

The plasma composition of karakul lambs fed isocaloric high- and low-fibre diets*

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Blood samples were withdrawn once weekly from the jugular vein of 10 karakul lambs (ca. 17 kg) for 12 weeks. The lambs were randomly allocated to a treatment and fed either a high-fibre (HF, $n = 5$) or low-fibre (LF, $n = 5$) diet. Dietary carbohydrate was provided as either structural (HF treatment) or readily fermentable (LF treatment) whereas the energy and nitrogen ratios were kept constant. Blood samples were drawn once a week and plasma concentrations of glucose, free fatty acids (FFA), lactate, insulin and glucagon were determined. Differences in the efficiency of metabolizable energy utilisation were determined from the average daily intake (ADI), average daily gain (ADG) and feed conversion ratio (FCR). ADI, ADG and FCR as well as the plasma composition remained constant within a treatment over the 12-week period. All data within each group of lambs were subsequently pooled. The ADI was higher in the HF than the LF ($p \leq 0.05$), whereas the digestible energy and nitrogen intakes were similar for the two treatments. The plasma glucose and FFA concentrations were higher ($p \leq 0.05$) in the LF than in the HF lambs. Insulin levels were higher ($p \leq 0.05$) in the HF than in the LF lambs (1.39 and 1.66 ± 0.07 ng.ml⁻¹, respectively). There were no differences in the glucagon concentrations between groups. The insulin:glucagon ratio was, however, higher ($p \leq 0.05$) in the HF than the LF group. The LF lambs maintained a higher ADG ($p \leq 0.05$) than the HF lambs (160 and 115 ± 3.6 g.day⁻¹, respectively) and at the same time had a lower ($p \leq 0.05$) FCR than the HF lambs (5.9 and 10.1 ± 0.75 , respectively). The LF lambs were more efficient ($p \leq 0.05$) at converting dietary energy into body mass than the HF lambs, requiring 68.9 MJ ME per kg gain compared to 98.3 ± 5.48 MJ ME per kg gain of the HF lambs.

Bloedmonsters is weekliks vir 12 weke geneem uit die vena jugularis van 10 karakul lammers (ca. 17 kg). Die lammers is aan 'n behandeling toegeken en is óf 'n hoë-vesel- (HF, $n = 5$) óf lae-vesel- (LF, $n = 5$) dieet gevoer. Die dieetkoolhidrate is as struktureel (HF-behandeling) of maklik fermenteerbaar (LF-behandeling) aangebied, terwyl die energie- en stikstofverhouding konstant gebly het. Bloed is elke week getrek en die plasmakonsentrasies van glukose, vrye vetsure (VVS), laktat, insulien en glukagon is bepaal. Die eksperimentele periode het 12 weke geduur en die gemiddelde daaglikse inname (GDI), gemiddelde daaglikse toename (GDT) en voeromsetverhouding (VOV) is gebruik om die verskil in die doeltreffendheid van ME-benutting tussen diëte te bepaal. GDI, GDT en VOV sowel as die plasmamestelling het konstant gebly binne behandelings oor die 12 weke. Alle data van dieselfde behandeling is daarna saamgevoeg. Die GDI was hoër vir die HF- as die LF-lammers ($p \leq 0.05$), maar die veteerbare energie en stikstofinname was dieselfde vir die twee behandelings. Die LF-lammers het ook 'n hoër ($p \leq 0.05$) plasmaglukose en VVS konsentrasies as die HF-lammers gehad. Insulinvlakke was hoër ($p \leq 0.05$) in die HF- as die LF-lammers (1.39 en 1.66 ± 0.07 ng.ml⁻¹, onderskeidelik). Daar was nie 'n verskil in plasmaglukagonkonsentrasie tussen twee groepe lammers nie, maar die insulien:glukagon-verhouding was wel hoër ($p \leq 0.05$) in die HF- as die LF-lammers. Die LF-lammers het 'n hoër GDT ($p \leq 0.05$) as die HF-lammers gehandhaaf (160 en 115 ± 3.6 g.dag⁻¹, onderskeidelik) en het terselfdertyd 'n laer ($p \leq 0.05$) VOV as die HF-lammers gehad (5.9 en 10.1 ± 0.75 , onderskeidelik). Die LF-lammers was meer doeltreffend ($p \leq 0.05$) in die omset van die dieetenergie na liggaamsmassa as die HF-lammers en het net 68.9 MJ ME per kg toename nodig gehad in vergelyking met 98.3 ± 0.75 MJ ME per kg toename benodig deur die HF-lammers.

