Energy values and energy balance in rats fed on supplements of guar gum or cellulose

BY I. R. DAVIES, J. C. BROWN AND G. LIVESEY*

AFRC Institute of Food Research, Norwich Laboratory, Colney Lane, Norwich NR4 7UA

In five experiments where guar gum (GG) or Solka-floc cellulose (SF) supplemented a semi-synthetic diet (100 g/kg) for male Wistar rats at 21°, it was found that GG acutely depressed both *ad lib.* and meal-fed food intakes by 40–50 %. The effect was temporary, with the GG having no effects on food intake in the longer term. Dietary energy balance over 28 d with animals fed on equal amounts of a basal ration showed partial digestible energy values, calculated from the intake and faecal loss of energy, for the supplements which averaged 0 kJ/g SF and 10 kJ/g GG, so that GG contributed substantial amounts of absorbable energy. Despite this additional energy from GG, there was very often no additional gain of body fat. Rather, in some experiments, fat deposition was actually decreased by supplementation with GG. GG is inferred to have a putative thermogenic effect which is often greater than the energy it supplies. This effect occurred to a greater extent in circumstances associated with a higher 'energy status', indicated by higher efficiencies of conversion of gross dietary energy to retained body energy, higher fat:lean tissue deposition ratios and the occurrence of larger deposits at the epididymal fat pad site. There was some evidence that deposition at this site was more extensively affected by GG than deposition of fat in the body as a whole. Possible implications of the present findings are discussed.

Non-starch polysaccharides: Guar gum: Cellulose: Energy balance: Rat

A popular view is that high-fibre diets, which are also of lower energy, will help slimmers lose weight (Eyton, 1982). Evidence is mounting, but fragmentary, to suggest that fibre enhances satiety and lowers hunger (Blundell & Burley, 1987; Stevens *et al.* 1987). But the usefulness of non-starch polysaccharide (NSP) in body-weight control is controversial. Several studies suggest that diets of increased dietary fibre content are associated with enhanced weight loss in adults when energy intake is below maintenance requirements. For example, Rytigg *et al.* (1985) found that an additional 10 g fibre (cereal–citrus (4:1, w/w)) each day taken as tablets with a 5000 kJ diet significantly ($P < 0.001$) increased weight loss by 40 %, from a loss of 4·2 kg to a loss of 6·3 kg in 11 weeks when compared with a placebo in a double-blind investigation. Enhanced weight loss has been observed also with 10–20 g guar gum (GG) daily in man (Evans & Miller, 1975; Krotkiewsky, 1984) and with 25 g cellulose daily (Mickelsen *et al.* 1979). Studies such as these lend support to, though do not prove, the suggestions by Heaton (1973, 1980), Cleave (1974) and Burkitt & Trowell (1975) that a cause of obesity in Western societies is the replacement of whole foods by fibre-depleted foods. In contrast with these studies it has been reported that 5 g cereal-fibre–citrus-fibre tablets (Rossner *et al.* 1985) and 20 g wheat bran or isphagula granulate (Hylander & Rossner, 1983) had no significant effect on weight reduction in human subjects prescribed sub-maintenance diets. The possibility of weight reduction with diets of increased fibre intake has recently been reviewed by an *ad hoc* expert group (Federation of American Societies for Experimental Biology, 1987), which returned an open verdict.

* For reprints.

It is difficult with studies of weight loss in man to obtain precise control over experimental variables. This may explain much of the information which is suggested to be contradictory (Federation of American Societies for Experimental Biology, 1987). It may be that the findings are not really contradictory but that the intake of fibre has been too small to observe reliable effects. Other explanations for the differing observations may be lack of control over food intake or perhaps subjects may aim to lose weight at a regular rate and adapt food intake to weight loss. Moreover, weight loss rather than energy loss is examined so that replacement of body fat with body water may obscure effects on energy balance. Control should be more easily obtained with laboratory animals. The present study was undertaken to provide detailed information on the effects of two well-defined but dissimilar neutral NSP, GG and cellulose, on food intake, apparent digestibility of dietary gross energy and on energy balance in rats. Separate information from five experiments of similar general design are reported, but with either juvenile animals or young adult animals, fed either *ad lib.* or by meal feeding. *Ad lib.* feeding was to achieve a higher food intake, hence likelihood of fat deposition, than the meal-fed animals; the young adult animals were also considered likely to deposit more fat than the juvenile animals.

MATERIALS AND METHODS
Experimental

Five separate energy balance studies were carried out. The features common to the five studies will be described first and individual features are described further for each experiment.

In all experiments the species and source of animals were CFHB Remote Wistar rats from Interfauna, UK Ltd, (Huntingdon). Housing was at 21°, two rats per wire-bottomed cage to minimize effects of isolation, and light supplied between 06.00 and 18.00 hours. Water was available *ad lib.* During the few days before experiments began all animals were provided a stock pelleted diet (Rat and Mouse no. 3 expanded; Special Diet Services Ltd, Witham). In all experiments, animals then received a basal semi-synthetic diet which contained no NSP (diet NNSP; Table 1). This was provided for at least 4 d, to allow either complete fermentation or elimination of NSP previously ingested. Then, in each experiment, equal numbers of animals were provided either diet NNSP as a basal ration, or the basal ration supplemented (100 g/kg basal diet) with GG (diet GG) or Solka-floc cellulose (diet SF) as described in Table 1.

The three diets (treatments) were provided for 28 d, the energy-balance period. The food was provided by methods described later (pp. 417–418), in such a way that the intake of the ingredients in the basal ration (those in diet NNSP, Table 1) was equal in each dietary treatment. This was so that differences observed between dietary treatments (diets NNSP, GG and SF; Table 1) could be attributed to the effects of the NSP which supplemented the intake. In all experiments the intake of food and the spillage, which was usually < 2 % of intake, were measured daily. When spillage occurred, a quantity of food equal in weight to the spillage of the previous day was added to the day's diet to ensure equality of intake of the basal ration between the treatment groups over the longer term. Faeces were collected from paper trays under the wire-bottomed cages daily before feeding, and stored at −20° before freeze-drying, grinding (with pestle and mortar) and analysis. Urine was discarded with the paper trays daily. The live weights of animals were recorded before feeding, usually every 4 d. At the end of the balance period animals were killed for analysis of body composition.

The food intake and faecal loss during the balance period was determined from the morning of the first day of the dietary treatments to the same time 28 d later. Deposition

Table 1. *Compositions of the basal, non-starch-polysaccharide-free diet and the supplemented diets*

Ingredients*	(g/kg basal diet)
Non-starch polysaccharide-free diet (basal diet):	
Starch†	360
Sucrose	300
Casein†	200
Maize oil	80
Mineral mix‡	40
Vitamin mix§	20
Supplemented diets are basal diet with addition of 100 g/kg basal diet of one of the following:	
Cellulose†	
Guar gum†	

* For feeding regimen, see pp. 417–418.

† Starch was 'Snoflake' maize flour from Corn Products Ltd, Manchester; edible casein, 30 mesh, was from G. Fiske & Co. Ltd, Richmond, Surrey; cellulose was Solka-floc cellulose (grade B92030) from Johnson, Jorgensen and Wettre Ltd, London and guar gum was from Sigma Chemical Co., London.

