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The influence of dietary fibre on body composition, visceral organ weight, digestibility and energy balance in rats housed in different thermal environments

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The present study was undertaken to provide detailed information on the effect of dietary fibre (DF) level on body composition, visceral organ weight, nutrient digestibility and on energy and protein metabolism of rats housed in cold (16°), warm (24°) or hot (32°) thermal environments. High- or low-fibre diets (257 *v.* 56 g DF/kg dry matter (DM)) were studied in a 6-week balance experiment (initial body weight about 100 g). Heat production was measured using open-air circuit respiration chambers. Pea fibre and pectin were used to adjust the DF level in the high-fibre diet. The ranking order of daily gain of rats kept in different environments was: 24° > 16° > 32°, while the ranking order for carcass protein was: 16° > 24° > 32°. Rats on the high-DF diet had a lower daily gain than those on the low DF diet, and more protein in DM of empty body weight (EBW) and less fat. The relative weights (g/kg EBW) of liver, heart and kidney decreased when increasing the environmental temperature. The relative weight of the heart was highest in rats on the high DF level, while liver and kidney weights were unaffected by DF. Per kg EBW, the stomach, small intestine, caecum and colon and the length of colon were significantly greater in rats consuming the high-fibre diet compared with those on the low-fibre diet. Rats kept at low temperature had a significantly heavier gastrointestinal (GI) tract than those kept at the highest temperature. Digestibility of protein, DM and energy was lowest for rats fed on the high-fibre diet. Heat production (HP) of fed rats as well as fasting HP decreased significantly as environmental temperature increased. HP as a proportion of metabolizable energy (ME) was significantly lower for rats at 24° compared with the other environmental temperatures. The proportion of energy retained as protein was slightly higher in rats fed on the high-fibre than on the low-fibre diet. Based on the results of the present study the authors measured a net energy value of 5·4 kJ/g DF fermented; approximately 50% of the DF came from peas. Possible implications of the present findings are discussed.

Visceral organs: Gutfill: Heat increment: Non-starch polysaccharides

A general view is that high-fibre diets have a low energy density due to a low digestibility (e.g. Just *et al.* 1983*b*; Eggum *et al.* 1982, 1984) and a low net energy value of fibres digested (Eggum *et al.* 1982; Livesey, 1992). The microbial capacity to ferment non-starch polysaccharides in single-stomached animals is well established. The end-products of the microbial degradation are various gases (H_2, CO_2, CH_4), lactic acid and short-chain fatty acids (SCFA). The SCFA produced are rapidly absorbed from the gut lumen (Rechemmer *et al.* 1988). In single-stomached animals such as rats and pigs these end-products can contribute a substantial amount of energy (Argenzio & Southworth, 1974; Eggum *et al.* 1984; Bach Knudsen *et al.* 1991).

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Dietary fibre (DF) may also affect the length and weight of the gastrointestinal (GI) tract as well as the size of internal organs. Liver, kidney and empty segments of the GI tract expressed as a percentage of body weight are increased by DF both in pigs and rats (Pond *et al.* 1988; Anugwa *et al.* 1989; Hansen *et al.* 1992). Moreover there is also an indication that the differences in weights of visceral organs are highly related to differences in fasting heat production (HP) among animals due to different previous nutritional treatments (Koong *et al.* 1985; Ferrell & Koong, 1986).

Because a larger part of the digestible energy (DE) of fibrous feedstuffs is lost as heat (heat increment) during the digestive and metabolic processes than from feedstuffs higher in starch or fat, the energy value of a fibrous diet may be influenced by the thermal environment in which the animals are maintained (Stahly & Cromwell, 1986). Changes in the thermal environment can influence feed intake, metabolism, nutritional requirement and efficiency of nutrient utilization (Dauncey & Ingram, 1986; Rothwell & Stock, 1986; Close, 1989; Hoffmann *et al.* 1991). Both heat stress and cold stress increase energy expenditure and result in an increased requirement for maintenance. A higher requirement of energy for maintenance during cold exposure alters the fat deposition to a greater extent than protein deposition, resulting in a leaner carcass. A hot environment has a similar influence on carcass composition but this is due to a reduced feed intake (Verstegen *et al.* 1973; Stahly & Cromwell, 1986).