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Introduction

The efficiency with which ruminants use metabolizable energy (ME) for growth and fattening is lower for roughage than concentrate-based diets (Black, 1983). Bulls fed an 85% concentrate diet grew 35% faster than those fed an isocaloric amount of hay (Bailey, 1989a,b; Bailey & Lawson,

1989). Many hypotheses have been proposed to explain the differences in the efficiency of utilisation of roughage and concentrate diets, with special attention being given to individual nutrients (Gill *et al.*, 1984; Black *et al.*, 1987a,b). The cause of the decreased metabolic efficiency on fibre diets has been thought to be due to inefficient usage of acetate by the

animal. This postulate has been tested in feeding trials with lambs and calves and the results have been controversial (Ørskov *et al.*, 1966; Ørskov & Allen, 1966a,b,c; Ørskov *et al.*, 1991; Ørskov & MacLeod, 1993).

Hayden *et al.* (1993) reported that steers undergoing 'compensatory growth' were metabolically more efficient than normal growing steers, and this seemed to be correlated to the plasma concentration of various hormones, including insulin. Sano *et al.* (1995) reported that propionate increased both insulin and glucagon secretion, insulin responsiveness to glucose was, however, variable (Sano *et al.* 1993). It seems possible, therefore, that the improved efficiency of ruminants fed concentrate rather than roughage type diets, may be due to hormonal changes resulting from increased propionate production in the rumen of concentrate fed animals.

The purpose of this study was to determine the magnitude of the difference in the efficiency of ME utilisation when diets with different fibre content were fed to karakul lambs, while observing the plasma concentration of metabolites and hormones.

Methods

Diets

Two diets were fed, one with a high-fibre (HF) and one with a low-fibre (LF) content. The diets were pelleted to avoid selection by the animal. The composition is shown in Tables 1 and 2. Since the efficiency of ME utilisation differs between foodstuffs (Ulyatt *et al.*, 1970), the same ingredients were used to make up the two experimental diets. The HF diet contained 70% roughage, whereas the LF diet contained only 30%. The protein : energy ratio of the two diets was the same. A suitable mineral and vitamin mix was added to ensure sufficient intake of all essential nutrients. Water was freely available.

Animals

Ten Karakul lambs were housed indoors in metabolism crates (1.5 m × 0.75 m) and initially fed chopped lucerne hay. The lambs were inoculated against enterotoxaemia and blue tongue, and treated for internal parasites. After a 10 day acclimatisation period, the lambs were divided at random into two groups and assigned to either the HF (high-fibre) or LF (low-fibre) group, after determining their mass (22.4 ± 1.8 kg), and adapted to either the HF or LF diet by gradually replacing the

Table 1 The ingredient composition (% dry matter) of the experimental diets

Component	HF	LF
<i>Eragrostis tef</i>	70.00	30.00
Maize meal	19.70	57.00
Sunflower oilcake	3.20	5.45
Molasses	4.50	4.50
Urea	1.00	1.00
Limestone	0.59	1.00
Sodium bicarbonate	0.05	0.15
Salt	0.25	0.30
Monosodium phosphate	0.55	0.20
Mineral & vitamin mix	0.10	0.10

Table 2 The proximate analysis of the experimental diets expressed as a percentage of dry matter (except where otherwise indicated)

Component	HF	LF
Dry Matter of total diet	90.27	90.70
Organic Matter	90.99	92.90
Metabolizable Energy (MJ.kg ⁻¹)	9.75	11.63
Nitrogen	2.43	2.90
Crude Protein	10.44	12.49
Energy : protein ratio	0.93	0.93
Crude Fibre	21.90	13.44
Starch	13.90	34.50
Calcium	0.52	0.53
Phosphate	0.34	0.34

lucerne hay with the allocated experimental diet over a 14-day period. The lambs were acclimatised for a further 14 days before the trial started, at which time their masses were 24.7 and 25.1 ± 0.93 kg for the HF and LF groups, respectively. The *ad libitum* intake was determined during this period. Lambs were fed twice daily and feed refusals were measured daily.