‡ Produced the following levels in the diet (g/kg basal diet): $CaHPO_4$ 13, $CaCO_3$ 8·2, KCl 7·03, Na_2HPO_4 7·4, $MgSO_4.H_2O$ 4·0, $MnSO_4.H_2O$ 0·18, $ZnCO_3$ 0·1, $FeSO_4.7H_2O$ 0·144, $CuSO_4$ 0·023, KIO_3 0·001.

§ Contained vitamins as follows (mg/kg basal diet): nicotinic acid 60, cyanocobalamin in mannitol 50, calcium-D-pantothenate 40, thiamin hydrochloride 10, riboflavin 10, pteroyl monoglutamic acid 5, D-biotin 1, vitamin K_1 2, Rovimix E-25 (containing 7·5 mg vitamin E, Roche) 300, Rovimix A-500 (containing 3·75 mg vitamin A, Roche) 25, Rovimix D_3-500 (containing 0·19 mg vitamin D_3, Roche) 15, choline bitartrate 1800.

of energy, lean dry mass and fat in one experiment (JAG) was over the same period with animals killed in the unfed state. In all other experiments, because animals were used to assess the effect of the treatments on stomach emptying or other physiological effects (not reported), the animals were killed at the end of the balance period in the fed state, on average at about 15.00 hours after providing food on the 29th day. This allocation of food was neglected subsequently as it was considered to result in no error exceeding 1 % for deposition of fat and lean dry matter (expressed per 28 d) and the error would have been less than this when relating differences in body composition to differences in treatment.

Juvenile-animal meal-feeding studies

There were three experiments using juvenile rats (initial live weights 90–110 g) that were provided food as a single meal each day (JM1, JM2 and JM3 respectively). Training to meal-feed was identical in each of these experiments and was undertaken by allowing access to unlimited amounts of NNSP diet at 09.00 hours for 2, 2, 2, 1·5, 1·5, 1·5, and 1·5 h on 7 d respectively and at 15.00 hours for 2 and 1 h on the first 2 d respectively, immediately after ceasing to provide the stock pellet diet. During the 28 d dietary treatment, access to one of the experimental diets (NNSP, SF and GG) was for 1·5 h starting at 09.00 hours.

Expt JM1. This was performed first, with forty-two animals randomly allocated to the three dietary treatments (fourteen animals per treatment, two animals per cage). Observations were made on each cage of animals, giving seven observations per dietary treatment. The quantities of diets NNSP and SF provided each day during the 28 d of treatment were made dependent on the intake of food by animals provided diet GG. This was done for each supplement on a cage-by-cage basis to equalize the intake of basal dietary ingredients in each treatment ('equalized-feeding'). To achieve this conveniently, the start of the feeding period was staggered over 3 d with diet GG leading, followed by diet SF then diet NNSP.

Expt JM2. This was performed with thirty-six rats. All were trained to meal-feed as

described for JM1. Twelve animals were killed for body composition analysis at the end of the training (equivalent to day 0 of the balance period) and the remaining twenty-four were allocated to the three dietary treatments (diets NNSP, SF and GG; Table 1); eight animals per treatment, two animals per cage making four observations (cages) per treatment. Again, the equalized-feeding arrangement with a staggered start was adopted as described for JM1.

Expt JM3. This was performed after studies JM1 and JM2 and was as described for study JM1 starting with forty-two animals, but differed in that the quantities of food provided were prescribed to be equal to the mean daily intakes for the corresponding treatment group in study JM1. Doing so allowed all treatments to commence on the same day and all animals to ingest the same amount of each ingredient in the basal ration.

Young-adult-animal meal-feeding study

One experiment was performed (YAM). The initial live weights of animals were 230–260 g. Forty-eight animals, caged in pairs, were trained to meal-feed using the procedure described for the JM1, JM2 and JM3 animals. Six animal pairs were killed for body composition analysis at the start of the 28 d treatment period and three groups of six pairs were fed one of the treatment diets (NNSP, SF, GG; Table 1) using the equalized-meal feeding arrangement and staggered start as described for JM1.

Juvenile-animals ad lib. diet GG feeding study

One experiment was performed (JAG). Live weights of animals were initially 90–110 g. Eighty animals were caged in pairs and fed on diet NNSP (Table 1) *ad lib.* for either 4 or 5 d. The forty pairs were then allocated randomly to one of five equal groups of eight pairs. One group continued to receive diet NNSP *ad lib.* while another was fed on diet GG (Table 1) *ad lib*: these two groups constituted a controlled study of the effects of diet GG on food intake. Two of the remaining groups were each fed, cage-by-cage, to equalize intakes of the basal dietary ingredients in these groups with that in the diet GG *ad lib.*-fed group. To do so conveniently the equalized feeding of diets NNSP and SF began 1 d after feeding diet GG. The one remaining group had been killed at the start of the balance period. The last four groups of animals constituted the energy balance part of the experiment.

Sampling and analysis

Tissue collections. Tissues were removed from animals after intraperitoneal injection of sodium pentobarbital (60 mg/ml in water; 1 ml/kg live weight) and cervical dislocation. In all experiments the epididymal fat pads, stomach, small intestine, caecum and colon plus rectum were each removed. A saline (9 g sodium chloride/l) wash to remove digesta was followed by blotting of the tissues with absorbent paper to remove surface water. In Expts JM1 and YAM the liver, kidney, testes and selected skeletal muscles (the plantaris, soleus and gastrocnemius muscles from the left side) were also removed. The remaining carcass and skin and the tissues were then weighed before and after freeze-drying.

Body composition. For Expts JM1 and YAM the skin with subcutaneous fat was denatured with 0·1 M-hydrochloric acid (220 ml per skin) overnight, homogenized in a blender, freeze-dried and ground in a coffee mill. Other dry tissues were ground to a powder (using a pestle and mortar) and the remaining carcass was broken into small pieces and ground in a coffee mill. Of each granular or powdered tissue and remaining carcass, 100 mg/g was taken, combined by mixing in a coffee mill, and analysed for fat to estimate total body fat. For Expts JM2, JM3 and JAG the bodies, empty of digesta, and the fat pads were freeze-dried separately, then combined, cut to pieces and ground in a coffee mill before analysis of body fat.

Table 2. *Equations used to predict body compositions from live weights of rats at the start of the balance period*

(The regression model fitted was fat or lean dry mass (g/kg live wt) = $b \times$ live weight (g) $+ c$, where b was set to zero when the coefficient did not improve the derived predictive equation (i.e. was not significant, $P > 0.05$))

Expt	b	c	RSD	Range for fat or LDM (g/kg)	Range for live wt (g)	n
Fat						
YAM	0	107	20	71–144	253–291	12
JM1, JM2, JM3	0	59	13	49–94	109–128	12
JAG	0	117	13	90–148	151–181	16
LDM						
YAM	0	232	6	224–242	253–291	12
JM1, JM2, JM3	−1·85	470	11	219–276	109–128	12
JAG	0	199	6	185–208	151–181	16

RSD, residual standard deviation for the regression; n, the number of animals used to obtain the relationships; LDM, lean dry mass; JAG, JM1, JM2, JM3 and YAM, age and mode of feeding of guar-gum-supplemented where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of the guar gum diet (for details of diets and procedures, see Table 1 and pp. 416–418).

