (g/kg DM)	Cellulose (g/kg NSP)	AX (g/kg NSP)	ß-Glucan (g/kg NSP)
1	WFI	1	W	163	83	623	32	156	563	94
	WFA	2	W	170	82	569	59	186	644	68
	WFPT	3	W	174	85	570	52	173	615	96
	WFWB	4	W	171	81	584	58	259	586	52
2	WFII	5	W	172	91	618	31	129	581	97
	WFOBI	6	W + O	171	87	600	48	104	458	313
	RO	7	O	167	106	573	67	134	299	463
	ROOB	8	O	177	105	554	79	127	304	481
3	OG	9	O	166	86	593	72	139	306	458
	OFI	10	O	177	79	614	50	160	320	400
	OFII	11	O	178	91	564	89	146	292	483
	OB	12	O	175	101	512	108	111	287	546
4	WFIII	13	W	188	97	591	28	107	607	107
	WFßGlc	14	W + O	189	92	605	56	18	321	589
	WFIR	15	W + O	187	83	610	40	75	525	275
	WFOBII	16	W + O	186	100	597	53	113	434	321
5	LF	17	W	204	153	571	60	233	550	67
	HFWB	18	W	203	150	509	95	221	632	53
	HFOB	19	W + O	219	161	509	89	157	326	416

AX, arabinoxylans; O, diets based on oats; W + O, diets based on wheat plus oats; W, diets based on wheat.
* For details of ingredients and procedures, see Table 1 and p. 374 and Bach Knudsen & Hansen (1991), Bach Knudsen *et al.* (1993*a*,*b*) and Bach Knudsen & Canibe (2000).

Corrections were done for hydrolytic losses and detector response by using known sugar standards. The content of polysaccharide residues was calculated as anhydro-sugars.

Calculations and statistical analyses

The content of cellulose was calculated as:

$$\text{cellulose} = \text{NSP}_{\text{glucose}} - \beta\text{-glucan},$$

and the content of arabinoxylans (AX) as:

$$\text{AX} = (\text{arabinose} + \text{xylose} + \text{uronic acids}).$$

In the pigs, all digestibilities were calculated relative to the Cr_2O_3 content as described previously (Bach Knudsen & Hansen, 1991; Bach Knudsen *et al.* 1993*a*,*b*; Bach Knudsen & Canibe, 2000). For the calculation of starch digestibility, it was assumed that free glucose in ileal digesta was derived from starch.

Diets were grouped based on oat (RO, ROOB, OG, OFI, OFII, OB), wheat plus oat (WFOBI, WFßGlc, WFIR, WFOBII, HFOB) and wheat (WFI, WFA, WFPT, WFWB, WFII, WFIII, LF, HFWB) see Bach Knudsen & Hansen (1991), Bach Knudsen *et al.* (1993*a*,*b*) and Bach Knudsen & Canibe (2000) for full details. Results were examined separately for each of the two treatments (faecal digestibilities in pigs and conventional rats, ileal digestibilities in pigs and faecal digestibilities in nebacitin-treated rats) according to the following model:

$$y = \mu + s + g + (s \times g) + d(g) + (s \times d(g)) + \gamma,$$

where y is the dependent variable (i.e. NSP etc.), μ the overall mean, s the effect of species, g the effect of diet group, s × g the interaction between species and diet group, d(g) the random effect of diet within groups, s × d(g) the random effect of interaction of species × diet within diet groups and γ is the random residual error. The statistical analyses were performed using the procedure MIXED of SAS release 8.02 (Statistical Analysis Systems, Cary, NC, USA). Differences between species for diet groups were regarded as significant at $P < 0{\cdot}05$.

Results

Dietary composition

The diets were composed of wheat and oat fractions and contained contrasting levels of the main NSP polysaccharides: AX, ß-glucan and cellulose. AX were the main constituents of eleven predominantly wheat-based diets and ß-glucan of eight diets based either on oats or wheat flour with added oat bran or a ß-glucan-enriched fraction. It was only in three diets where cellulose provided more than 200 g/kg NSP.

Nebacitin-treated rats as a model

Faecal digestibilities in nebacitin-treated rats and ileal digestibilities in pigs of nutrients within the diet groups (i.e. diets based on oats, oats + wheat, wheat) are given in Table 3.