Experimental procedure

Representative samples of the feeds were taken before, during (daily) and after the trial, bulked and stored for later analysis. The diets were analysed for dry matter (DM), organic matter (OM), nitrogen (N), crude fibre (CF), starch, calcium (Ca) and phosphate (P) by standard methods of the Association of Analytical Chemists (A.O.A.C., 1990). The metabolizable energy (ME) content was calculated from tables published by the National Research Council (N.R.C., 1985). A catheter was inserted into the jugular vein when necessary and three blood samples were drawn at 30-min intervals once every week. Blood samples were immediately centrifuged at 4°C to obtain the plasma. The mass of each lamb was determined twice weekly. Voluntary intake was calculated from gross intake and the number of days fed. Average daily gain (ADG) was calculated from the change in mass over the 12-week period. Feed conversion ratio (FCR) was calculated from the voluntary intake and ADG, whereas the energy conversion ratio (ECR) was calculated from the ME intake and ADG.

Analyses

Plasma samples were analysed for glucose, free fatty acid (FFA) and hormone concentrations. Glucose and lactate were determined using a commercially available kit (Boehringer Mannheim, Germany). FFA were determined according to the method of De Villiers *et al.* (1977), whereas insulin and glucagon were estimated with commercially available radio-immunoassay kits (Amersham, UK; Serona Diagnostics, Italy; respectively).

Statistics

Data were analysed statistically using the Statgraphics 6.0 (Manugistics, Inc., Maryland, USA) personal computer package in which the two-sample test with pooled variance pro-

vided a *t* statistic for unpaired samples with unequal variances. The rate of growth over the entire period was measured individually as the increment of mass against time.

Results

Blood metabolite and hormone concentrations

The venous concentrations of glucose, FFA, insulin and glucagon, as well as the insulin : glucagon ratios are shown in Table 3. Glucose concentrations ($p \leq 0.05$) were significantly greater (9.7%) in the LF fed compared to the HF fed group. The venous FFA concentrations were 14.6% higher ($p \leq 0.05$) in the LF than in the HF group. Contrary to results of other authors (Bassett, 1972; Zainir *et al.*, 1989) the plasma insulin concentrations in the LF group were lower (by 0.27 ± 0.08 pg.ml⁻¹, $p \leq 0.05$) than in the HF group. The insulin : glucagon ratio was significantly lower ($p \leq 0.05$) in LF compared to the HF fed lambs.

Voluntary intake

Mean feed intakes of the lambs are shown in Table 4. Although feed was freely available to the lambs, the mean daily intakes of dry (DM) and organic matter (OM) within a diet did not appear to increase significantly over this period. Regression analysis of daily feed intake against time revealed that the rate constant (i.e. increase in intake) did not differ from zero in either of the two groups:

$$\text{HF: } y = 0.0014 \pm 0.0014x + 1.21 \pm 0.13 \quad (r^2 = 0.2528)$$

$$\text{LF: } y = 0.0022 \pm 0.0016x + 0.95 \pm 0.15 \quad (r^2 = 0.1946)$$

where *y* = average daily DM intake and *x* = days

The HF group consumed significantly more DM (208 ± 49.6 g.day⁻¹, $p \leq 0.05$) than the LF group. The HF and LF treatment groups consumed 102.5 and 86.0 ± 1.3 g of DM per MJ ME, respectively. Although intakes were different, the two groups consumed similar amounts of metabolizable energy (ME) and nitrogen (N), since the protein : energy ratio was similar in the two diets. The intakes of crude fibre (CF) and starch differed significantly ($p \leq 0.05$), as a result of the different inclusion levels of hay and maize, respectively.

Average daily gain and feed and energy conversion ratios

The initial mass, final mass and average daily gain (ADG) of the lambs are shown in Table 5. Although the final mass of the lambs did not differ significantly between groups, the ADG was significantly higher in the LF than the HF fed group ($p \leq 0.05$). The average daily gain of the lambs was calculated from the rate constant of the regression of mass against time:

$$\text{HF: } y = 0.128 \pm 0.0019x + 24.61 \pm 0.18 \quad (r^2 = 0.9975)$$

$$\text{LF: } y = 0.161 \pm 0.0053x + 25.28 \pm 0.50 \quad (r^2 = 0.9915)$$

where *y* = ADG and *x* = days.