Total body wet and dry masses were taken to be the sum for the corresponding weights of each tissue and remaining carcass. Body water was the difference between body wet and dry masses. Dry lean body mass was the difference between dry body mass and body fat mass.

Analysis of fat, heats of combustion and dry masses. Fat was analysed from about 1·5 g dry tissue preparation using a Soxtec system (Tecator, Hoganes, Sweden) to extract fat quantitatively by refluxing for 1·5 h with a 50 ml solvent mixture of dichloromethane (AnalaR)–methanol (AnalaR) (9:1, v/v). The quantity extracted was determined gravimetrically.

Heats of combustion of 0·5–1 g dry matter were determined in a Gallenkamp adiabatic bomb calorimeter (Gallenkamp, Loughborough) using benzoic acid thermochemical standard.

Dry weights of tissues were obtained after freeze-drying for more than 10 d to reduce the moisture content to about 20 g/kg.

Calculations

Estimates of the deposition of fat and dry lean matter. The accumulation of body fat and dry lean mass during the 28 d balance period was calculated in terms of energy, taking 1 g fat to contain 39·5 kJ and 1 g dry lean mass to contain 20 kJ (Livesey *et al.* 1990). For the beginning of the balance period the lean dry matter and fat were estimated from the live weights of animals and formulas (Table 2). For Expts JM1 and JM3, the equation derived for animals killed at the start of Expt JM2 was used. This potentially introduced an absolute error of equal magnitude in each treatment group.

Calculation and expression of energy values, energy deposition and unrecovered energy. Partial digestible energy values, i.e. the change in digestible energy intake with each supplement divided by the change in supplement intake over the 28 d balance period, were calculated according to an equation (see Livesey *et al.* 1990) which involves small magnification of measurement errors (Livesey, 1989). Partial digestibility of energy for each

supplement, digestible energy intake, net energy deposited as the sum of the fat and dry lean energies deposited and a combined value for energy expenditure plus energy lost to urine, i.e. unrecovered energy, were each calculated as described previously (Livesey *et al.* 1990). Changes in net retained energy, fat and lean mass deposition apparently due to the supplements, are the differences between these variables with the unsupplemented diet (NNSP) and the supplemented diets (SF and GG); these values are expressed per unit weight of supplement ingested (kJ/g dry weight). The difference between the partial digestible energy values and the net retained energy (Livesey *et al.* 1990) gave the change in unrecovered energy (kJ/g).

Statistics

Analysis of variance was used. When the variate was found to be significantly ($P < 0.05$) related to basal dietary intake (e.g. digestible energy intake, energy accumulation and loss) analysis of covariance was used. Covariance was used in preference to using food intake as a blocking factor both because of the additional information it supplied and because there was no evidence of inequality of slopes for the dietary treatments on inspection of the residuals. The equalized-feeding arrangement resulted in the covariance adjusting the variances but not the means. All variates were checked to see if initial live weight was a concomitant variable, but there were no significant initial live weight effects. The degrees of freedom indicate the methods of analysis; with n numbers of pairs of animals per dietary treatment and three dietary treatments, $df = 3n - 3$ when one-way analysis of variance was used, and $df = 3n - 4$ when analysis of covariance was used. Degrees of freedom for intake values were determined only by the number of animals fed on the diet GG, except in Expt JM3 where intakes were prescribed (df 0).

Differences between dietary treatments indicated in the tables are given as least significant differences (LSD) with $P < 0.05$. Significance of differences ($P < 0.05$) in mean values between experiments (Table 9 only) was obtained after pooling of the standard deviations for each experiment (df = sum of df from each experiment less the number of experiments) and calculation of Student's t value for each comparison.

RESULTS
Food intake

The *ad lib.* food consumption of juvenile rats (Expt JAG) fell sharply on introduction of diet GG (Fig. 1(*a*)) and failed to recover to the levels reached by the diet NNSP-fed rats. However, when the intakes were expressed per unit metabolic body-weight (Fig. 1(*b*)), intakes were normal from about the eighth day and tended to be higher than for diet NNSP during the last 10 d of the period. A similar pattern of food intake was observed with meal-fed rats given diet GG (Fig. 2), the effect being slightly greater in young adult (Expt YAM) than in the juvenile rats (Expt JM1). The values for meal-fed rats per unit metabolic body-weight were approximately 0·5–0·6 of those of *ad lib.*-fed animals. Consequently mean intakes of meal-fed animals were only slightly above maintenance energy requirements (Pullar & Webster, 1977; Reeds *et al.* 1985) and during the first few days intakes were well below maintenance needs. In contrast, *ad lib.*-fed animals had sufficient food to be in positive energy balance for almost all of the 28 d period.

Gain of live weight

Supplementation with GG or SF-cellulose had no substantial effect on the gains of live weight in any experiment (Fig. 3). The weight gains in Expts JM2 and 3 are not shown, and were similar to that shown for Expt JM1 (Fig. 3).
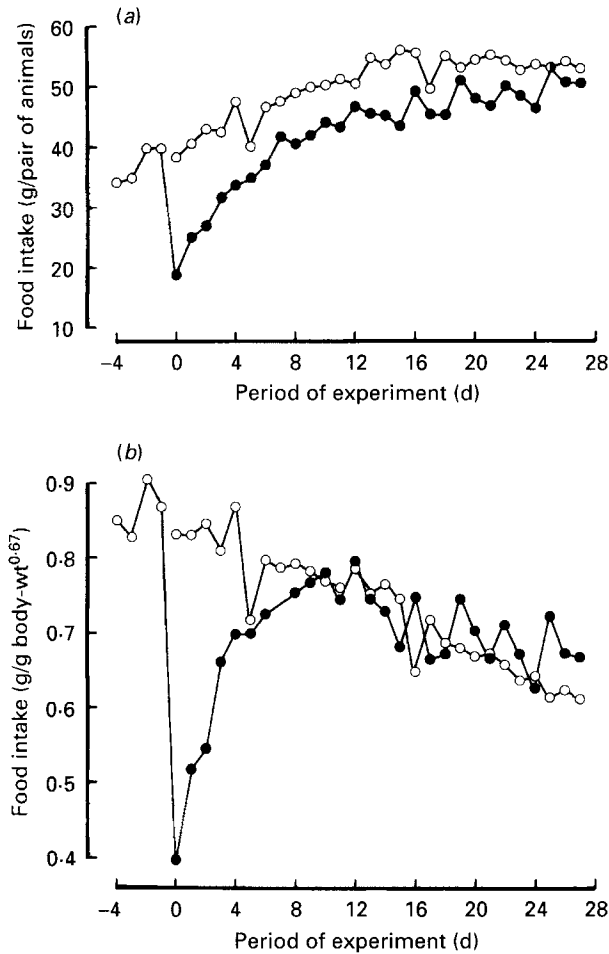
Fig. 1. Effect of supplementation with guar gum on *ad lib.* food intake in juvenile rats. (*a*) Mean values for absolute intake with their pooled standard error means equal to 3% of mean; (*b*) mean values for intake relative to metabolic body mass (g body-weight$^{0.67}$) with their pooled standard error means of 0.02 g/g body-weight$^{0.67}$; ($\bigcirc$), unsupplemented diet; ($\bullet$), diet supplemented with guar gum. For details of diets and dietary treatments, see Table 1 and pp. 416–418.