Total NSP digestibilities in the nebacitin-treated rats were 7–70 % and ileal digestibilities in the pigs −4–36 % (Fig. 1). Calculated for the three diet groups, digestibilities of total NSP and their constituents β-glucan and AX were much higher in nebacitin-treated rats compared with ileal digestibilities in pigs. Differences between rats and pigs were approximately 23–29 % for total NSP, 26–29 % for ß-glucan and 23–38 % for AX. Cellulose digestibilities, on the other hand, did not differ significantly between rats and pigs because of the large standard errors for both species.

Protein digestibility data in the nebacitin-treated rats had a smaller range (82–94 %) than ileal protein digestibilities

Table 3. Faecal digestibilities in nebacitin-treated rats and ileal digestibilities in pigs*
(Mean values with their standard errors)

		Rats		Pigs		
	Diet group	Mean	SE	Mean	SE	Statistical significance of difference (*P*)
Total NSP	Oat	54·1	5·46	25·3	5·58	0·001
	Wheat+oat	51·8	6·00	29·2	6·11	0·013
	Wheat	35·0	4·76	7·8	4·83	0·001
	All diets	46·9	3·14	20·8	3·19	0·001
ß-Glucan	Oat	84·1	7·21	40·4	7·31	0·001
	Wheat + oat	90·6	7·92	61·6	8·01	0·010
	Wheat	90·5	6·27	64·2	6·33	0·004
	All diets	88·4	4·14	55·4	4·19	0·001
AX	Oat	23·6	6·63	1·1	6·76	0·024
	Wheat + oat	34·0	7·29	5·8	7·40	0·011
	Wheat	40·2	5·78	2·5	5·87	0·001
	All diets	32·6	3·81	3·1	3·87	0·001
Cellulose	Oat	41·9	7·98	32·7	8·19	0·427
	Wheat + oat	23·0	9·77	39·9	8·97	0·219
	Wheat	15·1	6·96	4·0	7·12	0·272
	All diets	26·7	4·80	25·5	4·69	0·866
Protein	Oat	85·4	1·54	74·3	1·56	0·001
	Wheat + oat	89·9	1·69	85·6	1·70	0·006
	Wheat	88·8	1·34	89·4	1·35	0·596
	All diets	88·0	0·88	83·1	0·89	0·001
Fat	Oat	90·5	1·78	68·5	1·80	0·001
	Wheat + oat	94·9	1·95	84·4	1·97	0·001
	Wheat	94·4	1·61	88·1	1·56	0·001
	All diets	93·3	1·03	80·3	1·03	0·001
Starch	Oat	99·5	0·23	97·8	0·24	0·001
	Wheat + oat	99·7	0·25	98·8	0·26	0·018
	Wheat	99·7	0·20	99·4	0·20	0·185
	All diets	99·7	0·13	98·6	0·14	0·001
OM	Oat	90·4	1·56	82·9	1·57	0·001
	Wheat + oat	93·1	1·71	87·3	1·72	0·001
	Wheat	92·1	1·35	88·9	1·36	0·001
	All diets	91·9	0·89	86·4	0·90	0·001

AX, arabinoxylans, OM, organic matter.
* For details of diets and procedures, see Tables 1 and 2 and p. 374.

in pigs (67–92 %) (Fig. 1). For the diets based on oat and wheat plus oat, the protein digestibility in the nebacitin-treated rats was significantly higher ($P<0·05$) than ileal digestibility in pigs, the differences being 11·2 and 4·4 % respectively. Digestibilities for the wheat diets, however, were similar for nebacitin-treated rats and cannulated pigs.

For all diets, fat digestibility in the nebacitin-treated rats (86–98 %) was greater than ileal digestibility in the pigs (58–92 %) (Fig. 1). Hence, mean digestibilities for the diet groups were significantly higher ($P<0·05$) in these rats compared with ileal digestibilities in pigs. Differences were most pronounced for the diets based on oats followed by the wheat plus oat diets (22·0 and 10·5 % respectively).

