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Effects of dietary fat source and breed on the carcass composition, *n*-3 polyunsaturated fatty acid and conjugated linoleic acid content of sheep meat and adipose tissue

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Seventy-two 8-week-old ram lambs from three breeds, Suffolk, Soay and Friesland, were offered one of four diets based on dried grass and formulated to have a similar fatty acid content (60 g/kg DM) and containing: Megalac (high in 16 : 0, control; Volac Ltd, Royston, Herts., UK), whole linseed (18 : 3*n*-3), fish oil (20 : 5*n*-3 and 22 : 6*n*-3) or whole linseed plus fish oil. The lambs were slaughtered at approximately half of their mature live weight (43, 21 and 43 kg for Suffolk, Soay and Friesland lambs, respectively). Fish oil reduced DM intake and lamb live-weight gain ($P<0{\cdot}001$), while DM intake, live-weight gain and subcutaneous fat content were highest in Suffolk and lowest in Soay lambs. Linseed feeding doubled the proportion ($\times 100$) of 18 : 3*n*-3 in the *longissimus dorsi* from 1·4 to 3·1 and in the subcutaneous adipose tissue from 1·2 to 2·6 ($P<0{\cdot}001$). Suffolk and particularly Soay lambs contained higher proportions of 18 : 3*n*-3 than Friesland lambs in the *longissimus dorsi*, while in the adipose tissue, Suffolk lambs had the highest level. Feeding fish oil increased the muscle proportion ($\times 100$) of 20 : 5*n*-3 from 0·7 to 2·3 and 22 : 6*n*-3 from 0·3 to 0·8 ($P<0{\cdot}001$). By contrast, the proportions of the longer-chain *n*-3 polyunsaturated fatty acids were similar across all three breeds. All three lipid supplements containing *n*-3 polyunsaturated fatty acids increased the content of muscle *trans*-18 : 1 relative to the control values, but conjugated linoleic acid (*cis*-9,*trans*-11–18 : 2) only increased in the muscle of lambs fed linseed. Feeding linseed or fish oil lowered the *n*-6 : *n*-3 ratio in sheep meat, but neither diet nor breed had much effect on the polyunsaturated fatty acid: saturated fatty acid ratio.

Polyunsaturated fatty acids: Conjugated linoleic acid: Breed: Sheep

It has been recommended by the Department of Health (1994) that the intake of saturated fatty acids in the diet of man should be reduced, while that of polyunsaturated fatty acids (PUFA) be increased. In addition, the intake of PUFA of the *n*-6 series such as linoleic acid (18 : 2*n*-6) should not be altered, while the intake of the fatty acids of the *n*-3 series such as α-linolenic acid (18 : 3*n*-3), eicosapentaenoic acid (20 : 5*n*-3) and docosahexaenoic acid (22 : 6*n*-3) should be increased to approximately twice their current levels. This is due to the association between dietary long-chain fatty acids of the *n*-3 series and a reduction in the thrombotic tendency of blood and lower risk of CHD (Department of Health, 1994).

The contribution of ruminant animal meat and meat products to the supply of total and saturated fatty acids in the diet of man is well recognised (Enser *et al.* 1996, 1998). Sheep meat is characterised as having a low PUFA: saturated fatty acid ratio, although the 18 : 2*n*-6 : 18 : 3*n*-3 ratio and total *n*-6 : total *n*-3 ratio in lamb muscle are more favourable, with values of 1·9 and 1·3, respectively (Enser *et al.* 1996). While much work has focused on nutritional means of enhancing the PUFA content of sheep meat, relatively little attention has been directed at enhancing the *n*-6 : *n*-3 ratio. Linseed is high in 18 : 3*n*-3 and previous studies have shown that the duodenal flow of this fatty acid can be doubled by the inclusion of whole linseed in the diet of lambs (Wachira *et al.* 2000). Long-chain *n*-3 PUFA in the form of fish oil have been reported to be resistant to biohydrogenation in the rumen *in vitro* (Ashes *et al.* 1992). Although the level of protection *in vivo* has been reported to be somewhat lower, significant increases in the duodenal flow of eicosapentaenoic acid and

Abbreviations: CLA, conjugated linoleic acid; PUFA, polyunsaturated fatty acid.

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docosahexaenoic acid have been achieved (Wachira *et al.* 2000).

Changing sheep breeds also offers the potential of manipulating the fatty acid composition of sheep meat. Fisher *et al.* (2000) reported that Soay lambs, when compared with Suffolk, had higher concentrations of *n*-3 and *n*-6 PUFA in the *semimembranosus* muscle. This effect may be attributed to the leaner carcasses produced from Soay lambs, as ruminant animals have been shown to preferentially deposit PUFA in phospholipids rather than in neutral storage lipids (Ashes *et al.* 1992; Enser *et al.* 1998). However, relatively little work has been conducted to evaluate the effect of sheep breed on the *n*-3 fatty acid composition of sheep meat.

The objectives of the current experiment were to determine the effects of diets that differed in their supply of *n*-3 PUFA to the duodenum, and sheep breed, on animal performance, carcass composition and the fatty acid composition of lamb muscle and adipose tissue.

Materials and methods

Diets

Four isoenergetic and isonitrogenous diets based on dried grass were formulated to provide a similar fatty acid level (60 g/kg DM) from different fat sources (Table 1). The control diet contained Megalac (a Ca soap of palm oil fatty acids; Volac Ltd, Royston, Herts., UK), the linseed diet contained whole linseed, the fish oil diet contained South American herring oil with 500 μg butylated hydroxytoluene added/g as an antioxidant (Isaac Spencer & Co. Ltd, Fleetwood, Lancs., UK), while the linseed plus fish oil diet contained a mixture of whole linseed and fish oil (50 : 50, w/w). Dietary vitamin E was added to provide 200 mg α-tocopheryl acetate/kg fresh weight across all treatments and the diets were fed as pellets (10 mm diameter × 25 mm length).