The present study was undertaken to provide detailed information on the effects of dietary fibre on energy and protein metabolism in rats housed in different thermal environments. The variables studied also included the effect on body composition, visceral organ weights and nutrient digestibility.

MATERIALS AND METHODS

Experimental

The experiment was carried out according to a factorial design that comprised two levels of DF, high fibre and low fibre, i.e. 257 g and 56 g DF/kg dry matter (DM) respectively, and three environmental temperatures, cold ($16 \pm 0{\cdot}3°$), warm ($24 \pm 0{\cdot}5°$) and hot ($32 \pm 1°$). The relative humidity (RH) was set to 60 but was recorded to be 75 ± 5 RH in the cold, 60 ± 5 RH in the warm and 50 ± 5 RH in the hot environment. For practical reasons the experiment was carried out in two series of 6 weeks as outlined in Table 1. A balance period was introduced from Monday to Friday (4 d) in each week as described by Eggum (1973).

Heat production was estimated from calculations of gas exchange using two open-air circuit respiration chambers as described by Chwalibog *et al.* (1979). The gas exchange was measured over 24 h periods on each group of rats (n 6). Groups 1 and 5 were measured each day from Monday to Saturday. The remaining groups were measured on two consecutive days during each balance period. As the respiration measurements on the different groups were carried out on different days in the balance period the HP was adjusted to the middle of the balance period. The volume of the outgoing air from the two chambers was measured continuously from the differential pressure over both sides of an orifice and converted to standard temperature and pressure for dry air (STPD). A paramagnetic O_2 analyser (Magnos 4G, Hartmann & Braun, Germany) and an infra-red CO_2 analyser (Uras 3, Hartmann & Braun, Germany) were used for the measurements of concentrations of O_2 and CO_2 in samples of the outgoing and ingoing air. The concentrations of O_2 and CO_2, temperature, RH and rate of flow from each chamber were recorded automatically on-line every second minute.

The average daily HP was calculated according to Brouwer (1965). Both the respiratory quotient (RQ) and carbon–nitrogen balance (CN) methods were used to calculate HP

Table 1. *Experimental design*

Series*	Group	*n*	Temperature	Dietary fibre level
1	1	6	16°	High
	2	6	24°	High
	3	6	24°	Low
	4	6	32°	High
2	5	6	16°	Low
	6	6	24°	Low
	7	6	24°	High
	8	6	32°	Low

High, 257 g dietary fibre/kg dry matter; Low, 56 g dietary fibre/kg dry matter.
* Each series included an initial group of six rats.

(Christensen *et al.* 1988). Fasting HP was measured for 24 h at the end of the experiment. Fasting was initiated 24 h before the measurement of fasting HP but the rats had free access to water. Energy lost in urine was based on urinary N (48·8 kJ/g urinary N; Hoffmann & Klein, 1980). Daily feed intake was kept as close as possible to *ad lib.* intake by keeping feed refusals to a minimum. Water was always available. The animals were kept in individual cages placed at ambient temperatures of 16°, 24° and 32° respectively. These temperatures were also maintained in the respiration chambers. A 12 h (06·00–18·00 hours) light–dark cycle was operated.

After completion of the experiment the animals were killed with CO_2. The contents of the GI tract were removed and the weights of the digesta-free empty body (EBW), GI tract, liver, heart and kidney of each rat were recorded.

Animals and diets

In each series thirty male Wistar rats with initial live weights (LW) of 90–105 g were randomly allocated to five groups (Table 1). One group of six rats in each series (initial) was killed and used to estimate the initial body composition. All the other rats were kept in individual metabolic cages throughout the experiment. However, for gas exchange measurements the rats were measured in groups of six as described by Eggum *et al.* (1982). This was done for technical reasons. All the experimental rats were starved for 48 h before they were killed.

The added fibre sources were pea fibre (Nutrio P-Fibre 150C provided by Danisco, Brabrand, Denmark) and pectin (Mexpectin; Grindsted Products, Brabrand, Denmark) both rich in soluble dietary fibre (SDF). The diets were formulated to supply equal amounts of digestible protein and fat per unit metabolizable energy (ME). Consequently the chemical compositions of the high- and low-fibre diets differed. The protein concentration was reduced every second week by reducing the fishmeal and casein levels. The average composition of the high- and low-fibre diets is shown in Table 2.