Intake and faecal loss of dry matter and energy

In all the experiments the intake of the basal dietary ration was similar between dietary treatment groups (NNSP, SF, GG) due to the equalized-feeding (Table 3). The supplements increased the intake of gross energy.

Loss of dry matter to faeces was related to the intake of food and was increased by both diets SF (about fourfold) and GG (about twofold). Similarly, loss of energy to faeces was related to gross energy intake and was increased by diet SF (about fivefold) and diet GG (about threefold). The apparent digestibility of gross energy of each diet was different, being approximately 0.98 for diet NNSP, 0.90 for diet SF and 0.95 for diet GG in each experiment.
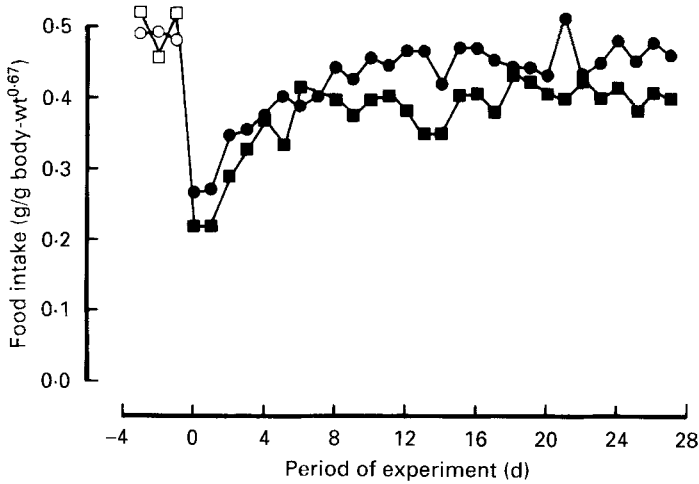
Fig. 2. Effect of supplementation with guar gum on meal-fed food intake in both juvenile and young adult rats. (□, ○), Unsupplemented diet fed to young adult (Expt YAM) and juvenile (Expt JM1) animals respectively; followed by (■, ●), diets supplemented with guar gum and fed to the same young adult (Expt YAM) and juvenile (Expt JM1) animals respectively. Points are mean values with their pooled standard error means of 0·03 g/g body-weight$^{0·67}$ for both Expt YAM and Expt JM1. For details of diets and dietary treatments, see Table 1 and pp. 416–418.

Gross and partial digestible energy values, partial digestibility of energy and the estimated heat of combustion of additional dry matter lost to faeces

The gross energy values (heats of combustion) of dry supplements were 17·34 (SE 0·08) kJ/g SF (*n* 4) and 17·54 (SE 0·10) kJ/g GG (*n* 4).

The change in the digestible energy intake due to the change in supplement intake from the basal to the supplemented diets, or partial digestible energy value (Kleiber, 1975; Livesey, 1989, 1990; Livesey *et al.* 1990) ranged (Table 4) between −1·9 and +2·2, with a mean value for all experiments of about 0 kJ/g SF. Values for GG, by contrast, ranged between 8·2 and 11·6, with a mean value for all experiments of about 10 kJ/g. These energy values correspond to partial digestibilities of energy for SF of between −0·11 and +0·13, with a mean of about zero, and for GG of between 0·47 and 0·66, with a mean value of about 0·55 (Table 4). The average heat of combustion apparent for the additional substance(s) lost to faeces was between 16 and 20 kJ/g for animals fed on diet SF, and was higher, between 26 and 32 kJ/g, for animals fed on diet GG.

Influence of the supplements on body composition

No treatment differences occurred in lean dry mass (Table 5) apart from the value for diet SF in Expt JM1.

In all experiments there was a tendency (not always significant) for the mean body water content to be higher with diet GG than with diet NNSP whether expressed in absolute terms (g) or as a proportion of total wet weight (Table 5). Differences in total wet body mass between animals fed on diet GG and those fed on diet NNSP almost exactly arose from a balance between the higher water content mentioned and a lower fat content of diet GG-fed animals described later (pp. 426–428). Changes in total dry body matter with diets GG or SF also appeared related to changes in fat content.

In three of the five experiments fat content tended to be lower in animals fed on diets SF and GG compared with diet NNSP (Table 5). The effect was significant for diet SF in Expt
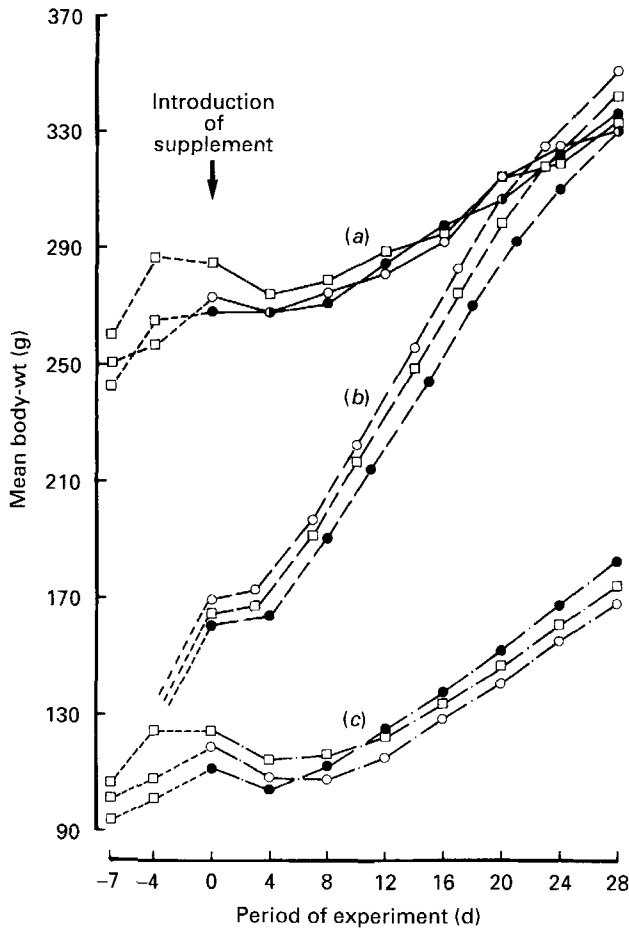
Fig. 3. Effect of supplementation with guar gum and Solka-floc cellulose on the gain of live weight. Values are for three dietary groups ((□), no non-starch polysaccharide; (○), Solka-floc cellulose-supplemented; (●), guar gum-supplemented) and three experiments ((a), young adults, meal-fed (YAM); (b), juvenile *ad lib.*-fed guar gum (JAG); (c), juvenile meal-fed (JM1)). Points are mean values with their pooled standard error for each experiment of 1% of the means. For details of diets and dietary treatments, see Table 1 and pp. 416–418.

JM1 and for diet GG in Expts YAM, JM1 and JAG. These effects of the supplements were similar when fat was expressed as a proportion (g/kg) of the body dry matter, and where observed, tended to be greater for diet GG than for diet SF. While diet GG did not always show within an experiment an effect of lowering body fat, it is notable that in no experiment was there a significant elevation of fat content, a result which could have been expected due to the substantial supplementary digestible energy.