Animals, experimental design and carcass analysis

Seventy-two 8-week-old ram lambs were used: twenty-four Suffolk × Lleyn, twenty-four British Friesland × Lleyn and twenty-four Soay lambs with initial mean live weights of 26, 24 and 12 kg, respectively. The lambs were housed individually on raised floor penning and gradually adapted over a 5 d period to a mixed diet containing equal quantities of the four diets on a fresh weight basis. After 2 weeks on the adaptation diet, the lambs within each breed were blocked and allocated by live weight to one of the four dietary treatments. Fresh feed was offered daily at 115 % of the previous recorded intake with feed refusals collected three times per week. Feed samples were taken once per week and stored at −20°C prior to analysis. Live weight was recorded once per week and animals were slaughtered at approximately half their potential mature live weight (43 kg for Suffolk and Friesland crosses and 21 kg for Soay) and the carcasses scored for fat and

Table 1. Ingredients and chemical and fatty acid composition of four diets containing different fat sources

Diet...	Control	Linseed	Fish oil	Linseed plus fish oil
Ingredients (g/kg)				
Dried grass	738	715	749	732
Sugarbeet pulp (molassed)	105	105	105	105
Megalac*	44	–	–	–
Whole linseed	–	105	–	52
Fish oil	–	–	36	18
Soybean meal	58	20	55	38
Molasses	25	25	25	25
Mineral and vitamin premix	20	20	20	20
Ammonium chloride	5	5	5	5
NaCl	5	5	5	5
Chemical composition (g/kg DM)				
DM (g/kg)	893	897	901	896
Organic matter	878	889	885	887
Crude protein (N × 6·25)	134	138	135	136
Neutral-detergent fibre	459	460	471	462
Fatty acids (g/kg DM)				
12 : 0 (lauric acid)	0·5	0·2	0·2	0·2
14 : 0 (myristic acid)	0·7	0·4	3·5	2·0
16 : 0 (palmitic acid)	22·0	5·5	11·7	8·4
16 : 1*n*-7 (palmitoleic acid)	0·2	0·5	3·3	1·8
18 : 0 (stearic acid)	2·4	1·9	1·9	1·8
trans-18 : 1	0·1	–	0·1	–
18 : 1*n*-9 (oleic acid)	13·3	7·1	7·3	7·8
18 : 1*n*-7 (vaccenic acid)	0·5	0·5	1·3	0·8
18 : 2*n*-6 (linoleic acid)	11·4	8·9	10·4	10·6
18 : 3*n*-3 (α-linolenic acid)	6·6	25·5	8·4	19·5
20 : 5*n*-3 (eicosapentaenoic acid)	0·2	0·6	5·7	3·0
22 : 6*n*-3 (docosahexaenoic acid)	–	–	3·3	1·6
Total fatty acids	59·5	52·9	66·9	63·0

* Calcium soap of palm oil fatty acids; Volac Ltd, Royston, Herts., UK.

conformation using scales of 1–15 (Fisher *et al.* 2000). The carcasses were then weighed (hot carcass weight) and hung by the hind legs for 24 h at 1°C before being re-weighed (cold carcass weight) and the *longissimus dorsi* pH recorded. Post-slaughter samples from the *longissimus dorsi* were dissected and trimmed of all visible fat. Adipose tissue samples (full thickness, 50 × 50 mm) were dissected from the loin of the cold carcass. Samples were then vacuum packed and stored at −20°C prior to subsequent analysis. The left forelimb of each carcass was also dissected into lean, bone, subcutaneous and intermuscular fat.

Chemical analysis

Feed samples were bulked and analysed for DM, organic matter (Association of Official Analytical Chemists, 1990), N (Kjeltec 1035 analyser; Foss UK Ltd, Cheshire, UK) and neutral-detergent fibre (Van Soest *et al.* 1991). Samples of *longissimus dorsi* were blended in a food processor and the lipids extracted from duplicate 10 g samples using chloroform–methanol (2 : 1, v/v; Folch *et al.* 1957). After the addition of the fatty acid standard, heneicosanoic acid methyl ester (Sigma, Gillingham, Kent, UK), the solvents were removed under N_2 and the lipids hydrolysed with 2 M-KOH in methanol–water (1 : 1, v/v) containing 1 g hydroquinone/l as antioxidant, at 60°C for 1 h. After dilution with water and removal of non-saponifiable compounds by three extractions with light petroleum (boiling point 40–60°C), the hydrolysate was acidified and the fatty acids extracted into light petroleum. After neutralising and drying with solid $NaHCO_3$ and anhydrous sodium sulfate, the fatty acids were methylated with a solution of diazomethane in diethyl ether and their composition compared by GLC. Samples were injected in the split mode, 70 : 1, onto a 50 m × 0·25 mm internal diameter CP-Sil 88 WCOT for fatty acid methyl esters (catalogue no. 7488; Chrompak Ltd, Welwyn Garden City, Herts., UK) with He as the carrier gas. The output from the flame ionisation detector was quantified using a computing integrator (Spectra Physics 4270; Darmstadt, Germany) and linearity of the system was tested using saturated (fatty acid methyl ester 4) and monounsaturated (fatty acid methyl ester 5) methyl ester quantitative standards (Thames Restek UK Ltd, Windsor, Berks., UK).

A sample of adipose tissue was blended in a food processor. Lipid was extracted by homogenising duplicate 1 g samples in chloroform containing 100 mg 2,6-di-*tert*-butyl-*p*-cresol/l as antioxidant and then adding anhydrous sodium sulfate to remove water. After filtration, samples were taken and hydrolysed and the fatty acids processed and analysed as described earlier. Feed fatty acid samples were attained by direct hydrolysis in 5 M-KOH in aqueous methanol (1 : 1, v/v) for 3 h at 60°C after the addition of 21 : 0 methyl ester as the internal standard. A standard of mixed isomers of conjugated linoleic acid (CLA) methyl esters was obtained from Sigma Chemical Co. (Poole, Dorset, UK). At the column loadings used, only one significant peak was detected in the samples corresponding to a peak in the CLA standard which was taken to be *cis*-9,*trans*-11-CLA (Enser *et al.* 1999). Fatty acid results are presented as g/kg DM for the feeds and as mg/g fresh tissue or proportion (× 100) of the total fatty acids for the muscle and adipose tissue.