Analytical methods

The digest-free (empty) bodies of the rats were autoclaved, homogenized and then freeze-dried. All analyses were carried out on freeze-dried materials except for the diets. DM was determined by oven-drying at 105° for 20 h. N and energy were determined on duplicate samples by a modified Kjeldahl method (KjellFoss 16200 Autoanalyser; Foss Electric A/S, Denmark) and by bomb calorimetry (IKA-C 400; Janke & Kunthel, KG IKA-Werk, Heitersheim, Germany) respectively. Protein was calculated as N × 6·25. Ash was analysed

Table 2. *Ingredients and chemical composition of high- and low-fibre diets*

Fibre level...	High	Low
Ingredients (g/kg)		
Barley	494	243
Wheat	34	—
Wheat starch	—	561
Soya-bean meal	40	—
Fish meal	37	96
Casein	16	41
Sugar-beet molasses	2	—
Animal fat	3	—
Soya-bean oil	25	30
Pea fibre	306	—
Pectin	20	—
Dicalcium phosphate	14	10
Monocalcium phosphate	—	14
Calcium carbonate	4	—
NaCl	3	3
Mineral/vitamin mixture	2	2
Chemical composition (g/kg DM)		
Protein (N × 6·25)	172	155
HCl-fat	60	59
Starch	431	682
S-NSP	91	9
I-NSP	155	39
NSP	246	48
Klason lignin	11	8
Dietary fibre from:		
Pea fibre	129	—
Pectin	18	—
Basal diet	110	56
Ash	48	46
Energy (MJ/kg DM)	18·94	18·67

DM, dry matter; HCl-fat, hydrochloric acid-fat; S-NSP, soluble non-starch polysaccharides; I-NSP, insoluble non-starch polysaccharides; NSP, non-starch polysaccharides.

according to the method of the Association of Official Analytical Chemists (1975) while fat was extracted with diethyl ether after acid hydrolysis (Stoldt, 1952). Carbon was measured as described by Neergaard *et al.* (1969). Starch was analysed by the enzymic method described by Bach Knudsen *et al.* (1993). Total non-starch polysaccharide (NSP) was determined using a modification of the methods of Theander & Åman (1979), Theander & Westerlund (1986) and Englyst *et al.* (1982) as described by Bach Knudsen *et al.* (1993). Klason lignin in the diets was determined gravimetrically as the residue resistant to 12 M-H_2SO_4 (Theander & Westerlund, 1986). DF was determined as the sum of total NSP and Klason lignin.

Calculations and statistical analyses

All calculations of gas exchange were carried out on the average of groups (six rats) as kept in the respiration chambers, while the other data were calculated on an individual basis. Since one temperature (24°) was replicated for both the high- and low-fibre diets in each series it was possible to estimate and correct for any series effect in comparisons between high and low fibre at the other temperatures. Analysis of variance was done using the GLM procedure (SAS, 1985), with the effect of fibre, temperature and interactions between fibre

and temperature as main effects and adjusting for the period effect. When there was no significant interaction between fibre and temperature, as in most cases, the results in the Tables are presented as main effects. When significant effects were obtained, differences between means were compared by the least squares means (LSMeans) test (SAS, 1985).

RESULTS

Growth and carcass characteristics

As seen in Table 3, daily weight gain was highest (4·39 g) in the 24° environment, with the lowest daily gain (2·67 g) in the hot (32°) environment. The proportion of protein in the carcass DM was highest (689 g/kg DM) in the 16° environment, and lowest (620 g/kg DM) in the hot (32°) environment and the proportion of fat in the carcass was opposite to the values for protein.

Compared with rats on the low-fibre diet the animals on the high-fibre diet had a lower daily gain (3·14 *v.* 3·72 g) but with a higher gutfill in the gastrointestinal tract (23 *v.* 15 g/kg LW), in spite of the fact that the animals, at the time of killing, had been fasted for 48 h. Rats fed on the high-fibre diet contained less DM (314 g/kg EBW) but more protein (676 g/kg DM) than rats fed on the low-fibre diet (332 g DM/kg EBW and 622 g protein/kg DM).