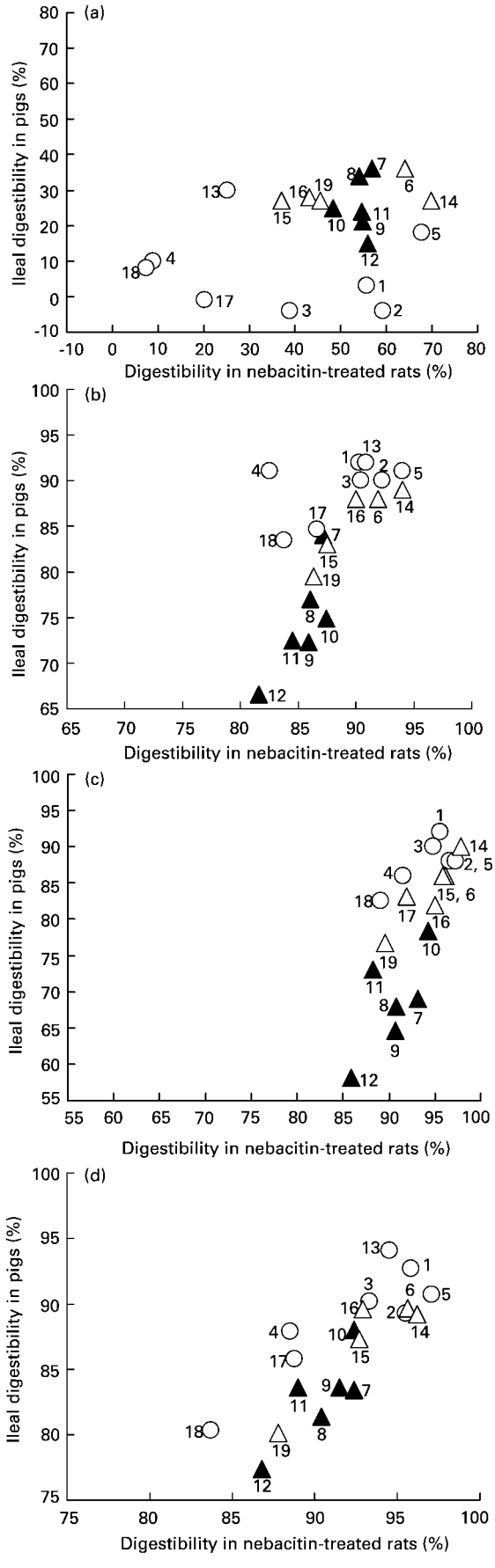
Digestibility of starch was nearly complete in the nebacitin-treated rats as well as in the cannulated pigs for the wheat diets, whilst for the oat and the wheat plus oat diets, ileal starch digestibility in the pigs was slightly, but significantly lower than digestibility in the nebacitin-treated rats.

Organic matter digestibilities in the nebacitin-treated rats ranged from 84 to 96 %, ileal digestibilities in the pigs from 77 to 94 % (Fig. 1). For all diet groups, digestibilities were significantly higher ($P<0·05$) in the nebacitin-treated rats than in the cannulated pigs with differences for the oat, the wheat plus oat and the wheat diets being 7·5, 5·8 and 3·3 % respectively.

Faecal digestibility in conventional rats and pigs

Faecal digestibilities in conventional rats and pigs for the diet groups are presented in Table 4. Total NSP breakdown was 46–88 % in the conventional rats and 54–95 % in the pigs (Fig. 2). For all diet groups, NSP breakdown was lower (3·9–8·5 %) in the rats than in the pigs, but the differences were significant only for the wheat plus oat and the wheat diets. For the single NSP constituents, the results varied somewhat. β-Glucan digestibility was generally high in the rats and the pigs and differed only significantly between the two species for the wheat diets, for which it was lower in the rats (3·1 %). For all diet groups, the digestibilities of AX and especially of cellulose were also lower in the rats than the pigs, (difference: AX 3·6–8·0 %, cellulose 7·5–51·2 %), but because of the large variations in both species the differences were not always significant.

Faecal protein digestibility in the conventional rats had a smaller range (82–94 %) compared with that in the



pigs (75–98 %) (Fig. 2). Concerning the diet groups, digestibility for the oat diets was significantly higher ($P<0{\cdot}05$) in the rats than the pigs, and lower for the wheat plus oat (significant; $P<0{\cdot}05$) and the wheat diets (NS). The reversed directions of the results led to an overall good agreement between rats and pigs.

Faecal fat digestibility varied also more in the pigs (64–93 %) than in the rats (83–95 %) (Fig. 2). With the exception of the wheat diets, fat digestibility was significantly higher in the rats than the pigs, differences being 14·4 ($P<0{\cdot}0001$), 5·0 ($P<0{\cdot}011$) and 2·2 % for the oat, the wheat plus oat and the wheat diets respectively.

Digestibilities of starch were complete in rats and pigs; the calculated significance of differences are without physiological importance.