Statistical analysis

Live-weight gain for each animal was determined by regression analysis of live weight (kg) *v.* time. Both DM intake and live-weight gain were expressed in relation to metabolic live weight (live weight$^{0·75}$). All data were subjected to ANOVA as a factorial randomised block design with the initial live weight being used as a covariate where appropriate. The 11 df for the treatments were separated into main effects of fat source (diet), lamb breed (breed) and the interaction between fat source and lamb breed (diet × breed). Analysis was conducted using Genstat 5 (1995; Lawes Agricultural Trust, Rothamsted, Herts., UK).

Results

Feed analysis and animal performance

The chemical composition of the four diets was similar with mean values for organic matter, crude protein (N × 6·25) and neutral-detergent fibre of 885, 136 and 463 g/kg DM, respectively (Table 1). The total fatty acid content of the diets was also similar at approximately 60·0 g/kg DM except for the linseed diet, which had a lower value at 52·9 g/kg DM. The inclusion of Megalac in the control diet resulted in the highest concentration of palmitic (16 : 0) and oleic (18 : 1*n*-9) acids, while the inclusion of whole linseed resulted in the highest concentration of α-linolenic acid (18 : 3*n*-3). The highest concentrations of the long-chain *n*-3 fatty acids eicosapentaenoic acid (20 : 5*n*-3) and docosahexaenoic acid (22 : 6*n*-3) were obtained in the fish oil diet, while the linseed plus fish oil diet contained levels of 18 : 3*n*-3, 20 : 5*n*-3 and 22 : 6*n*-3 intermediate to that of the linseed and fish oil diets. Stearic acid (18 : 0) and vaccenic acid (*trans*-11–18 : 1) concentrations were low in all the diets.

When compared with lambs offered the control diet, the inclusion of fish oil reduced DM intake and daily live-weight gain (Table 2). For lambs offered the control, linseed, fish oil or linseed plus fish oil diets, the mean DM intakes were 132, 125, 94 and 110 g DM/kg live weight,$^{0·75}$ respectively (SED 4·3, $P<0·001$), while live-weight gains were 20·8, 20·6, 15·8 and 19·6 g/kg live weight$^{0·75}$ (SED 1·35, $P<0·01$). However, there was no significant effect of dietary fat source on the food conversion ratio (kg DM intake/kg gain). Daily food intake and live-weight gain were highest in Suffolk lambs, which had a higher intake than Friesland, which in turn had a higher intake than the Soay. In addition, the food conversion ratio was lower in Suffolk lambs than either Soay or Friesland (food conversion ratio 5·6, 6·5 and 6·9, respectively; SED 0·51, $P<0·05$). There was a significant interaction between dietary fat source and breed for daily food intake. When fed the control diet, Suffolk lambs ate more than Friesland lambs, which in turn ate more than Soay lambs. However, when fed either the linseed or fish

Table 2. Effects of dietary fat source and breed on the performance, carcass weights and forelimb measurements of sheep†
(Mean values)

Diet...	Control			Linseed			Fish oil			Linseed plus fish oil				Statistical significance of effect		
Breed...	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	SED	Diet	Breed	Diet × Breed
Animal performance																
Initial live weight (kg)	24·5	12·2	25·5	24·5	12·3	25·6	24·4	12·4	25·7	24·3	12·4	25·2	0·989	NS	***	NS
Final live weight (kg)	44·3	22·2	42·9	43·5	21·0	44·5	42·5	20·0	42·3	43·7	20·9	42·7	0·743	**	***	NS
Intake (g DM/kg $LW^{0·75}$)	153	113	132	141	101	134	96	82	104	127	97	107	7·5	***	***	*
Daily LW gain (g/kg $LW^{0·75}$)	25·3	18·9	18·1	25·2	15·2	21·4	18·1	13·0	16·2	24·0	16·5	18·2	2·34	***	***	NS
FCR (kg feed/kg gain)	6·1	6·4	8·6	5·6	7·2	6·4	5·4	6·5	6·6	5·3	6·0	6·0	1·03	NS	*	NS
Carcass weights																
Hot carcass (kg)	19·4	10·1	19·6	20·3	9·9	20·5	19·8	9·0	19·5	20·3	9·6	20·3	0·61	NS	***	NS
Cold carcass (kg)	18·7	9·8	19·0	19·7	9·6	19·2	19·2	8·7	18·9	19·7	9·2	19·6	0·60	NS	***	NS
24 h muscle pH	5·7	5·6	5·7	5·8	5·6	5·7	5·6	5·8	5·8	5·8	5·6	5·6	0·09	NS	NS	NS
Conformation class‡	7·7	4·0	8·0	8·8	4·0	7·7	9·6	3·8	7·3	9·2	3·7	6·8	0·69	NS	***	NS
Fat class‡	8·5	3·3	8·2	8·5	3·3	6·5	10·6	2·8	9·5	9·5	2·8	8·8	0·55	*	***	NS
Forelimb																
Weight (g)	1163	576	1144	1212	564	1192	1164	521	1136	1197	550	1182	36·8	NS	***	NS
Bone (%)	24·2	25·1	24·4	24·1	25·8	25·1	24·7	24·9	24·9	24·8	23·9	23·1	1·10	NS	NS	NS
Lean (%)	56·8	58·4	58·5	57·8	59·6	57·8	53·3	59·1	56·0	56·4	58·6	59·0	1·50	NS	**	NS
Subcutaneous fat (%)	7·5	6·3	7·2	7·5	6·1	7·0	9·2	5·8	8·5	7·8	6·2	7·5	1·24	NS	**	NS
Intermuscular fat (%)	11·5	10·2	10·0	10·6	8·6	10·2	12·8	10·2	10·6	11·0	11·3	10·4	1·67	NS	*	NS

LW, live weight; FCR, feed conversion ratio.
*$P<0·05$, **$P<0·01$, ***$P<0·001$.
† For details of diets and procedures, see Table 1 and p. 698.
‡ Scale 1–15 (Fisher *et al.* 2000).

oil diets, there was little difference in daily food intake between Suffolk and Friesland lambs, while Soay lambs had a similar intake (g DM/kg live weight$^{0.75}$) to Friesland lambs when offered the linseed plus fish oil diet.