Visceral organs

The relative weights of liver, heart and kidney (Table 4) decreased with increasing temperature (liver: 41·1 to 35·1; heart: 4·0 to 3·4; kidney: 9·0 to 7·4 g/kg EBW). The weight of the heart was significantly higher (3·9 g/kg EBW) in rats fed on the high-fibre diet than in rats fed on the low-fibre diet (3·5 g/kg EBW), whereas the weights of the liver and kidney were unaffected by DF level. Per kg EBW, the stomach, small intestine, caecum and colon and the length of colon were significantly ($P < 0·01$) greater in rats consuming the high-fibre diet compared with rats fed on the low-fibre diet. This increase was nearly twofold for caecum and colon but also the length of these organs increased considerably. The GI tract was also influenced by environmental temperature. Rats kept at low temperature had a significantly heavier stomach, small intestine, colon and caecum than those kept at the highest temperature.

Digestibility

As expected, digestibilities of protein, DM and gross energy were lowest ($P < 0·01$) for the high-fibre diet (Table 5). Generally there was a higher digestibility at 24° compared with the other two temperatures; however, the absolute differences were small, but significant.

Energy metabolism

The same amount of feed was offered to all rats regardless of the treatment. However, feed intake of rats at 32° was only half of what was offered (Table 6). Consequently ME intake per day was lower for rats in the 32° environment. Since their live weights were different, energy utilization is expressed per kg metabolic body weight ($W^{0·75}$). However, ME intake on a metabolic-body-weight basis was significantly different only for the two fibre levels at 24°. HP was calculated both by the RQ and CN methods. The results from the two procedures were very close in this experiment. The difference in fasting HP of rats given the high- or low-fibre diets was only marginal. However, HP of fed rats, as well as fasting HP, decreased significantly as environmental temperature increased. HP as a proportion of ME (HP(CN):ME) was significantly lower for rats at 24° compared with the other environmental temperatures. The proportion of energy retained as protein was slightly

Table 3. *Effects of dietary fibre on growth rate and body composition of rats housed in cold, warm or hot thermal environments**

		Dietary fibre		Temperature			
	Initial	High	Low	16°	24°	32°	RMSE
Body weight (g)							
Initial	95·8	93·2[a]	104·0[b]	98·0	98·6	99·3	6·0
Final	—	217·8[a]	257·9[b]	229·7[a]	276·3[b]	207·6[c]	11·9
Daily gain	—	3·14[a]	3·72[b]	3·24[a]	4·39[b]	2·67[c]	0·30
Gutfill (g/kg LW)	68	23[a]	15[b]	20[a]	17[ab]	21[ac]	4
Carcass composition							
DM (g/kg EBW)	255	314[a]	332[b]	319[a]	333[b]	318[b]	19
Protein (N × 6·25) (g/kg DM)	673	676[a]	622[b]	689[a]	638[b]	620[c]	46
Carbon (g/kg DM)	505	506[a]	530[b]	503[a]	525[b]	526[b]	20
Fat† (g/kg DM)	191	207[a]	259[b]	170[a]	274[b]	255[b]	37
Ash (g/kg DM)	120	121[a]	108[b]	122[a]	109[b]	112[b]	9
Energy (MJ/kg DM)	23·01	23·89[a]	25·02[b]	23·89[a]	24·98[b]	24·50[ab]	1·09
Water/protein	4·12	3·25	3·25	3·12[a]	3·15[a]	3·49[b]	0·14

RMSE, root mean square error; LW, live weight; EBW, empty-body weight (without digesta); DM, dry matter.
[a, b, c] Mean values with different superscript letters in the same row for high *v.* low fibre level and different temperature levels respectively, were significantly different ($P < 0·05$).
* For details of diets and procedures, see Table 2 and pp. 688–691.
† Fat analyses were carried out only on seven of the initial rats and one third of the other rats (n 16).