For the single diet groups, faecal organic matter digestibilities differed slightly, but significantly, between the rats and pigs ($P<0{\cdot}05$). Because of the reversed direction of the differences, the agreement for all diets was good.

Discussion

Nebacitin-treated rats as a model

There may be several reasons for the higher digestibility of NSP estimated in nebacitin-treated rats compared with the ileal digestibility of pigs. The microbial activity expressed by the concentration of ATP in digesta materials was reduced by 80–90 % in these rats (KE Bach Knudsen, unpublished results). Because of the remaining activity, it is not possible to separate totally the digestive processes carried out by the rats' enzymes on the one hand from the fermentative processes by the microbial enzymes on the other. However, it is important to note that the hydrolytic digestive processes in the stomach and small intestine of pigs are also a mix of activities deriving from endogenous enzymes (major) and microbial enzymes (minor). For instance, the loss of NSP in the upper intestinal tract of pigs is a result of microbial action (Bach Knudsen, 2001; Bach Knudsen & Jørgensen, 2001).

Rats with a reduced microflora have, compared with normal rats, a longer retention time in the gut because of an enlarged caecum (Boisen *et al.* 1985). However, the retention time depends on the dietary fibre levels. On a diet providing 40 g dietary fibre/kg, mean transit times (MTT) were found to be 32 and 47 h in conventional and nebacitin-treated rats respectively, while MTT was more uniform (22 and 25 h respectively) when a dietary fibre level of 180 g/kg was fed (Raczynski *et al.* 1982). The diets used in the current studies were all low in dietary fibre (28–108 g/kg), probably leading to long transit times that may have favoured actions of the remaining microflora on easily fermentable carbohydrates. This refers especially to ß-glucan and also for AX in the diets

Fig. 1. Ileal digestibilities in pigs and faecal digestibilities in nebacitin-treated rats of total NSP (a), protein (b), fat (c) and organic matter (d). (○), Wheat-based diets; (△), wheat plus oat-based diets; (▲), oat-based diets. For details of diets and procedures, see Tables 1 and 2 and p. 374.

Table 4. Faecal digestibilities in conventional rats and pigs*
(Mean values with their standard errors)

		Rat		Pig		
	Diet group	Mean	SE	Mean	SE	Statistical significance of difference (*P*)
Total NSP	Oat	84·9	3·84	88·8	3·86	0·126
	Wheat+oat	83·8	4·21	92·3	4·23	0·006
	Wheat	63·5	3·32	70·3	3·35	0·005
	All diets	77·4	2·20	83·8	2·21	0·001
β-Glucan	Oat	99·2	0·58	99·8	0·58	0·510
	Wheat + oat	99·0	0·63	99·9	0·64	0·279
	Wheat	95·8	0·50	98·9	0·50	0·001
	All diets	98·0	0·33	99·5	0·33	0·002
AX	Oat	75·7	4·23	82·4	4·30	0·003
	Wheat + oat	83·8	4·68	91·8	4·71	0·002
	Wheat	68·1	3·70	71·7	3·72	0·477
	All diets	75·9	2·45	81·9	2·46	0·242
Cellulose	Oat	63·2	7·44	70·7	7·51	0·487
	Wheat + oat	30·3	9·13	81·5	8·23	0·001
	Wheat	29·7	6·45	49·3	6·51	0·048
	All diets	41·1	4·47	67·2	4·30	0·001
Protein	Oat	86·6	1·36	82·3	1·37	0·008
	Wheat + oat	89·0	1·49	93·3	1·50	0·015
	Wheat	90·5	1·18	94·1	1·19	0·103
	All diets	88·7	0·78	89·9	0·78	0·165
Fat	Oat	87·2	1·85	72·8	1·86	0·001
	Wheat + oat	91·8	2·02	86·8	2·04	0·011
	Wheat	91·0	1·67	88·8	1·61	0·144
	All diets	90·0	1·07	82·8	1·07	0·001
Starch	Oat	99·9	0·03	100·0	0·03	0·014
	Wheat + oat	99·9	0·03	100·0	0·03	0·018
	Wheat	99·8	0·03	100·0	0·03	0·001
	All diets	99·9	0·02	100·0	0·02	0·001
OM	Oat	93·6	1·02	92·6	1·02	0·017
	Wheat + oat	94·7	1·11	96·0	1·12	0·006
	Wheat	94·2	0·88	95·1	0·88	0·011
	All diets	94·2	0·58	94·5	0·57	0·076