Slaughter weight (kg) was lower in lambs fed the fish oil diet, although there was no significant effect of dietary treatment on carcass weight (kg). Soay lambs were observed to have a lower carcass weight than lambs from either of the other two breeds (mean cold carcass weights 19·3, 9·3 and 19·4 kg for Suffolk, Soay and Friesland lambs respectively; SED 0·30, $P<0·001$), while carcass fat and conformation scores were highest in Suffolk and lowest in the Soay lambs with Friesland lambs having intermediate values. Lambs fed either diet containing fish oil had higher fat scores than those offered either of the other two dietary treatments (mean fat scores 11·3, 10·3, 14·2 and 12·2 for lambs offered the control, linseed, fish oil or linseed plus fish oil diets respectively; SED 0·95, $P<0·01$). The content of lean in the forelimb joint (expressed as % forelimb weight) was lower in Suffolk lambs than those from either of the other two breeds ($P<0·01$). By contrast, % subcutaneous and forelimb intermuscular fat was significantly higher in Suffolk than Soay lambs ($P<0·05$).

Fatty acids

Longissimus dorsi. Total muscle fatty acid concentration ranged from 36·59 to 28·62 mg/g with no significant effect of either diet or breed (Table 3). Animals offered the linseed diet contained twice the intramuscular proportion of 18 : 3*n*-3 than those on the control diet, with lambs offered the linseed plus fish oil diet having intermediate values (mean proportions (×100) of 1·4, 3·1, 1·4 and 2·1 for lambs fed the control, linseed, fish oil or linseed plus fish oil diets respectively; SED 0·158, $P<0·001$). Both Suffolk and Soay lambs contained more 18 : 3*n*-3 than the Friesland lambs (mean proportions (× 100) of 2·09, 2·06 and 1·79, for Suffolk, Soay and Friesland lambs respectively; SED 0·158, $P<0·01$). The proportion of the long-chain *n*-3 fatty acids 20 : 5*n*-3, 22 : 5*n*-3 and 22 : 6*n*-3 in lambs fed the fish oil diet was more than threefold that of lambs offered the control diet, with lambs fed the linseed plus fish oil diet having intermediate values. By contrast, the proportion of the longer-chain *n*-3 PUFA was similar across all three sheep breeds.

Lambs fed the control diet contained the highest proportion (× 100) of 18 : 2*n*-6 (mean values 4·9, 4·0, 3·4 and 3·5 for lambs fed the control, linseed, fish oil or linseed plus fish oil diets respectively; SED 0·36, $P<0·01$). Likewise, the proportion of 20 : 4*n*-6 was highest in lambs fed the control diet. Soay lambs had higher intramuscular levels of all the major *n*-6 PUFA than Suffolk or Friesland lambs. The proportion (× 100) of CLA (*cis*-9,*trans*-11–18 : 2) in muscle was higher in the lambs offered the linseed and the linseed plus fish oil (mean values 1·0, 1·6, 1·1 and 1·7 for control, linseed, fish oil and linseed plus fish oil diets respectively; SED 0·12, $P<0·001$). There was also a breed effect, with the Soay lambs having a significantly higher proportion of CLA (mean values 1·2, 1·5 and 1·3 for Suffolk, Soay and Friesland lambs, respectively; SED 0·10, $P<0·05$).

Lambs offered the control diet had higher levels of the major monoenoic fatty acid, 18 : 1*n*-9, than lambs offered the linseed diet, which in turn had higher levels than lambs offered the fish oil or linseed plus fish oil diets (mean proportion (×100) of 34·1, 30·9, 25·9 and 27·4 for lambs fed the control, linseed, fish oil and linseed plus fish oil diets respectively; SED 1·04, $P<0·001$). By contrast, lambs offered diets containing fish oil had the highest proportion of 16 : 1*n*-7 and 18 : 1*n*-7. Friesland lambs had a higher proportion of 18 : 1*n*-9 than Suffolk lambs, which in turn had a higher proportion than Soay lambs. The content of *trans*-18 : 1 was significantly higher in lambs offered any of the diets with an added PUFA source (mean values 3·8, 6·6, 7·0 and 8·6; SED 0·53, $P<0·001$) for lambs fed the control, linseed, fish oil or linseed plus fish oil diets respectively. There were no significant differences between breeds for the muscle levels of *trans*-18 : 1.

The content of 16 : 0 was lower in lambs offered the linseed diet compared with those offered the control or fish oil diets, while Suffolk lambs contained a lower proportion of 16 : 0 than either of the two other breeds. Lambs fed either the control or linseed diets had the highest proportion (× 100) of the saturated fatty acid 18 : 0 (14·5, 14·2, 11·9 and 12·1 for lambs fed the control, linseed, fish oil or linseed plus fish oil diets respectively; SED 0·58, $P<0·001$) while Suffolk lambs had a higher proportion than Soay lambs, which in turn were higher than Friesland lambs (mean values 14·1. 13·1 and 12·5, respectively; SED 0·50, $P<0·01$).

Subcutaneous adipose tissue. There was a significant effect of diet on the total content of fatty acids (mg/g tissue) in the adipose tissue, with lambs offered the fish oil diet having a significantly lower content (mean values 798·01, 792·15, 753·72 and 798·35 for the control, linseed, fish oil and linseed plus fish oil diets, respectively; SED 12·915, $P<0·01$; Table 4). Soay lambs were also observed to have the greatest concentration of fatty acids in the adipose tissue, with Friesland lambs having the lowest value (means values 785·54, 804·67 and 766·62 mg/g for the Suffolk, Soay and Friesland lambs, respectively; SED 11·271, $P<0·01$). There was a significant interaction between breed and feed for the total content of fatty acids. Friesland lambs were observed to have the greatest content of fatty acids in the adipose tissue when offered the linseed plus fish oil diet, Soay lambs the greatest content when offered the linseed diet, whilst Suffolk lambs had the greatest content when offered the control diet ($P<0·001$).