The mass gains of the lambs in the HF and LF groups as well as the regression of the mean of mass over time are shown in Figure 1. The lambs fed the LF diet clearly grew faster than those fed the HF diet. The difference is better illustrated by the time required to reach a target mass. If a target mass of 40 kg is selected, then lambs fed the LF diet would

Table 3 The venous concentrations of glucose, FFA, insulin and glucagon during the growth trial ($n = 5$ per group; mean \pm s.e.m.)

	HF	LF	s.e.m.	$p \leq$
Glucose (mmol)	5.08	5.57	± 0.11	0.05
FFA (mmol)	0.212	0.243	± 0.01	0.05
Lactate (mmol)	0.921	0.816	± 0.12	NS
Insulin (ng.ml ⁻¹)	1.66	1.39	± 0.07	0.05
Glucagon (pg.ml ⁻¹)	57.7	62.0	± 5.03	NS
Insulin/glucagon	28.8	22.4	± 1.73	0.05

s.e.m = standard error of the mean; NS = not significant

Table 4 Feed intake of lambs ($n = 5$ per group) during the growth trial (g.day⁻¹ except where otherwise indicated; mean \pm s.e.m.)

Intake	HF	LF	s.e.m.	$p \leq$
Dry Matter	1162.0	954.0	± 59.01	0.05
Organic Matter	1056.0	886.0	± 54.39	NS
Nitrogen	28.1	27.6	± 1.27	NS
Crude Protein	175.7	172.5	± 8.07	NS
Starch	161.1	329.1	± 13.80	0.05
Crude Fibre	264.8	128.9	± 9.08	0.05
Phosphate	4.1	4.2	± 0.22	NS
Calcium	10.6	10.6	± 0.54	NS
Metabolizable Energy (MJ.day ⁻¹)	11.3	11.1	± 0.58	NS

NS = not significant; s.e.m = standard error of the mean

Table 5 Live mass gain, feed conversion ratio (FCR) and energy conversion ratio (ECR) during the growth trial ($n = 5$ per group; mean \pm s.e.m.)

	HF	LF	s.e.m.	$p \leq$
Initial mass (kg)	24.7	25.1	± 0.93	NS
Final mass (kg)	34.4	38.6	± 1.97	NS
ADG (g.day ⁻¹)	115.0	160.9	± 3.6	0.05
FCR (kg.kg ⁻¹)	10.10	5.93	± 0.75	0.05
ECR (MJ ME.kg ⁻¹)	98.3	68.9	± 5.48	0.05

NS = not significant; s.e.m. = standard error of the mean

take 84–104 days to reach this, whereas lambs fed the HF diet would require 112–123 days. The lambs fed the LF diet grew 25.8% faster than the HF-fed lambs.

The feed (FCR) and energy (ECR) conversion ratios of each treatment group are given in Table 5. The FCR is determined by feed intake under *ad libitum* conditions, or else by ADG when intake is restricted. Intake differed between groups and was not restricted, thus the FCR reflected the difference in both intake and efficiency of utilisation. To obtain a better estimate of efficiency, the energy conversion ratio (ECR; MJ ME intake per kg live mass gain) was calculated, since the unrestricted energy (ME) intakes were similar.

The FCR of the LF-fed lambs was 37.7% ($p \leq 0.05$) better than that of the HF-fed lambs (5.9 and 10.1 ± 0.75 kg.kg⁻¹, respectively). When the efficiency of mass gain was measured as ECR, the LF group were 25.6% more efficient ($p \leq$