Estimates of the effects of the supplements on energy balance

The *ad lib.*-fed juvenile animals (Expt JAG) deposited more energy as lean and fat mass than the juvenile meal-fed animals (Expts JM1, JM2 and JM3) (Table 6) which is consistent with the higher food intakes (Figs. 1 and 2). Energy and fat deposition in the young adult meal-fed animals (Expt JAM) was, however, less than in the juvenile meal-fed animals. This is consistent with the lower food intake per metabolic body mass in the young adult animals (Fig. 2).

Table 3. *Effects of non-starch polysaccharide supplements on the intake and faecal loss of dry matter and energy over 28 d in rats*

	Expt‡	n	Dietary treatment§			SD	df
			NNSP	SF	GG		
Intake of	YAM	6	710	710	710	64	5
basal diet,	JM1	7	482	482	482	32	6
fresh wt	JM2	4	461	469	469	32	3
(g/pair per	JM3	7	495	490	483		0
28 d)	JAG	8	1074	1070	1074	66	7
Intake of	YAM	6	0	71	71	0·6	
supplement,	JM1	7	0	48	48	0·3	
fresh wt	JM2	4	0	47	47	0·3	
(g/pair per	JM3	7	0	49	48		
28 d)	JAG	8	0	107	107	0·7	
Gross energy	YAM	6	13·0	14·1	14·2		
intake	JM1	7	8·92	9·64	9·66		
(MJ/pair	JM2	4	8·53	9·35	9·31		
per 28 d)	JM3	7	9·10	9·77	9·67		
	JAG	8	20·1	21·8	21·9		
						LSD	
Faecal dry	YAM	6	19·4	81·9*	39·4*†	1·9	14
matter	JM1	7	13·5	53·0*	23·3*†	1·8	17
(g/pair	JM2	4	12·3	49·3*	23·5*†	2·7	8
per 28 d)	JM3	7	13·5	56·5*	24·5*†	2·1	18
	JAG	8	29·7	133·0*	60·8*†	5·1	20
Faecal energy	YAM	6	–‖	—	—	—	—
(kJ/pair	JM1	7	167	822*	427*†	34	17
per 28 d)	JM2	4	174	893*	514*†	31	8
	JM3	7	174	924*	471*†	44	18
	JAG	8	457	2350*	1360*†	113	20
Apparent	YAM	6	...	...	—	...	...
digestibility	JM1	7	0·981	0·915*	0·956*†	0·004	18
of gross	JM2	4	0·980	0·905*	0·948*†	0·006	9
dietary energy	JM3	7	0·981	0·905*	0·948*†	0·005	18
	JAG	8	0·977	0·891*	0·938*†	0·005	21

JAG, JM1, JM2, JM3 and YAM, age and mode of feeding of diet GG where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of diet GG; NNSP, no non-starch polysaccharide diet; SF, Solka-floc-cellulose-supplemented diet; GG, guar-gum-supplemented diet; n, the number of animals pairs fed on each diet; SD, standard deviation; LSD, least significant difference; df, degrees of freedom.

* Mean values were significantly different ($P < 0.05$) from those for diet NNSP.

† Mean values were significantly different ($P < 0.05$) from those for diet SF.

‡ For details, see pp. 416–418.

§ For details, see Table 1.

‖ Faecal energy densities not measured.

Both LSD and df are adjusted for covariance with food intake which, as expected, was highly significant ($P < 0.001$) in each case (values not shown).

In general, SF-cellulose had no effect (Table 6) on digestible energy intake, on deposition of energy in either fat or lean tissue or on unrecovered energy (energy expenditure plus losses to urine). Like SF, GG did not affect the deposition of dry lean mass, but it increased both digestible energy intake and unrecovered energy. The last was between 4 and 10 % higher with diet GG than with diet NNSP. Despite the higher intakes of digestible energy with diet GG, the deposition of both fat and energy were lower than in diet NNSP-fed animals, the effect being significant in Expts JAG and JM1 (Table 6).

Table 4. *Partial digestible energy values and digestibilities of the non-starch polysaccharide supplements and the estimated heats of combustion of additional dry matter lost to faeces of rats*

	Expt†	Supplement		LSD	df
		SF	GG		
Partial digestible	JM1	2·2‡§	11·6*‡§	0·8	18
energy value of	JM2	0·2§	9·4*‡§	0·6	9
supplement (kJ/g	JM3	0·3§	10·6*‡§	1·0	18
dry wt)	JAG	−1·9‡§	8·2*‡§	1·2	21
Partial digestibility	JM1	0·13‡	0·66*‡	0·04	18
of supplementary	JM2	0·02	0·54*‡	0·04	9
energy (kJ/kJ	JM3	0·02	0·60*‡	0·04	18
intake)	JAG	−0·11‡	0·47*‡	0·06	21
Estimated gross	JM1	16·6‡	27·1*‡§	1·8	18
energy of incremental	JM2	19·6‡§	31·4*‡§	0·8	9
faecal mass (kJ/g	JM3	17·4‡	26·7*‡§	1·4	18
dry wt)	JAG	18·7‡	30·4*‡§	1·6	21

JAG, JM1, JM2, JM3 and YAM, age and mode of feeding of diet GG where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of diet GG; SF, Solka-floc cellulose; GG, guar gum; LSD, least significant difference ($P < 0.05$); df, degrees of freedom.

* Mean values were significantly different from those of diet SF ($P < 0.05$).

† For details, see pp. 416–418.

‡ Mean values were different from zero.

§ Mean values were different from the heat of combustion of the corresponding supplements, SF being 17·34 (SEM 0·08), *n* 4 and GG being 17·54 (SEM 0·10), *n* 4.

Expressions of energy balance values as changes per unit weight of supplement ingested (Table 7) are less subject to bias due to errors in the equations predicting initial body composition (Table 2) than are the absolute values noted in Table 6. However, even with these more reliable expressions diet GG still showed the tendency to decrease fat deposition in four of the five experiments and significantly in two (Expts JM1 and JAG). The effects of SF and GG on the gain of lean tissue were < 2 kJ/g supplement (Table 7), that is < 10 % of gross energy of the supplements ingested, and in all experiments were considered to be negligibly different from zero. The magnitude of the effect on unrecovered energy with GG differed significantly ($P < 0.01$) between experiments and ranged from +5·7 to +23·1 kJ/g GG ingested. This corresponds to a range from 60 % of the partial digestible energy associated with GG being deposited to a remarkable 280 % being expended or lost to urine.

Effect of the supplements on the size of the epididymal fat pads and other tissues

Effects of the supplements on the gastrointestinal tract in Expts JM1 and YAM were similar to previous work with *ad lib.*-fed juvenile animals (Johnson & Gee, 1986) and are not reported. The supplements had no substantial effect on liver, kidney, testes, skeletal muscle, heart or spleen. These findings are, therefore, also not reported. The dry weights of one pair of fat pads were examined in all experiments, which provided supplementary evidence of influences on fat deposition (Table 8).