Similar to that in muscle, the highest proportion (×100) of 18 : 3*n*-3 in the adipose tissue was observed in lambs offered the linseed diet, which was more than twice the level of lambs offered the control diet, while lambs offered the linseed plus fish oil diet had an intermediate level between those fed either the fish oil or linseed plus fish oil diets (mean values 1·3, 2·6, 0·9 and 1·5 for lambs fed the control, linseed, fish oil and linseed plus fish oil diets, respectively; SED 0·09, $P<0·001$). The highest content of 18 : 3*n*-3 was also observed in Suffolk lambs, although Friesland lambs were observed to have similar levels when offered either the linseed or fish oil diets

Table 3. Effects of dietary fat source and breed on the fatty acid composition (proportion (×100) of total fatty acids) and total fatty acid content (mg/g) of the *longissimus dorsi* muscle of sheep†

(Mean values)

Diet...	Control			Linseed			Fish oil			Linseed plus fish oil				Statistical significance of effect		
Breed...	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	SED	Diet	Breed	Diet × Breed
12 : 0	0·19	0·15	0·21	0·18	0·13	0·15	0·20	0·14	0·16	0·15	0·15	0·22	0·040	NS	NS	NS
14 : 0	2·53	2·52	2·61	2·38	2·52	2·30	2·68	2·70	2·60	2·31	2·74	2·64	0·303	NS	NS	NS
16 : 0	25·08	25·97	25·12	21·14	22·30	21·89	24·29	24·88	25·73	23·17	24·56	23·78	0·910	***	*	NS
16 : 1*n*-7	1·85	1·89	1·94	1·47	1·81	1·82	2·32	2·38	2·45	1·74	2·36	1·97	0·171	***	**	NS
18 : 0	14·65	15·07	13·81	15·55	14·85	12·37	12·47	11·18	12·12	13·41	11·37	11·67	1·033	***	**	NS
trans-18 : 1	3·82	4·23	3·44	6·41	5·93	7·50	8·10	7·06	6·01	9·03	9·10	7·64	0·949	***	NS	NS
18 : 1*n*-9	34·09	32·10	36·09	31·28	30·92	30·38	24·36	25·17	28·03	27·31	26·06	28·84	1·871	***	*	NS
18 : 1*n*-7	1·30	0·96	1·40	0·94	1·03	1·26	2·03	1·82	1·98	1·56	1·49	1·49	0·207	***	NS	NS
CLA‡	0·88	1·08	1·01	1·37	1·47	1·82	1·07	1·34	0·89	1·43	1·95	1·59	0·221	***	*	NS
18 : 2*n*-6	4·75	5·60	4·25	3·57	4·22	4·14	3·13	3·66	3·29	3·35	3·43	3·66	0·578	***	NS	NS
18 : 3*n*-3	1·44	1·73	1·16	3·13	3·16	2·99	1·43	1·54	1·15	2·28	1·82	1·86	0·283	***	*	NS
20 : 3*n*-6	0·12	0·13	0·13	0·08	0·09	0·12	0·17	0·21	0·17	0·09	0·13	0·11	0·025	***	*	NS
20 : 4*n*-6	0·99	1·14	1·24	0·66	0·97	0·94	0·59	1·08	0·72	0·68	0·90	0·96	0·239	*	NS	NS
20 : 4*n*-3	1·26	0·06	0·30	0·11	0·13	0·26	1·43	1·38	1·22	0·46	0·61	0·49	0·236	***	NS	*
20 : 5*n*-3	0·81	0·65	0·57	0·85	1·00	1·23	2·36	2·38	2·22	1·54	1·63	1·66	0·330	***	NS	NS
22 : 4*n*-6	0·06	0·05	0·10	0·06	0·04	0·08	0·10	0·05	0·05	0·01	0·04	0·04	0·021	NS	NS	NS
22 : 5*n*-3	0·70	0·63	0·62	0·69	0·70	0·84	1·37	1·27	1·24	1·02	1·05	1·00	0·138	***	NS	NS
22 : 6*n*-3	0·30	0·31	0·22	0·33	0·37	0·50	0·98	0·71	0·69	0·68	0·57	0·63	0·117	***	NS	NS
Total fatty acids (mg/g)	31·48	34·16	31·35	30·95	31·23	28·62	36·59	30·93	36·26	30·30	36·41	31·25	4·921	NS	NS	NS

CLA, conjugated linoleic acid.
*$P<0·05$, **$P<0·01$, ***$P<0·001$.
† For details of diets and procedures, see Table 1 and p. 698.
‡ *cis*-9,*trans*-11–18 : 2.

Table 4. Effects of dietary fat source and breed on the fatty acid composition (proportion (×100) of total fatty acids) and total fatty acid content (mg/g) of the subcutaneous adipose tissue of sheep†

(Mean values)

Diet...	Control			Linseed			Fish oil			Linseed plus fish oil				Statistical significance of effect		
Breed...	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	Suffolk	Soay	Friesland	SED	Diet	Breed	Diet × Breed
12 : 0	0·16	0·13	0·27	0·15	0·13	0·18	0·14	0·16	0·22	0·14	0·13	0·26	0·031	NS	***	NS
14 : 0	3·03	3·12	3·80	2·96	2·97	2·85	3·70	3·99	3·88	3·38	3·45	4·12	0·252	***	**	*
16 : 0	26·30	25·81	25·72	18·67	19·09	18·42	25·46	24·97	25·56	22·70	21·58	23·52	0·939	***	NS	NS
16 : 1*n*-7	1·72	2·30	2·28	1·52	1·90	1·90	2·94	3·03	3·29	1·97	2·56	2·30	0·148	***	***	NS
18 : 0	18·68	16·27	14·67	17·99	16·57	13·95	14·89	10·90	12·44	14·18	12·10	10·30	1·079	***	***	*
trans-18 : 1	4·82	6·23	5·01	11·22	8·88	12·27	11·11	11·64	9·23	15·53	13·19	13·54	1·031	***	NS	***
18 : 1*n*-9	28·87	29·87	29·96	24·92	27·80	26·27	18·97	21·21	23·59	19·51	21·81	22·17	1·152	***	***	NS
18 : 1*n*-7	0·69	0·66	0·81	0·62	0·61	0·79	1·48	1·29	1·51	0·99	1·03	1·00	0·068	***	***	*
CLA‡	0·79	1·32	1·05	1·57	1·96	2·10	0·71	1·78	0·85	1·40	2·56	1·74	0·162	***	***	***
18 : 2*n*-6	3·53	2·03	2·39	2·03	1·51	2·31	1·41	1·05	1·77	1·67	1·09	1·65	0·163	***	***	***
18 : 3*n*-3	1·68	1·09	1·05	3·04	1·93	2·93	0·93	0·85	0·89	1·94	1·02	1·48	0·151	***	***	***
20 : 5*n*-3	0·02	0·00	0·04	0·10	0·01	0·09	0·80	0·22	0·59	0·29	0·19	0·18	0·053	***	***	***
22 : 5*n*-3	0·11	0·06	0·08	0·20	0·09	0·19	0·95	0·40	0·70	0·44	0·37	0·32	0·066	***	***	***
22 : 6*n*-3	0·00	0·00	0·035	0·06	0·00	0·06	0·45	0·06	0·25	0·19	0·09	0·08	0·037	***	***	***
Branched chain fatty acids	4·21	5·64	6·98	3·26	6·22	4·22	3·60	6·43	3·79	3·09	3·60	8·41	1·30	NS	***	*
Total fatty acids (mg/g)	826·97	813·82	753·25	781·03	852·07	743·36	740·25	780·77	740·16	795·55	770·89	828·59	23·123	**	**	***