Table 4. *Organ weights per kg empty body weight (EBW, without digesta) and length and weight of the empty gastrointestinal tract of rats fed on high- or low-fibre diets and maintained at different temperatures**

		Dietary fibre		Temperature			
	Initial	High	Low	16°	24°	32°	RMSE
Organ weight (g/kg EBW)							
Liver	53·3	36·5	38·0	41·1[a]	35·5[b]	35·1[b]	4·5
Heart	5·3	3·9[a]	3·5[b]	4·0[a]	3·7[a]	3·4[b]	0·4
Kidney	11·4	8·3	8·1	9·0[a]	8·3[b]	7·4[c]	0·7
Stomach (g/kg EBW)	8·0	7·0[a]	5·0[b]	7·1[a]	5·8[b]	5·1[c]	0·6
Small intestine							
Weight (g/kg EBW)	61·0	23·0[a]	14·7[b]	20·8[a]	18·9[ab]	16·7[b]	3·0
Length (mm)	907	1024[a]	957[b]	1091[a]	968[b]	913[b]	102
Caecum (g/kg EBW)	5·8	5·2[a]	2·5[b]	4·4[a]	3·8[b]	3·3[c]	0·5
Colon							
Weight (g/kg EBW)	9·2	5·5[a]	3·2[b]	4·6[a]	4·4[b]	4·0[b]	0·5
Length (mm)	126	168[a]	138[b]	155	160	145	19
Total digestive tract (g/kg EBW)	84·0	40·7[a]	25·3[b]	36·9[a]	32·9[b]	29·2[c]	3·7

RMSE, root mean square error.
[a, b, c] Mean values with different superscript letters in the same row for high *v.* low fibre level and different temperature levels respectively were significantly different ($P < 0·05$).
* For details of diets and procedures, see Table 2 and pp. 688–691.

Table 5. *The influence of dietary fibre and environmental temperature on apparent digestibility of crude protein, dry matter and energy in rats**

	Dietary fibre		Temperature			
	High	Low	16°	24°	32°	RMSE
Crude protein	0·727[a]	0·861[b]	0·790[a]	0·800[b]	0·792[ab]	0·010
Dry matter	0·822[a]	0·916[b]	0·867[a]	0·873[b]	0·866[a]	0·006
Energy	0·818[a]	0·925[b]	0·872[ab]	0·876[a]	0·867[b]	0·006

RMSE, root mean square error.

[a, b] Mean values with different superscript letters in the same row for high *v.* low fibre level and different temperature levels respectively were significantly different ($P < 0·05$).

* For details of diets and procedures, see Table 2 and pp. 688–691.

Table 6. *The influence of dietary fibre (F) and environmental temperature (T) on energy utilization by rats*†

Temperature...	16°		24°		32°			Significances		
Fibre level...	High	Low	High	Low	High	Low	RMSE	T	F	T×F
DM intake (g/d)	17·9[a]	18·4[a]	17·6[a]	17·4[a]	8·9[b]	9·2[b]	1·4	***	NS	NS
GE intake (kJ/d)	335·9[a]	343·0[a]	330·1[a]	325·5[a]	167·6[b]	172·1[b]	25·7	***	NS	NS
ME intake (kJ/d)	266·3[a]	308·5[b]	265·4[a]	295·3[b]	133·6[c]	154·6[c]	21·8	***	***	NS
ME (kJ/$W^{0·75}$ per d)	1035·4[a]	1038·7[a]	885·4[b]	1008·6[a]	569·4[c]	579·0[c]	48·6	***	*	*
HP(RQ) (kJ/$W^{0·75}$ per d)	914·4[a]	909·6[a]	694·6[b]	763·1[c]	490·0[d]	497·0[d]	34·0	***	*	**
Fasting HP (kJ/$W^{0·75}$ per d)	734·4[a]	662·3[a]	516·9[b]	531·6[b]	413·7[c]	420·6[c]	22·2	*	NS	NS
HP(CN) (kJ/$W^{0·75}$ per d)	928·0[a]	931·6[a]	687·5[b]	761·2[c]	506·1[d]	512·2[d]	40·3	***	*	*
HP(CN):ME	0·900[a]	0·901[a]	0·783[b]	0·761[b]	0·934[a]	0·901[a]	0·07	***	NS	NS
RE(CN) (kJ/$W^{0·75}$ per d)	107·3[a]	107·1[a]	197·9[b]	247·4[b]	63·4[a]	66·8[a]	51·1	***	NS	NS
RE-protein (kJ/$W^{0·75}$ per d)	90·0[a]	85·8[a]	102·6[a]	106·4[a]	68·5[b]	58·0[b]	14·0	***	NS	NS
RE-fat (kJ/$W^{0·75}$ per d)	17·3[a]	21·3[a]	95·3[b]	141·0[b]	−5·1[a]	8·8[a]	43·7	***	NS	NS

DM, dry matter; GE, gross energy; ME, metabolizable energy; HP(RQ), heat production estimated by RQ method; $W^{0·75}$, metabolic body weight; HP(CN), heat production estimated by CN method; RE(CN), retained energy estimated by CN method; RE-protein, retained energy in protein; RE-fat, retained energy in fat; RMSE, root mean square error; NS, not significant.