The epididymal fat pads were smallest in animals fed on diet GG in all experiments and significantly so when the fat pads were large (Expts JM1, YAM and JAG). These effects

Table 5. *Effects of non-starch polysaccharide supplements on empty body compositions after 28 d of feeding in rats*

| | Expt§ | n | Dietary treatment | | | | | Cov | |
			NNSP	SF	GG	LSD	df	Mean	SD
Wet mass	YAM	6	616	613	611	21	14	0·026	0·004‡
(g/pair)	JM1	7	331	314*	333†	8	17	0·029	0·003‡
	JM2	4	352	367*	382*†	12	8	0·029	0·005‡
	JM3	7	335	326	336†	10	18	–‖	
	JAG	8	652	665	625*†	14	20	0·019	0·002‡
Dry mass	YAM	6	227	223	215	15	14	0·091	0·020‡
(g/pair)	JM1	7	117	107*	109*	5	17	0·012	0·002‡
	JM2	4	119	125*	126*	6	8	0·007	0·002‡
	JM3	7	111	109	108	4	18	–	–
	JAG	8	267	270	231*†	21	20	0·014	0·003‡
Water (g/pair)	YAM	6	388	389	396	28	14	0·016	0·004‡
	JM1	7	214	207*	224*†	6	17	0·019	0·002†
	JM2	4	233	243*	256*†	9	8	0·022	0·003‡
	JM3	7	225	218	228†	10	18	–	–
	JAG	8	384	394	394	23	21	0·005	0·003
Fat (g/pair)	YAM	6	69·4	63·5	60·6*	6·0	14	0·007	0·001‡
	JM1	7	34·6	28·6*	26·1*	3·6	17	0·005	0·001‡
	JM2	4	28·6	30·1	31·8	4·1	9	0·002	0·002
	JM3	7	28·3	29·1	25·6	4·5	18	–	–
	JAG	8	124	116	89*†	14	20	0·011	0·002‡
Lean dry mass	YAM	6	158·2	160	155	11	15	0·003	0·002
(g/pair)	JM1	7	82·6	78·7*	82·9†	3·5	17	0·006	0·001‡
	JM2	4	90·8	94·4	94·4	3·8	8	0·008	0·001‡
	JM3	7	82·5	80·0	82·8	3·2	18	–	–
	JAG	8	143	154	141	14	21	0·000	0·002
Water	YAM	6	631	635	647	28	15	−0·01	0·04
(g/kg wet wt)	JM1	7	646	659*	673*†	11	18	−0·02	0·03
	JM2	4	660	661	669	10	9	0·08	0·04
	JM3	7	669	665	678†	12	18	...	–
	JAG	8	589	594	630	31	21	−0·10	0·05
Fat	YAM	6	303	282*	281*	18	14	0·010	0·003‡
(g/kg dry wt)	JM1	7	294	266*	238*†	24	17	0·020	0·008‡
	JM2	4	239	243	253	26	8	0·028	0·009‡
	JM3	7	255	268	236	35	18	...	–
	JAG	8	463	428*	368*†	32	20	0·018	0·005‡

JAG, JM1, JM2, JM3 and YAM, age and mode of feeding diet GG where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of diet GG; *n*, number of animal pairs fed on each diet; NNSP, no non-starch polysaccharide diet; SF, Solka-floc cellulose diet; GG, guar gum diet; LSD, least significant difference ($P < 0.05$); df, degrees of freedom; Cov, covariance regression coefficient (and SD its standard deviation) between the residual variate after adjustment for treatment effects, and the residual of gross energy intake from the basal portion of the diet – units are kJ/kJ change in basal ration intake.

  * Mean values were significantly different from those for diet NNSP ($P < 0.05$).

  † Mean values were significantly different from those for diet SF ($P < 0.05$).

  ‡ Mean values for Cov were significantly different from zero ($P < 0.05$).

  § For details, see pp. 416–418.

  ‖ Lack of variance in food intake precluded attempts to calculate the food intake effect.

are apparent also after normalization for lean dry mass and expressed relative to that for diet NNSP-fed animals (Table 8). Diet SF had either smaller or no effects. Normalization of dry fat pad weights for the quantity of body fat still showed effects, but less often. Pooling of values from all experiments showed both diets SF and GG to decrease the size

Table 6. *Effects of guar gum and Solka-floc cellulose on energy balance over 28 d*

	Expt§	n	Dietary treatment			LSD	df	Cov	
			NNSP	SF	GG			Mean	SD
Digestible energy	YAM	6	−‖	—	...	—	—	—	—
intake (MJ/pair	JM1	7	8·75	8·82*	9·23*†	0·03	17	0·96	0·01‡
per 28 d)	JM2	4	8·25	8·45	8·79*†	0·35	8	0·95	0·05‡
	JM3	7	8·93	8·85	9·30*†	0·03	18	—	—
	JAG	8	19·6	19·4	20·6*†	0·1	20	0·98	0·02‡
Fat deposition	YAM	6	0·33	0·18	0·14	0·28	14	0·42	0·05‡
(MJ/pair per 28 d)	JM1	7	0·78	0·57*	0·50*	0·14	17	0·28	0·06‡
	JM2	4	0·67	0·69	0·78	0·16	9	−0·05	0·06
	JM3	7	0·57	0·58	0·46	0·16	18	—	—
	JAG	8	3·43	2·99	1·99*	0·57	20	0·48	0·10‡
Lean tissue deposition	YAM	6	0·53	0·65	0·62	0·21	14	0·04	0·03
(MJ/pair per 28 d)	JM1	7	0·46	0·38*	0·47†	0·07	17	0·12	0·02‡
	JM2	4	0·68	0·72	0·73	0·06	9	0·18	0·02‡
	JM3	7	0·46	0·41	0·46	0·06	18	--	—
	JAG	8	1·60	1·72	1·50	0·26	21	0·07	0·04
Net energy	YAM	6	0·87	0·84	0·76	0·42	14	0·32	0·07‡
(MJ/pair per 28 d)	JM1	7	1·24	0·95*	0·97*	0·14	17	0·39	0·05‡
	JM2	4	1·35	1·41	1·51	0·17	9	0·12	0·06
	JM3	7	1·03	0·99	0·92	0·14	18	--	—
	JAG	8	5·03	4·72	3·50*†	0·69	20	0·54	0·11‡
Unrecovered energy	YAM	6		—	—	—	--	--	--
(expenditure plus	JM1	7	7·51	7·87*	8·26*†	0·19	17	0·62	0·05‡
loss to urine)	JM2	4	7·00	7·04	7·28*†	0·19	8	0·84	0·08‡
(MJ/pair per 28 d)	JM3	7	7·90	7·86	8·28*†	0·12	18	--	—
	JAG	8	14·6	14·7	17·1*†	0·66	20	0·47	0·10‡

JAG, JM1, JM2, JM3 and YAM, age and mode of feeding of diet GG where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of diet GG; *n*, number of animal pairs fed each diet; NNSP, no non-starch polysaccharide diet; SF, Solka-floc cellulose supplemented diet; GG, guar gum supplemented diet; LSD, least significant difference ($P < 0.05$); df, degrees of freedom; Cov, covariance regression coefficient (and SD its standard deviation) between the residual variate, after adjustment for treatment effects, and the residual of gross energy intake from the basal fraction of the diet – units are kJ/kJ change in basal ration intake.
* Mean values were significantly different from those for diet NNSP ($P < 0.05$).
† Mean values were significantly different from those for diet SF ($P < 0.05$).
‡ Mean values for Cov were significantly different from zero ($P < 0.001$).
§ For details, see pp. 416–418.
‖ Faecal energy densities not determined, therefore no values computed.

of the fat pads normalized for body fat. This suggests a small redistribution of body fat in addition to a lowering of body-fat content in some experiments or a change in the developmental stages of the animals.