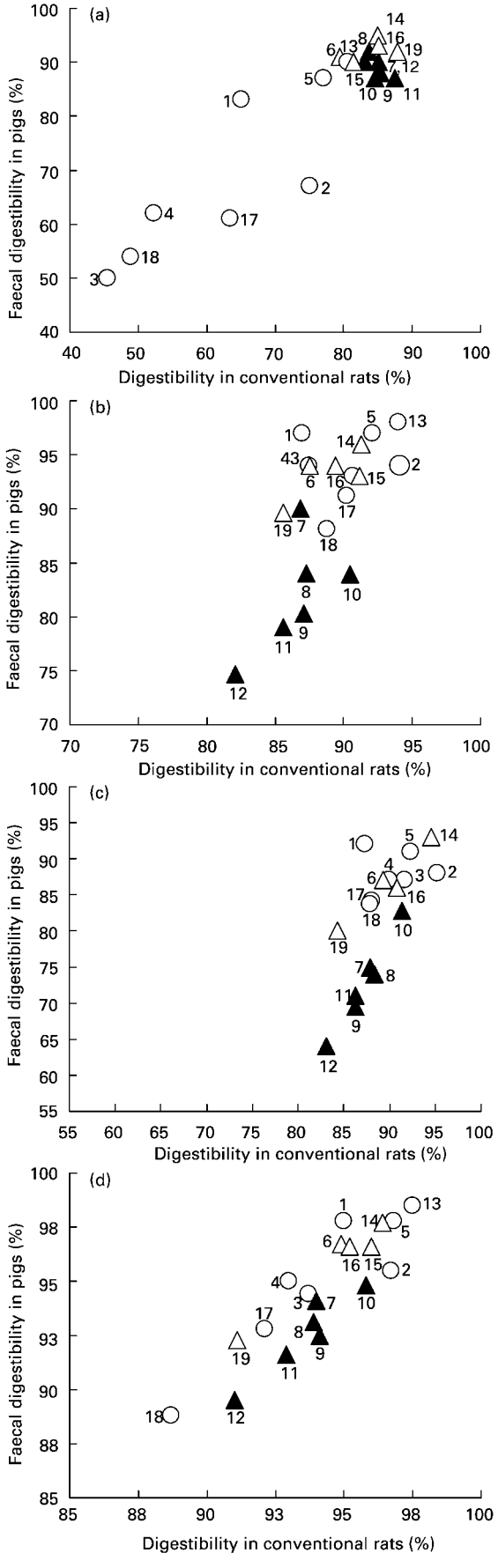
AX, arabinoxylans; OM, organic matter.
* For details of diets and procedures, see Tables 1 and 2 and p. 374.

containing wheat flour. The high cellulose breakdown found for the oat and wheat plus oat diets in the nebacitin-treated rats and in the pigs may at least in part be due to a reason other than microbial breakdown. Cellulose was determined by difference between total NSP-glucose and ß-glucan and made up only a small part of total NSP (20–160 g/kg) except for the diets containing wheat bran (WFWB, HFWB). Small analytical errors in the determination of total NSP-glucose and/or ß-glucan may have contributed to the high digestibilities.

Suppression of the microflora resulted in higher activities of pancreatic enzymes in the distal small intestine and large intestine (Boisen *et al.* 1985) compared with conventional rats, in which pancreatic enzymes are rapidly destroyed by the gut flora (Mason, 1984). Enzymatic digestion of protein still in the hindgut and more time available for protein hydrolysis because of longer MTT are the most likely reasons for the higher protein digestibilities in nebacitin-treated rats compared with pigs. Higher protein digestibilities of dried and toasted pea diets in nebacitin-treated rats compared with ileal digestibility in pigs have also been found by Canibe *et al.* (1997). In contrast, with the slaughter method a close agreement was found between conventional rats and pigs for the apparent ileal digestibilities of N from meat and bone meal and blood meal (Donkoh *et al.* 1994; Pearson *et al.* 1999). It is difficult to decide whether the good agreement between rats and pigs in these latter studies are due to the fact that in both species digestibilities were measured in ileal samples, or whether the proteins investigated, i.e. animal protein sources, had an effect. Our present studies suggest that the type of protein may play a role in the results, because significant differences between the nebacitin-treated rats and ileal digestibilities in pigs were found for the oat and wheat plus oat diets, but not for the wheat diets.