[a, b, c, d] Mean values with different superscript letters in the same row were significantly different ($P < 0·05$).

* $P < 0·05$; ** $P < 0·01$, *** $P < 0·001$.

† For details of diets and procedures, see Table 2 and pp. 688–691.

higher in rats on the high-fibre diet than on the low-fibre diet. This is in agreement with the carcass analysis (Table 3).

DISCUSSION

Growth and carcass characteristics

During the experimental period of 6 weeks the body composition of the rats changed significantly (Table 3). This was especially the case for DM which increased with age. The protein content of the rats was in the same range (initial: 172 g/kg LW, after 6 weeks:

209 g/kg LW) as found by Neergaard (1981). The rats fed on the high-fibre diets retained somewhat more protein and less fat in the carcass DM than rats fed on the low-fibre diet. This difference in body composition can be partly explained by the fact that the rats fed on the low-fibre diet had a higher ME intake. The rats receiving the high-fibre diet also dissipated a higher proportion of ME intake as heat and thus left less energy for fat synthesis.

Rats on the high-fibre diet had a higher gutfill in spite of a 48 h fasting period; the difference was nearly twofold between the high- and low-fibre diets (Table 3). This demonstrates that gutfill can make up a significant part of LW depending on diet composition. As discussed by Just (1982), this increase in gutfill and thereby LW caused by feeding a fibrous diet will at least partly cancel the influence of fibre on energy utilization when expressed relative to body weight. Fasting results in loss of body energy and thereby changes carcass composition towards a lower fat content. In spite of a higher gutfill in rats fed on the high-fibre diet indicating a lower influence of starvation, the differences in carcass fat content between the two groups of rats were considerable.

Visceral organs

Measurements confirmed that intake of high-fibre diets caused a significant extension of the GI tract. This hypertrophy of gut tissues after consuming a fibrous diet was also confirmed by other rat studies (Goodlad & Mathers, 1990; Hansen *et al.* 1992). The visceral organs of rats and pigs have a high rate of energy expenditure relative to their size (Ferrell & Koong, 1986; Pekas & Wray, 1991). The present experiment suggests a relationship between visceral organ size and energy expenditure only in the 16° environment. Rats on the high-fibre diet had the highest fasting HP in accordance with their heavier digestive tract compared with rats on the low-fibre diet. The relative sizes of liver, heart and kidney were hardly affected by the fibre level. On the other hand the relative size of these organs decreased significantly as the temperature was increased.

The differences in fasting HP between environmental temperatures (Table 6) could in part be explained by the differences in visceral organ sizes. In the present experiment low temperature caused a substantial increase in the size of the very active metabolic organs such as liver, kidney and GI tract.

Digestibility

The low ambient temperature caused a marginal, but significant, reduction in digestibilities of protein, energy and DM. This is in agreement with results reported in studies with pigs (Fuller & Boyne, 1972; Phillips *et al.* 1982; Le Dividich & Noblet, 1986). Christopherson & Kennedy (1983) suggested that low ambient temperature increases the rate of passage and reduces the retention time in the digestive tract. Therefore, there is less time for microbial fermentation in the hind-gut and lower digestibility of fibrous material. It would therefore be expected to have a higher influence on the fibrous diet. Such a tendency was also seen for rats kept at 16°. On the other hand, rats kept in the cold environment developed a significantly longer small intestine. This might have an effect only on the nutrients digested by endogenously secreted enzymes. The reason for the decrease in digestibility from the 24° to 32° environments could be explained by a change of the small-intestinal mucosa due to temperature differences as discussed by Sengupta & Sharma (1993). In their experiment rats under acute heat stress at 37° had a lower capacity for absorption. The lower feed intake of the rats at 32° in the present study could also influence digestibility positively. However, in experiments with pigs and rats (Just *et al.* 1983*b*; Larsen *et al.* 1991) only marginal increases were found in the apparent digestibilities of

nutrients when reducing daily feed intake. It is therefore not likely that the differences in feed consumption affected digestibility in the present study.