DISCUSSION

The present paper addresses three issues regarding the effects of two dissimilar neutral NSP, SF-cellulose and GG, on body-weight, energy and fat deposition in the rat. These are effects on food intake, digestibility of energy and on the deposition of digested energy in the body.

It needs to be stressed, however, that the observed effects may be limited to the circumstances of the experiments. These studies were performed with animals housed in pairs below thermoneutrality (21° rather than 28°). Intake of food was sometimes

Table 7. *Changes in energy deposition and expenditure plus loss to urine relative to the dry weight of supplement intake*

| | | Supplement | | | |
| | | SF | GG | | |
	Expt†	mean	mean	LSD	df
Change in net fat	YAM	−2·1	−2·7	3·9	14
deposition (kJ/g	JM1	−4·3‡	−5·8‡	2·9	17
of supplement)	JM2	+0·4	+2·3	3·4	9
	JM3	+0·2	−2·3	3·5	18
	JAG	−4·3	−13·5‡	5·3	20
Change in net lean	YAM	+1·7	+1·3	2·9	15
tissue gain (kJ/g	JM1	−1·6‡	+0·2*	1·4	18
of supplement)	JM2	+0·8	+0·8	1·3	8
	JM3	−1·1	+0·0	1·3	18
	JAG	+1·1	−0·9	2·4	21
Change in net energy	YAM	+0·4	−1·4	5·9	14
deposited (kJ/g	JM1	−5·9‡	−5·6‡	2·9	17
of supplement)	JM2	+1·2	+3·7‡	3·6	9
	JM3	−0·9	−2·3	2·9	18
	JAG	−3·2	−14·4*‡	6·4	20
Change in unrecovered	YAM	−§	—	—	—
energy (expenditure	JM1	+8·1‡	17·2*‡	2·9	17
plus losses to urine)	JM2	+1·0	5·7*‡	2·6	8
(kJ/g of supplement)	JM3	+1·2	12·9*‡	2·5	18
	JAG	+1·3	23·1*‡	6·1	20

JAG, JM1, JM2, JM3 and YAM, age and mode of feeding of diet GG where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of diet GG; SF, Solka-floc cellulose; GG, guar gum; LSD, least significant difference ($P < 0.05$); df, degrees of freedom.

* Mean values were significantly different from those of diet SF ($P < 0.05$).

† For details, see pp. 416–418.

‡ Mean values were different from zero ($P < 0.05$).

§ Faecal energy densities not determined, therefore no value computed.

restricted due to the meal-feeding and equalized feeding and also due to spontaneous decreases in the intake of food by rats fed on GG. Intakes of the supplements were about 7–8 % of gross energy intake, which compares with a range of between 1 and 14 % for unavailable carbohydrate in human studies (see Livesey, 1990).

The present study clearly demonstrates that GG acutely and markedly depresses food intake in both meal-fed and *ad lib.*-fed animals at 21°. The mechanism of this effect is not clear and could be one or a combination of possibilities such as, a lack of palatability, mechanical difficulties with eating a diet that readily forms a gel on contact with moisture or more profound effects on regulatory mechanisms. Effects on stomach emptying are excluded, as GG is without significant effect on stomach emptying of dry matter in the pig (Rainbird & Low, 1986) and in the rat (I. R. Davie & G. Livesey, unpublished results). This acute effect of GG on food intake is consistent with observations in man showing GG to lower hunger (Evans & Miller, 1975; Krotkiewsky, 1984), though whether similar mechanisms operate in both species is not known. The occurrence of an effect with the soluble fibre (GG) but not with the insoluble fibre (SF-cellulose; values not shown) is consistent with observations in humans with GG *v.* wheat bran when measuring hunger and weight loss (Krotkiewsky, 1984) and with psyllium gum *v.* wheat bran when measuring

Table 8. *Effects of the supplementary guar gum and Solka-floc cellulose on the sizes of the epididymal fat pads of rats*

| | Expt‡ | n | Dietary treatment§ | | | LSD | df |
			NNSP	SF	GG		
Tissue dry weight	YAM	6	7·8	7·0*	5·9*†	0·7	14
(g/pair)	JM1	7	3·3	2·5*	2·3*	0·4	17
	JM2	4	1·6	1·6	1·4	0·3	9
	JM3	7	2·0	2·0	1·7	0·4	18
	JAG	8	10·8	9·1*	7·5*†	1·4	20
Ratio dry wt to lean	YAM	6	1·00	0·88*	0·78*	0·11	14
dry body mass (relative	JM1	7	1·00	0·79*	0·69*	0·13	18
to NNSP)	JM2	4	1·00	0·98	0·83*	0·18	9
	JM3	7	1·00	1·05	0·86	0·21	18
	JAG	8	1·00	0·78*	0·71*	0·16	20
Ratio dry wt to body	YAM	6	1·00	0·98	0·85*†	0·07	15
fat mass (relative	JM1	7	1·00	0·91	0·94	0·13	18
to NNSP)	JM2	4	1·00	0·98	0·79*†	0·09	9
	JM3	7	1·00	0·97	0·96	0·14	18
	JAG	8	1·00	0·92	0·96	0·12	21
	Pooled‖	32	1·00	0·95*	0·92*	0·03	76

JAG, JM1, JM2, JM3 and YAM, age and mode of feeding of diet GG where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of diet GG; *n*, number of animal pairs fed on each diet; NNSP, no non-starch polysaccharide diet; SF, Solka-floc cellulose supplemented diet; GG, guar-gum diet; LSD, least significant difference ($P < 0.05$); df, degrees of freedom.
* Mean values were significantly different ($P < 0.05$) from those for diet NNSP.
† Mean values were significantly different ($P < 0.05$) from those for diet SF.
‡ For details, see pp. 416–418.
§ For details, see Table 1.
‖ Data pooled from all experiments.

food intake (Stevens *et al.* 1987). However, the present effect of GG on intake is a temporary phenomenon (Fig. 1), and would, therefore, indicate caution also in human studies when attempting to extrapolate from acute effects of fibres on food intake to the consideration of energy balance in the longer term.

When accounting for the effects of the quantity of food ingested in a practical way, i.e. by feeding to equalize the intake of the basal ration, the GG and the SF-cellulose fed as supplements have no marked effects on body-weight gain or lean tissue gain, and only small effects on fat deposition under the prevailing experimental conditions. With SF-cellulose, this is clearly due to the additional gross energy from the supplement being lost to faeces. For GG, however, the additional energy available from supplementation (partial digestible energy value of 10 kJ/g) appears to be balanced by an increased loss of heat or of energy to urine (unrecovered energy). Effects of NSP on urinary energy losses are not expected (Southgate & Durnin, 1970; Kelsay *et al.* 1978; Miles *et al.* 1988; Wisker *et al.* 1988). Consistent with these observations our preliminary work shows GG fed to rats either decreases or has no effect on urinary energy (urinary energy loss decreased by 3 (SE 3) kJ/g GG). Hence, we infer an elevation of energy expenditure and a putative thermogenic effect of the GG. The extent of this effect is sometimes sufficient to cause more energy to be expended than is supplied, hence the negative values for net energy retention (Table 7).