The apparent crude fat digestibility was generally greater in rats than in pigs, with the most notable difference found with the oat-based diets. Both rats and pigs have been shown to digest up to 300 g/kg fat in the diet without problems (Jakobsen, 1992) and both species secrete diluted bile (Björnhag, 1992). However, the feeding regimen was different, with rats having free access to the diet, whereas the pigs were meal fed, and this may have contributed to the higher digestibilities in the rats.

The combined effect of the overestimation of NSP, starch, protein and fat digestibilities is a digestibility of



organic matter in nebacitin-treated rats that was on average 5·5 % higher than the ileal digestibility of organic matter in pigs.

Conventional rats as a model for total tract digestibility in pigs

The faecal digestibility of total NSP and its fractions AX and cellulose was less in the rats than the pigs, but the magnitude of the differences between the two species varied for the single diet groups. Lower NSP digestibilities in rats than in pigs were also found in other studies in which the breakdown of pea NSP has been measured in rats and pigs (Goodlad & Mathers, 1991; Canibe *et al.* 1997). The lower digestibility of NSP in the rats is presumably a reflection of the faster digesta passage in the rat than the pig and possibly differences in the ability of the microflora in handling cell walls with a complex structure. MTT in rats were 52, 29, 32 and 22 h when fed diets containing 52, 141, 158 and 206 g dietary fibre/kg respectively (Bach Knudsen *et al.* 1991). In pigs fed 274–296 g dietary fibre/d, MTT were 52–64 h (van Soest *et al.* 1983). Since the bacterial degradation of cell wall polysaccharides in secondary lignified tissues is generally considered a slow process (van Soest, 1984), one would expect the biggest difference in the digestibility of NSP between the two species for the diets containing lignified wheat bran, i.e. some of the wheat-based diets. However, the greatest differences were found for the wheat plus oat diets, which contained highly fermentable fibres. In this respect, the results from the present study agree with those found in comparative studies of rats and pigs (Canibe *et al.* 1997) and of rats and human subjects (Bach Knudsen *et al.* 1994). In both cases, the greatest differences between rats and pigs or between rats and human subjects were observed for pectin polysaccharides, which in the digestive contents of pigs and human subjects are highly fermentable.

Rats and pigs of similar body weights as those used in our present studies were also used in other comparative digestibility trials (Smith *et al.* 1987). Nevertheless, there may arise the question of whether pigs and rats of the body weights and respective ages as those used in our studies are comparable with regard to gut development, and this may affect NSP fermentation in particular. In pigs there is evidence that the small intestine is developed at about 20 kg body weight, while the hindgut is still developing after 150 kg (Nielsen, 1962). There may also be concern that the low fibre level in the diets and the absolute amounts of fibre intake could have affected the results of our comparisons.

In rats as well as in pigs, an increasing fibre content in the diets or increasing feeding levels resulted in a higher passage rate, leaving theoretically less time for fermentation (Stanogias & Pearce, 1985; Bach Knudsen *et al.*

Fig. 2. Faecal digestibilities in pigs and conventional rats of total NSP (a), protein (b), fat (c) and organic matter (d). (○), Wheat-based diets; (△), wheat plus oat-based diets; (▲), oat-based diets. For details of diets and procedures, see Tables 1 and 2 and p. 374.

1991). Accordingly, increasing neutral-detergent fibre levels in the diet of pigs was associated with decreasing digestibilities of neutral-detergent fibre, cellulose and hemicellulose, but the magnitude of this effect was related to the fibre source (Stanogias & Pearce, 1985). There are conflicting results in the literature on whether feeding levels affect the digestibilities of fibre and nutrients in pigs (Just *et al.* 1983; Roth & Kirchgessner, 1984). Digestibilities of neutral-detergent fibre were improved when the body weight of pigs increased from 45 to 100 and 150 kg (Shi & Noblet, 1994). In rats, on the other hand, the fermentation of NSP was independent of the dietary fibre level (Nyman & Asp, 1985). Increasing intakes of fibre by increasing feeding levels of the same diets from 5 to 13 g/d had also no effect on the digestibility of insoluble fibre, but led to a slight although significant decrease in the digestibility of soluble fibre (Larsen *et al.* 1991). In addition, a study conducted in rats over 27 weeks showed that after a certain adaptation time the extent of fermentation remained rather stable independent of the increase in body weight during the study (Brunsgaard *et al.* 1995).