CLA, conjugated linoleic acid.
*$P<0·05$, **$P<0·01$, ***$P<0·001$.
† For details of diets and procedures, see Table 1 and p. 698.
‡ *cis*-9, *trans*-11–18 : 2.

Table 5. Effects of dietary fat source and breed on the polyunsaturated fatty acid:saturated fatty acid ratio, and *n*-3:*n*-6 fatty acids in the *longissimus dorsi* muscle in sheep† (Mean values)

	Diet effects						Breed effects				
Fatty acid ratio	Control	Linseed	Fish oil	Linseed plus fish oil	SED	Statistical significance of effect	Suffolk	Soay	Friesland	SED	Statistical significance of effect
P:S‡	0·15	0·18	0·12	0·14	0·013	***	0·15	0·16	0·15	0·011	NS
$\sum n\text{-}6:\sum n\text{-}3$§	2·08	0·94	0·68	0·78	0·247	***	1·02	1·15	1·21	0·119	NS
18 : 2*n*-6:18 : 3*n*-3	3·51	1·32	2·49	1·80	0·208	***	2·05	2·23	2·54	0·180	*

P, polyunsaturated fatty acid; S, saturated fatty acid.
*$P<0·05$, ***$P<0·001$.
†For details of diets and procedures, see Table 1 and p. 698.
‡P:S calculated as (18 : 2*n*-6 + 18 : 3*n*-3)/(12 : 0 + 14 : 0 + 16 : 0 + 18 : 0).
§*n*-6 : *n*-3 calculated as (18 : 2*n*-6 + 20 : 3*n*-6 + 20 : 4*n*-6 + 22 : 4*n*-6)/(18 : 3*n*-3 + 20 : 5*n*-3 + 22 : 5*n*-3 + 22 : 6*n*-3).

($P<0·001$ for the interaction between dietary fat source and breed).

The proportion ($\times 100$) of 18 : 2*n*-6 was low on all treatments, with an overall mean value of 1·9. Animals offered either of the diets containing fish oil had the lowest proportion of 18 : 2*n*-6, while those offered the control diet had the highest (mean values 2·6, 2·0, 1·4 and 1·5 for lambs fed the control, linseed, fish oil and linseed plus fish oil diets, respectively; SED 0·09, $P<0·001$). Soay lambs had the lowest proportion of 18 : 2*n*-6 when compared with either Suffolk or Friesland lambs (mean values 2·1, 1·4 and 2·03 for Suffolk, Soay and Friesland lambs, respectively; SED 0·08, $P<0·001$). There was a significant interaction between dietary fat source and breed, with Suffolk lambs fed the control diet having a higher proportion of 18 : 2*n*-6 than Friesland lambs.

Similar to that in the muscle, the content of *trans*-18 : 1 was greatest in lambs offered the linseed plus fish oil diet and lowest in those offered the control diet with animals offered either the fish oil or linseed diets having intermediate values (mean proportion ($\times 100$) of 5·4, 10·8, 10·6 and 14·1 for lambs fed the control, linseed, fish oil and linseed plus fish oil diets, respectively; SED 0·50, $P<0·001$). There was a significant interaction between diet and breed for the proportion of *trans*-18 : 1, with Soay lambs having the lowest value of the three breeds when offered the linseed diet, while Friesland lambs had the lowest value when offered the fish oil diet ($P<0·001$). Lambs offered the control diet had the highest level of 18 : 1*n*-9 while animals offered either diet containing fish oil (fish oil or linseed plus fish oil) had the lowest levels. Suffolk lambs were observed to have the lowest content of 18 : 1*n*-9 when compared with either of the other two breeds.

The proportion of CLA in the adipose tissue was significantly higher in lambs offered either of the diets containing linseed (mean values ($\times 100$) 1·0, 1·9, 1·1 and 1·9 for lambs fed the control, linseed, fish oil and linseed plus fish oil diets, respectively; SED 0·09, $P<0·001$). The proportion of CLA was also higher in Soay lambs than Friesland lambs, which in turn had higher values than Suffolk lambs (mean values 1·1, 1·9 and 1·4 for Suffolk, Soay and Friesland lambs, respectively; SED 0·08, $P<0·001$), although Friesland lambs were observed to have a similar content of CLA to Soay lambs, when fed the linseed diet ($P<0·001$ for the interaction between dietary fat source and breed).

Nutritional indices of the longissimus dorsi

There was no significant interaction between dietary fat source and breed on the 18 : 2 : 18 : 3 ratio, total *n*-6 : *n*-3 ratio or the PUFA : saturated fatty acid ratio and the mean values for the main effects are therefore presented in Table 5. Feeding the linseed diet significantly reduced the 18 : 2 : 18 : 3 and *n*-6 : *n*-3 ratios compared with lambs fed the control diet, while the provision of the fish oil diet resulted in the lowest *n*-6 : *n*-3 ratio. Lambs fed the linseed plus fish oil diet had 18 : 2 : 18 : 3 and *n*-6 : *n*-3 ratios intermediate between the linseed diet and fish oil diet. Suffolk lambs were observed to have a slightly lower 18 : 2 : 18 : 3 ratio compared with Soay lambs, which in

turn had a lower ratio than Friesland lambs ($P<0{\cdot}05$) although there was no significant effect of breed on the total *n*-6 : *n*-3 ratio. The PUFA : saturated fatty acid ratio was low on all dietary treatments although lambs fed the linseed diet were observed to have a significantly higher ratio than those offered the control diet, while the inclusion of fish oil was observed to reduce the PUFA : saturated fatty acid ratio.