There was a difference of 201 g DF/kg DM between the two types of diet (high fibre 257 *v.* low fibre 56 g DF/kg DM). The reduced energy digestibility (0·108) of the high-fibre diet compared with the low-fibre diet (high fibre 0·818 *v.* low fibre 0·925) can mainly be attributed to the differences in DF even though there were also differences in protein and starch content due to the experimental design. The present experiment was not designed for estimating the partial digestibility of the fibre sources included. However, it can be calculated that the unavailable carbohydrates (organic matter − protein − fat − starch) have a digestibility of 0·71 and 0·77 in the high- and low-fibre diets respectively. In the calculation it is assumed that starch has a digestibility of 1·0 (Larsen *et al.* 1991) and dietary fat 0·6 (Eggum *et al.* 1982). A relatively small amount of the unavailable carbohydrate in the high-fibre diet in the present study consisted of pectin (7%) found to have a high digestibility of 0·93 (Livesey *et al.* 1995). The value from the high-fibre diet is in the same range as the estimate of 0·78 for NSP digestibility of raw pea (Goodlad & Mathers, 1990) but is in contrast to the work of Nyman *et al.* (1990) who found that only 53% of the NSP from pea was fermented. These values are also comparable with the apparent digestibility of unavailable carbohydrate of 0·7 for mixed diets reported by Livesey (1992) who did an extensive analysis of the literature. A negative correlation between DF and digestibility of protein, DM and energy is well established in pigs and rats (Just *et al.* 1983*a*, *b*; Eggum *et al.* 1982, 1984). Hansen *et al.* (1992) compared different sources of DF and found that the decrease in apparent energy digestibility was more pronounced for wheat bran and oat bran than for pea fibre as used in the present study. The effect of DF on nutrient digestibility may be partly explained as an increased rate of passage through the digestive tract as demonstrated in pigs (Varel *et al.* 1988) and rats (Hansen *et al.* 1992). Transit time also depends on the length of the entire gut, especially the length of the caecum–colon. Our measurements in the present study showed an increased gut length of rats fed with the high-fibre diet (Table 4). This might partly compensate for the effect of increased rate of passage. DF has also been found to cause an increased mucus secretion in the digestive tract that could, as discussed by Satchithanandam *et al.* (1990), result in a more rapid transit time and impaired nutrient absorption. The effect of DF on digestibility of other dietary constituents is certainly influenced by the fibres in the cell walls that might hinder the access of digestive enzymes to the cell contents (Bach Knudsen *et al.* 1993). Peas and pea fibre are also known to contain anti-nutritional factors depressing digestibility (Liener, 1989).

Energy expenditure

Methane was not measured in the present experiment and consequently not included in estimation of ME. In a similar study with high- and low-fibre diets fed to growing pigs (H. Jørgensen, X. Zhao and B. O. Eggum, unpublished results) the production of CH_4 contributed only 1·2 and 0·2% of digested energy on high- and low-fibre diets respectively. Relating energy expenditure to the applied experimental treatment is usually done by normalizing to metabolic body size or lean body mass. By doing so the treatment effect might be blurred because variation in energy expenditure has been attributed to variations in chemical composition of the body or composition of gain (Ferrell *et al.* 1979; Jørgensen *et al.* 1990). In the present experiment when feeding the same daily amount of DM on both high- or low-fibre levels several procedures of normalization were carried out. Just (1982) suggested that normalization to metabolic body size corrected for differences in gutfill is more correct. Because of the 48 h fast before slaughtering in the present study it was not possible to predict the amount of gutfill when the respiration trial was running. In a second procedure, lean body mass was used in normalization but this did not contribute to

Table 7. *Estimation of requirement of metabolizable energy for maintenance at energy equilibrium in dependence on environmental temperature, kJ/$W^{0.75}$ per d, calculated as quotient a/b_2 from the regression equation: RE/$W^{0.75}$ per d = $a_i + b_1$ ME/$W^{0.75}$ per d + temperature$_i$ + b_{2i} ME/$W^{0.75}$ per d × temperature$_i$*

Temperature (°)	a	b_2	a/b_2
16	−338	0·429	788
24	−241	0·485	497
32	−226	0·507	446

a/b_2, maintenance ME(kJ)/$W^{0.75}$.

explaining the variation in HP. Therefore, the normalization chosen as the most appropriate in the present study was metabolic body size ($W^{0.75}$). In the present experimental conditions we did not find any significant difference in energy expenditure when relating values to the amount of ME intake (HP(CN):ME) between high- and low-fibre diets.