From these rat experiments, we assume that the body weight of the rats used in our present experiments had no influence on the results of the comparisons. We can only speculate that differences in the anatomy and physiology of the large intestine and microbial number and composition between pig and rat may have contributed to the differences in NSP degradation. However, it cannot be excluded that the extent of NSP breakdown in pigs and rats would have agreed better at higher fibre levels, because under these conditions NSP degradation might have been lower in the pigs. In contrast, the rat may be a less suitable model for heavier pigs because heavier pigs have a bigger fermentative capacity.

In general, there was a good agreement between rats and pigs with regard to faecal protein digestibility. Thus, the present studies are consistent with previous investigations (Eggum *et al.* 1982; Beames *et al.* 1996). However, as in earlier studies (Eggum & Beames, 1986) protein derived from oats was significantly better digested in the rat than the pig, presumably due to the lower ileal N losses for the oat diets in the rats compared with the pigs.

The digestibility of fat in rats was consistently higher than in pigs, with the biggest difference being seen for the oat-based diets. In contrast to our present results, a previous comparison between rats and pigs showed slightly lower faecal fat digestibilities in rats than in pigs (Jakobsen, 1992). These results were derived from diets that differed for pigs and rats in many respects, but had in common that they contained pure fats. In the present investigations, pure fats (soyabean oil and/or lard) were constituents of all diets based on wheat and wheat plus oats. For these diets, differences between rats and pigs were smaller than for the diets based on oats as the only cereal. Earlier results observed with barley-based diets also showed a significantly higher fat digestibility in rats than in pigs. These findings applied to animals with normal as well as with reduced gut microflora (Eggum *et al.* 1982). Similarly, in human ileostomy subjects, higher amounts of fat were excreted in ileostomy effluent with oat-bran bread compared with wheat bread (Lia *et al.* 1996).

Species differences in the digestion of feed macrostructures

In the rats, as in the pigs (Bach Knudsen & Hansen, 1991; Bach Knudsen *et al.* 1993*a*,*b*), the apparent digestibilities of protein and fat decreased at higher dietary levels of NSP. However, there were differences in the way the two species handled the types of cereal components. The cells of the aleurone and sub-aleurone layers of oat have thick walls (Wood, 1986) and were present particularly in the diets containing oat bran and coarse oat products. Studies on pigs have shown that the aleurone cells from oats retain their integrity to a high degree in the stomach and upper small intestine of pigs (Johansen *et al*. 1997) with consequently lower ileal and faecal digestibility of protein in oats compared with wheat in pigs (Bach Knudsen & Hansen, 1991; Bach Knudsen *et al.* 1993*a*,*b*; Bach Knudsen & Canibe, 2000). In contrast, our present results suggest that in the rats these rigid cell walls had no major effect on the digestibility of protein and fat, which is in agreement with other studies indicating that intact cell structures seem to be less important for rats than for human subjects (Livesey, 1991; Wisker *et al.* 1996). Rats probably finely chew large particles, and smaller particles may be formed in the stomach and small intestine of rats than of human subjects (Livesey, 1991). If the same is true in relation to pigs, this could explain the greater differences between the two species in the protein and fat digestibilities for the oat-based diets and might also explain the slightly (although significantly) higher starch digestibilities in the nebacitin-treated rats compared with ileal digestibilities in pigs for the oat diets.

Conclusions

The close correlation between faecal digestibility of total NSP and AX in rats and pigs and the complete breakdown of β-glucan in both species suggest that the rats may be a suitable model for the fermentation of cereal NSP in the pig, when it is taken into account that the results in rats will be somewhat lower than in pigs. In the case of faecal protein digestibility, there are discrepancies between species that seem to be related to the ability of the rat to handle intact cell structures and particles differently from the pig. The latter point also refers to the small intestinal and total tract digestibility of fat from oats, but apparently not for pure fat added to diets. The nebacitin-treated rat, however, could not predict the small intestinal digestibilities of NSP and nutrients in the pigs. Taken as a whole, there were no differences between conventional rats and pigs in the digestibility of organic matter, and this is in agreement with earlier studies.

Acknowledgements

The present study was supported by the Danish Agricultural and Veterinary Research Council. We would like to

thank Kathrine Høirup, Lene Hornum Rasmussen and Karin Eybye, Danish Institute of Agricultural Sciences, for excellent technical assistance, and G. Rave, Variationsstatistik, Christian Albrechts-University of Kiel, for his help with the statistical calculations.

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