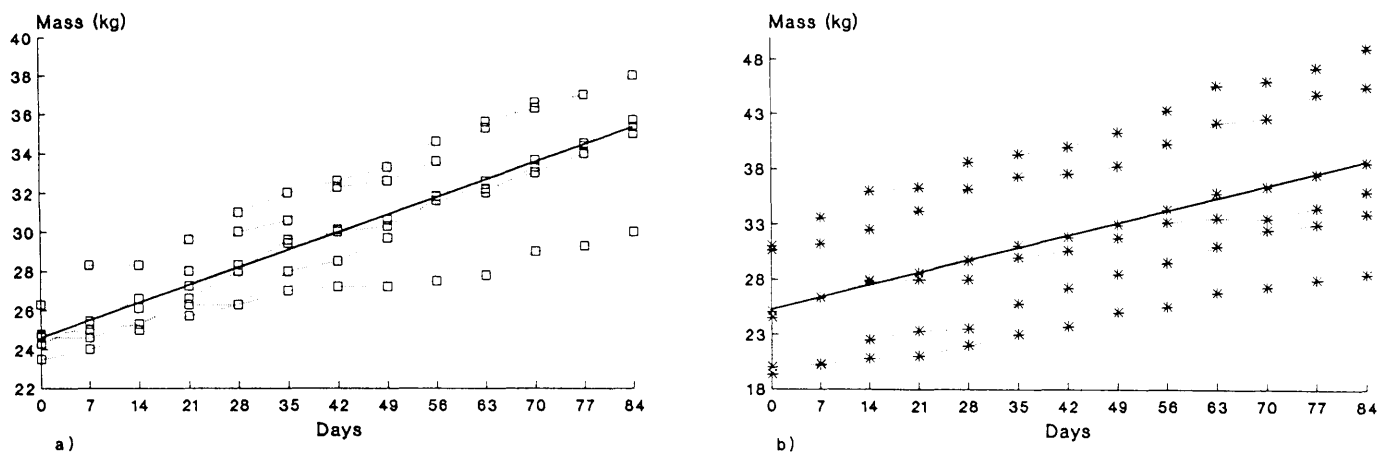


Figure 1 The increase in mass of the lambs during the experimental period as well as the regression of the mean (solid line) for (a) the HF group (squares) and (b) the LF group (stars).

0.05) in using dietary energy for live mass gain than the HF group. This is similar to differences reported by Bailey (1989a,b).

Discussion

One of the consequences of feeding a low-fibre diet containing high amounts of readily fermentable carbohydrates is an elevated plasma glucose concentration when compared to roughage-fed lambs. In the present study there was a 10% increase in glucose concentration in the LF compared to the HF lambs. Similar results have been reported by Abdul-Razzaq *et al.*, (1988) and Bailey (1989a,b). The higher plasma concentration of glucose in concentrate-fed animals is most probably due to increased propionate production in the rumen as well as greater glucose absorption from the small intestine (Janes *et al.*, 1985).

Plasma FFA concentration was also elevated in the LF compared to the HF lambs. Circulating FFA concentrations appear to be positively related to FFA turnover or irreversible loss rate (Pethick *et al.*, 1983). Thus it would appear that there was a greater lipolytic rate in the LF compared to the HF lambs. This is contrary to other authors who found that decreasing the fibre content of a diet lowered plasma FFA concentrations.

Differences in blood composition that relate to diet are probably a consequence of differences in metabolism and not the cause (Cole & Hallford, 1994; Cole *et al.*, 1993). Normal tissue growth may be influenced by metabolic hormones either directly or by way of altering partitioning (Van Houtert & Leng, 1993). Thus the differences in metabolite concentrations observed in this study could be the result of altered endocrine status.

In the present study the insulin concentrations were lower in the LF than in the HF lambs. This result was unexpected, as the uptake of glucose and propionate was expected to be higher in the LF than the HF-fed group (Sano *et al.*, 1993, 1995). Although Abdul-Razzaq *et al.*, (1988) and Abdul-Razzaq & Bickerstffe (1989) reported higher plasma insulin concentrations in low-fibre than in roughage-fed diets, Godden & Weekes (1981) found no differences in insulin or glucose concentrations between low- and high-fibre diets. Beerman *et al.* (1987) reported lower insulin concentrations in lambs that

had elevated blood glucose levels and a high growth rate. These authors treated lambs with steroids (cimaterol), and these lambs maintained a faster growth rate, a higher feed utilisation efficiency and had lower blood insulin concentrations than did untreated lambs. Farningham & Whyte (1993) found that sheep infused with propionate had increased glucose levels and that under these conditions glucagon was more involved in glucose regulation than insulin. These conflicting results might be explained by the observation of de Boer *et al.* (1985) that it is the balance or ratio of hormones to each other that is important and not the concentrations themselves.