The circumstance of this putative thermic effect for GG is examined in Table 9. For those experiments with the juvenile rats, where the initial live weights are almost similar (Expts

Table 9. *Summary of observations on the effect of guar gum (GG) on energy balance in the juvenile rats, with experiments ranked in order of decreasing apparent energy status*

Expt	n	Covariance for conversion of GE to NE for basal ration (kJ/kJ)	Fat: lean tissue gain on the basal diet (kJ/kJ)	Epididymal fat pads dry wt on basal diet (g)	Change in body fat (kJ/g GG)	Change in EE+UE (kJ/g GG)	Partial digestible energy value (kJ/g GG)
JAG	8	0·54[c]	2·2[c]	10·8[c]	−14·4[a]	23·1[d]	8·2[a]
JM1	7	0·39[b]	1·7[b]	3·3[b]	−5·6[b]	17·2[c]	11·6[c]
JM3	7	—	1·4[ab]	2·0[a]	−2·3[b]	12·9[b]	10·6[c]
JM2	4	0·12[a]	1·0[a]	1·6[a]	+3·7[c]	5·7[a]	9·4[b]
Pooled SD		0·09	0·5	0·8	3·6	3·6	0·9
df		45	62	62	60	59	62

[a,b,c,d] Mean values in the same vertical column with unlike superscript letters were significantly different ($P < 0.05$).

JAG, JM1, JM2, JM3 and YAM, age and mode of feeding of diet GG (see Table 1) where J is juvenile and YA is young adult, M is meal-feeding and AG is *ad lib.*-feeding of diet GG; n, number of animal pairs observed per dietary treatment; GE, gross energy; NE, net energy retained in the body; EE+UE, energy expenditure plus urinary energy loss.

JM1, JM2, JM3 and JAG) there is a progressive increase (Table 9), from Expt JM2 to Expt JAG, in the efficiency of conversion of increasing gross basal (diet NNSP) dietary energy to net energy retained in the body. The inefficiency at the highest value is close to the energy expenditure obligatory for energy deposition in the tissues (Pullar & Webster, 1977), whereas the lower efficiencies are indicative of animals being close to maintenance requirements. The increased efficiency of energy conservation as retained energy is associated also with a progressive increase in the fat:lean tissue deposition and a progressive increase in the weights of the epididymal fat pads (Table 9). It is clear that there is a progressive increase in the energy status of the rats from Expt JM2 to Expt JAG. This is accompanied by a progressive increase in the ability of GG to depress fat deposition and a progressive increase in the putative thermic effect of the GG (Table 9). Table 9 also shows that there is no similar progressive effect on the partial digestible energy value of GG. This is important because it establishes the fact that these significantly overt trends are not due to errors associated with the measurement of food intake or of faecal energy losses. The observation (Tables 4 and 9) that the partial digestible energy value of GG did not change progressively from Expt JAG to Expt JM2 also suggests that losses of bacterial matter to faeces do not change progressively, as would be expected if a progressive thermic effect of the GG (Table 9) occurred due to a relatively large increase in the supply of substrate for fermentation. This could arise, for example, due to the GG causing losses of starch from the small to the large intestine.

Part of the putative thermic effect (Table 9) may be regarded as obligatory thermogenesis, a response needed to handle the greater intake of energy, an observation also made with increased intake of the basal diet (covariances, Table 6). But values for net energy retention which are negative (Table 7) suggest effects additional to the GG simply providing extra energy which would permit both obligatory- and adaptive-dietary thermogenesis. Moreover, these negative values also indicate an effect greater than expected due to fermentation. This is because the sum of energy losses due to fermentation will be no more than about 30% of the gross energy content of that portion of the GG undergoing anaerobic fermentation (> 98%, see p. 431) and which is due to the heat of fermentation,

the production of molecular hydrogen and methane and the loss of efficiency due to absorption of energy as short-chain fatty acids which are oxidized to ATP with less efficiency than available carbohydrates (Nutrition Council, 1987). A possible explanation of the putative thermic effect of GG is that there occurs a modification to the pattern of food intake, with diet NNSP animals tending towards meal-feeding and diet GG animals tending towards nibbling (Cohn & Joseph, 1960; Spangler & Johnson, 1981). However, this would not obviously explain the trend in the meal-fed animals. Animals fed on diet GG were *ad lib.*-fed in all experiments except JM3, whereas to equalize intake of basal dietary materials the diet SF- and NNSP-fed animals were restrict-fed. Whether *ad lib.* feeding introduces an additional stress to increase thermogenesis by comparison with restrict-feeding at the same energy intake is not excluded by these studies, though it is unlikely. Further restrict-feeding was applied to both treatments in Expts JM3 and a similar though non-significant trend by diet GG to decrease fat deposition (Tables 6 and 7) and fat pad size (Table 8) was observed.

The decrease in the size of the epididymal fat pads in diet GG-fed animals is consistent in all experiments and is notable, since one might have expected larger fat pads as a result of the additional intake of digestible energy. Recent work with maize starch (G. Livesey, I. R. Davies and J. C. Brown, unpublished results) and sucrose (Livesey *et al.* 1990) indeed shows that the additional energy from these sources, in similar experiments to those presently reported, results in an expected increase in the size of these fat pads.

The partial digestible energy value of GG (about 10 kJ/g) is considerably below that of its apparent digestible energy value (17 kJ/g), i.e. its heat of combustion (17·34 kJ/g) multiplied by its apparent digestibility, which is close to 0·98 (Nyman & Asp, 1982; Nyman *et al.* 1986; a value confirmed for one of the present experiments (Expt JM1) and briefly reported elsewhere by Davies *et al.* 1987 and by Livesey & Davies, 1987). This difference arises due to additional losses of fat and protein to faeces (Nyman *et al.* 1986), which explains the higher (than 17 kJ/g carbohydrate) heat of combustion of the additional dry matter lost to faeces when this GG is ingested (Table 4).

It is not possible to make extrapolations of all the present results to man or even to other conditions in the rat, but a number of points merit consideration. The trends summarized in Table 9 do not support a view that GG, provided as a supplement, would help in the loss of body fat when energy intakes are close to or below maintenance requirements as might be supposed in humans during continuous slimming (Federation of American Societies for Experimental Biology, 1987; British Nutrition Foundation, 1990). The results, however, do not preclude a view that the GG may help prevent subsequent regain of body fat when intakes of energy are above the requirement for energy balance. There may also be benefit to be gained if a redistribution of lipid stores (Table 8) would occur on ingestion of non-starch polysaccharides.

The present study illustrates a problem when extrapolating from traditional energy values to effects on energy balance for carbohydrates which, like GG, might have pharmacological effects. It is that the partial digestible energy value (and the apparent digestible energy value) do not always predict what really happens to body fat deposition. Whether lower intakes of GG, less than 100 g/kg supplementation, have effects on body fat deposition and whether the presently observed effects are temporary, as found with effects on food intake, remains to be investigated.

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