Discussion

Animal performance

The lower food intake observed in lambs offered diets containing unprotected fish oil agrees with trends reported in the literature for sheep (Gulati *et al.* 1999) and dairy cows (Doreau & Chilliard, 1997*a*). By contrast, Offer *et al.* (1999) reported no significant effect on the DM intake of dairy cows after feeding 250 g fish oil/d, while Scollan *et al.* (2001) reported similar levels of performance in beef steers offered diets containing either protected fat, linseed or fish oil. The decrease in intake in lambs fed the fish oil diet may be attributed to a significant reduction in fibre digestion and microbial growth in the rumen reported by Wachira *et al.* (2000) in sheep fed similar diets to those reported in the present study. The increased fat classification of lambs fed the fish oil diet may also be attributed to a higher proportion of propionate in the rumen in lambs fed this diet (Wachira *et al.* 2000); this has been reported to favour lipogenesis and lead to fatter carcasses in lambs (Solomon *et al.* 1986).

The three breeds used were chosen to represent a range of genotypes. Suffolk lambs were used because they represent a major terminal sire breed for commercial lamb production, while Friesland lambs represent a breed selected for their milk production and have been shown to deposit fat differently from other sheep breeds (Zygoyiannis *et al.* 1990). Soay lambs were used as they represent a more feral breed that has been shown to have a high proportion of lean and, when finished on grass, flavour characteristics that differ markedly from those of other breeds (Fisher *et al.* 2000). The lower voluntary food intake and live-weight gain of Soay lambs are in agreement with those reported in a number of other studies (e.g. Sinnett-Smith & Woolliams, 1988). It is recognised that there is a seasonal depression in both voluntary food intake and digestibility and that this effect appears to be greater in northern latitude seasonal breeders, such as the Soay (Kay, 1979; Iason *et al.* 1994; Argo *et al.* 1999). However, lambs in the current experiment were finished indoors during the summer (May to September) when seasonal effects of the photoperiodic cycle would be expected to result in the greatest proportional intake by the Soay lambs (Argo *et al.* 1999).

Ewe-type breeds have a greater content of internal fat and consequently a lower content of subcutaneous fat than meat-sire breeds (Wood *et al.* 1980; Beriain *et al.* 2000), a result in accordance with the differences between Suffolk and Friesland lambs in the current study. However, the major differences in carcass characteristics could be attributed to the Soay lambs, which were typified as having low subcutaneous fat, low intermuscular fat and a higher proportion of lean body mass. Similar findings were reported by McClelland *et al.* (1976), Thonney *et al.* (1987) and Fisher *et al.* (2000), where Soay lambs were found to have a higher proportion of lean tissue and a reduced content of fat. Sinnett-Smith & Woolliams (1988) reported that breed differences in the fatness of sheep were a consequence of different balances of anabolic and catabolic processes in adipose tissue with a unique pattern for each breed.

Muscle fatty acids

Feeding whole linseeds lead to a muscle fatty acid composition similar to those reported in beef animals receiving grass silage supplemented with linseed (Scollan *et al.* 2001) and in lambs grazing grass (Enser *et al.* 1998; Rowe *et al.* 1999; Fisher *et al.* 2000), although the relative proportions of *n*-3 PUFA were higher in the current study. The increases in muscle PUFA reported here are also greater than those reported by Solomon *et al.* (1991) and Lough *et al.* (1992), who fed whole oil seeds to sheep. However, their animals were slaughtered at a greater live weight than those in the current study. Heavier, fatter carcasses contain a greater proportion of neutral lipids, which are more saturated, in relation to phospholipids, which have a greater content of PUFA (Ashes *et al.* 1992). The proportion of neutral lipids can vary from <1 to >30 % tissue weight, although for UK meat 5 % is rarely exceeded (Enser & Wood, 1997). By contrast, the content of phospholipids is relatively constant and comprise between 0·5 and 1·0 % muscle weight. Compared with lambs fed the control diet, the increased muscle content of 18 : 3*n*-3 in lambs fed the linseed diet reflects the doubling of the duodenal flow of 18 : 3*n*-3 reported by Wachira *et al.* (2000), with lambs fed the linseed plus fish oil diet having intermediate values for both duodenal flow and muscle fatty acid content. Similarly, the levels of 20 : 5*n*-3 and 22 : 6*n*-6 were approximately three times greater in lambs offered the fish oil diet compared with those on the control diet, which again reflects the greater duodenal flow (Wachira *et al.* 2000).

There was some evidence that elongation and desaturation of 18 : 3*n*-3 had occurred, with increased concentrations of 20 : 5 (eicosapentaenoic acid) occurring in the animals fed linseed compared with those fed the control diet. However, the levels of 22 : 5*n*-3 and 22 : 6*n*-3 were only slightly higher in the animals fed linseed, confirming the results in beef showing that limited conversion to these longer-chain products occurs (Scollan *et al.* 2001). One factor which influences these conversions is the 18 : 2 : 18 : 3 ratio in absorbed lipid, since both *n*-6 and *n*-3 fatty acids compete for the same enzymes during chain elongation and desaturation (Brenner, 1989). Nevertheless the results clearly show that high tissue concentrations of 20–22-*n*-3 PUFA can more easily be obtained by feeding fish oil than by encouraging chain elongation by feeding linseed.

Muscle levels of 18 : 2*n*-6 were highest in lambs fed the control diet, reflecting the differences in dietary concentration and flow at the duodenum (Wachira *et al.* 2000).