In the present study, the insulin : glucagon ratio was significantly higher in the HF compared to the LF lambs. A low insulin : glucagon ratio would represent a dominance of glycogenolytic and gluconeogenic actions, whereas a high ratio would promote glycogenesis and peripheral glucose use (de Boer *et al.* 1985). This lower ratio in the LF lambs may have shifted the hormonal site of glucose regulation to the liver, increasing hepatic gluconeogenesis when compared to the HF lambs. This may have caused increased peripheral glucose utilisation. These effects would explain the higher glucose concentration in the LF compared to the HF lambs. The higher FFA concentrations in the LF compared to the HF lambs may be the result of the lower insulin concentrations.

In many studies where concentrate and roughage diets are fed, either the dietary energy and nitrogen ratio between diets or the dietary energy intakes differ. In the present study, the voluntary intakes of the two groups of lambs were equivalent on the basis of ME and nitrogen intake and were not determined by gross intake. Forbes (1988) suggested that appetite is stimulated when absorption of energy-yielding nutrients falls below a certain concentration and that eating stops when these rise above a certain point. On the other hand the capacity of the gastrointestinal tract to accommodate the feed may limit intake. The results of Farningham & Whyte (1993) showed that propionate is an appetite depressant. Our results tend to support Forbes' and Farningham & Whyte's hypotheses, since the LF lambs consumed a smaller ration than did the HF lambs, but dietary ME and nitrogen intakes were similar and propionate concentrations in the rumen would have been higher.

Although the lambs were fed *ad libitum*, intakes did not

increase significantly over the 12-week period. It has been well documented that ruminants have a lower feed intake in winter months (Blaxter *et al.*, 1982). The experiments of Forbes *et al.* (1979) and Forbes (1980) suggest that this change in feed consumption is induced by a changing photoperiod. This feeding study took place during autumn and winter (April to July), which may, as a result of the shortening of the photoperiod, have prohibited the expected increase in feed intakes. This should not affect the validity of the results obtained since Blaxter *et al.* (1982) showed that an altering photoperiod would not affect the data provided that comparative studies were conducted at the same period of the year.

Cumulative live mass gain appeared to be linear over the study period even though growth is not linear but allometric in nature (Blaxter *et al.*, 1982). The reasons for an apparently consistent average daily gain are most likely the relatively short experimental period (12 weeks), the masking effect of experimental variation, as well as the constant concentration of daily feed intake. Furthermore, the partitioning of energy between nitrogen and fat is determined by the relationship between energy intake and energy deposition rate. This relationship is linear when animals are in a more mature growth phase (20–40 kg) and nitrogen is not limiting (Campbell, 1988).

Average daily gains were not very high. This appears to be the result of the low growth potential of Karakul lambs. Martins & Peters (1992) reported Karakul growth rates of 108–178 g per day. Karakul sheep are not selected for growth rate but reproduction and good quality lamb pelts. There was, however, still a significant difference between the HF and LF-fed groups. The 26% greater growth rate maintained by the lambs fed the LF compared to the HF diet is similar to values found by other investigators. Theriez *et al.* (1982) fed lambs 30 or 70% lucerne and 70 or 30% concentrate (similar to the LF and HF diets in this study) and found a 26% greater growth rate on the LF than on the HF diet.

As a result of the lower intake and higher growth rate of the LF compared to the HF lambs, the FCR was 38% higher for the HF group. This difference in FCR is partially derived from the difference in the quantity of food consumed, however, the difference in the FCR was greater than the difference in feed intake between the groups. Since the ME intake was similar, the ECR was a better reflection of efficiency of utilisation of ME, and was similar to the difference in growth rate. The HF lambs required 26% more ME per unit live mass gain than the LF lambs.

Results of this study show firstly that changing the form of carbohydrate fed from structural to ready fermentable, affected plasma metabolite concentrations and altered the endocrine status. A portion of the increased efficiency of utilisation of nutrients may depend upon these changes in circulating concentrations of hormones or altered tissue sensitivity to these hormones. Secondly, changing the form of carbohydrate altered the efficiency with which lambs used the ME available for growth. This may have been a result of the changes in hormonal concentrations altering the partitioning of nutrients and thereby increasing the efficiency of growth in the LF compared to the HF lambs. Thirdly, that voluntary intake was determined from the nutrient concentration and

not the quantity of feed consumed.

It is probable that digestion and absorption of the nutrients by the animals, as well as the intermediary metabolism of the metabolites may differ between treatments. These aspects formed the basis of further studies, using the diets described here.

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