According to the factorial approach of energy balance, energy utilization can be partitioned between factors attributable to maintenance or cost of growth. In order to calculate the maintenance requirement and the overall efficiency of ME utilization for energy retention (RE), energy retention per kg metabolic body weight (kJ RE/$W^{0.75}$ per d) was regressed (kJ ME/$W^{0.75}$ per d) with the following model:

$$\text{RE/W}^{0.75}\text{ per d} = a_i + b_1\,\text{ME/W}^{0.75}\text{ per d} + \text{temperature}_i + b_{2i}\,\text{ME/W}^{0.75}\text{ per d} \times \text{temperature}_i.$$

The model provides an estimate of the overall efficiency (b_1) of ME utilization for energy retention and by extrapolating ME to zero energy retention, a maintenance requirement was calculated as ME − maintenance/$W^{0.75}$ = a_i/b_{2i}. The results from the model (R^2 0·839) are presented in Table 7. The calculated maintenance requirements for the three temperatures correspond well with the estimated values obtained from fasting HP and are in agreement with values reported by Eggum & Chwalibog (1983) and Hoffmann *et al.* (1991). A reduction in environmental temperature from 24° to 16° increased the total HP by 28%, fasting HP by 33% and a calculation of maintenance requirement by the above equations increased this value by 59%. This shows that with equal supply of ME a decrease in temperature has a strong impact on body composition because less energy is available for synthesis of protein and fat. The present results are also in agreement with results reported by Rothwell & Stock (1986) who found that an increase in temperature above 24° suppresses feed intake and energy expenditure. Hoffmann *et al.* (1991) found in their experiment that the average thermoneutral temperature was 32° based on the lowest maintenance requirement. In the present experiment we did not find any significant difference in maintenance requirement between 24° and 32°, however, the 32° environment had a strong negative impact on feed intake.

Energy retention

Most of the variation in energy retention was in the amount retained as fat. Protein retention was very much the same irrespective of dietary composition. The strong correlation between the proportion of energy gained as fat and temperature level confirms the susceptibility of body composition of the growing rats to environmental temperature.

In calculating the difference in net energy between high- and low-fibre diets at 24° by using the obtained maintenance value given in Table 7, and assuming that the difference in net energy is only due to differences in fermented unavailable carbohydrates, a value of 5·4 kJ net energy/g fermented unavailable carbohydrate is obtained which is a utilization of 0·45 of the fermented material. This is very close to the utilization of 0·5 proposed by Livesey (1992). The experiment does not give a conclusive answer to the question to what extent a high-fibre diet is beneficial in losing body weight in man. But the results indicate that when feeding a high-fibre diet at an equal amount of ME as a low-fibre diet, less energy will be deposited, particularly as body fat.

Energy expenditure as heat in a cold environment could be used to meet the elevated maintenance needs. In a warm environment this HP is probably of no use. In other words, the heat generated from nutrient digestion and metabolism could play a useful role in a cold environment by minimizing the amount of nutrients or body tissue being oxidized for HP. However, in a hot environment, the dissipation of this heat may even become a physiological burden to the animal (Stahly & Cromwell, 1986). The present results indicate a stronger influence of fibre on energy retention at 24° than at 16°, although the effect was not significant. Considering the higher gutfill caused by the high-fibre diet this effect would be stronger. The present results also indicate that the lean body content was enhanced in rats housed either in a cold or a hot environment. A low amount of fat was retained due to less dietary energy being available for synthesis of fatty tissue.

CONCLUSION

The present study with rats demonstrates that dietary fibre has a low energy density. Besides a low digestibility, the net energy value of the absorbed nutrients from fibre is low but significant. Therefore, feeding equal amounts of ME results in a leaner carcass of rats fed on a high-fibre diet compared with rats on lower fibre diets. The study also shows that the size of the GI tract increases in rats given a high-fibre diet. A low environmental temperature seems to have a similar impact on the GI tract.

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