The lowest muscle content of 18 : 2*n*-6 was, however, achieved in animals fed the fish oil diet, an effect that cannot be explained by dietary differences alone. This effect of fish oil on muscle 18 : 2*n*-6 was in contrast to its lack of effect on 18 : 3*n*-3 levels and probably results from the difference in lipid class distribution of the two fatty acids in muscle: 18 : 3*n*-3 mainly in triacylglycerols, which, in ruminant animals, contain relatively little longer-chain PUFA and 18 : 2*n*-6 mainly in phospholipids where it competes for incorporation with longer-chain PUFA such as the fish oil fatty acids. The levels of 20 : 4*n*-6 in muscle followed the pattern for 18 : 2*n*-6, with more in the control than the other three treatments, which had similar amounts. The high 18 : 3 : 18 : 2 ratio in the linseed diet lowered both 20 : 3*n*-6 and 20 : 4*n*-6 in accordance with the expected competition between the two C_{18} fatty acids for Δ^6-desaturase. Fish oil, in contrast, decreased 20 : 4*n*-6 but increased 20 : 3*n*-6. This is in accordance with evidence reported by Ashes *et al.* (1992) that fish oil did not inhibit Δ^6-desaturase in sheep, contrary to the findings in rodents (Brenner, 1989).

Although there was no significant effect of breed on muscle fatty acid composition, the proportion of 18 : 2*n*-6 and 18 : 3*n*-3 tended to be higher in muscle from Soay lambs, a result in agreement with Fisher *et al.* (2000). In the earlier work, the *semimembranosus* muscle was examined and Soay lambs had a very low concentration of total fatty acids (16·68 mg/g), which will have been partly responsible for high proportions of PUFA since the phospholipid fraction was more significant. The phospholipid : neutral lipid ratio is also greater in red muscles such as *semimembranosus* than white muscle such as *longissimus dorsi* (Turkki & Campbell, 1967). In the present study, total fatty acid content in *longissimus dorsi* was not different between the breeds, which is surprising given the low level of carcass subcutaneous fat in Soay lambs (Table 2). A further difference between this present study and that of Fisher *et al.* (2000) is that their lambs were from differing grazing systems. There is a large variation in the fatty acid composition of grass between varieties and times of year (Dewhurst & King, 1998), which will subsequently affect the fatty acid composition of the sheep meat produced.

Many factors may contribute to the dietary effects on tissue levels of 18 : 1*n*-9 and make a full understanding of the mechanism difficult. The control group had the highest intake of 18 : 1*n*-9 and contained the highest muscle concentration. However, differences in rumen metabolism cannot explain why the amounts in the muscle of the linseed fed-lambs were higher than in those fed fish oil as these diets contained similar quantities of 18 : 1*n*-9 and this was reflected in the duodenal flows (Wachira *et al.* 2000). Competitive exclusion of 18 : 1*n*-9 from phospholipids by other more unsaturated fatty acids will account for some of the differences, since the amounts of C_{20} and C_{22} PUFA incorporated from fish oil were greater than those synthesised from 18 : 3*n*-3 in linseed. However, this cannot provide the whole explanation, since phospholipids in sheep *longissimus dorsi* comprise only about one-third of the lipid and contain a lower proportion of 18 : 1*n*-9 than the triacylglycerols. The fatty acid composition of the adipose tissue can be taken as an index of the availability of saturated and monounsaturated fatty acids for incorporation into the intramuscular fat. In lambs fed the diets containing fish oil, the adipose tissue concentrations of 18 : 0 were lower than in those offered the control or linseed diets, suggesting that the low 18 : 1*n*-9 might have resulted from a decreased substrate availability.

In general, the content of CLA in the intramuscular lipid followed the pattern for *trans*-18 : 1 from which most of it is probably formed by Δ^9-desaturase (for review, see Enser, 2001). The regressions of CLA (g/100 g lipid) *v.* CLA + 18 : 1 (g/100 g lipid) (Fig. 1) across feeds within breeds were similar for the Soay and Friesland lambs ($y = 0{\cdot}1543x + 0{\cdot}1737$, R^2 0·6891 and $y = 0{\cdot}1444x + 0{\cdot}2991$, R^2 0·7915 for Soay and Friesland lambs, respectively). However, the regression for the Suffolk lambs revealed a lower content at higher substrate levels ($y = 0{\cdot}078x + 0{\cdot}5682$, R^2 0·2986). Since the proportions of 16 : 1 were also lower in the Suffolk lambs in both muscle and adipose tissue, then breed differences in Δ^9-desaturase activity could produce such an effect.

The levels of 12 : 0 and 14 : 0 in muscle were not influenced by diet. However, 16 : 0 constituted a significantly higher ($P < 0{\cdot}01$) proportion of the total fatty acid content in lambs offered the control and fish oil diets. These two treatments had the highest dietary 16 : 0 content owing to the inclusion of a protected palm oil source in the control diet and the fact that fish oil contains a relatively high content of saturated fat, of which 16 : 0 is a major fatty acid (Enser, 1991). In contrast to the current findings, diets containing protected fish oil or fishmeal had no significant effect on the proportion of 16 : 0 in muscle fatty acids in some studies (Ashes *et al.* 1992; Mills *et al.* 1992), although feeding fishmeal was reported to increase tissue 16 : 0 tissue levels in the work of Mandell *et al.* (1997). It is also possible that in the current work, feeding lambs diets containing linseed decreased *de novo* fatty acid synthesis (Doreau & Chilliard 1997*b*).

Adipose tissue

The long-chain C_{20} and C_{22} fatty acids were present at very low levels in the subcutaneous adipose tissue of lambs fed any of the dietary treatments. This may be attributable to the low proportion of phospholipid in adipose tissue as well as a low incorporation of long-chain fatty acids into the triacylglycerol fraction in ruminant animals (Storry *et al.* 1974; Ashes *et al.* 1992; Enser *et al.* 1996). The adipose tissue of lambs fed the linseed diet contained more than twice the level of 18 : 3*n*-3 compared with that of lambs fed the control diet or that reported in lambs at retail (Enser *et al.* 1996). This reflects a doubling in flow of 18 : 3*n*-3 at the duodenum for animals fed the linseed compared with the control diet as discussed previously. There is also evidence to suggest that in ruminant animals 18 : 3*n*-3 is preferentially deposited in triacylglycerol rather than in membrane lipids compared with 18 : 2*n*-6 (Marmer *et al.* 1984; Enser *et al.* 1996), a result in accordance with the current findings, where the overall 18 : 2*n*-6 : 18 : 3*n*-3 ratio was 1·2 in the subcutaneous adipose tissue and 2·0 in the *longissimus dorsi*.

Published effects of sheep breed on fatty acid composition

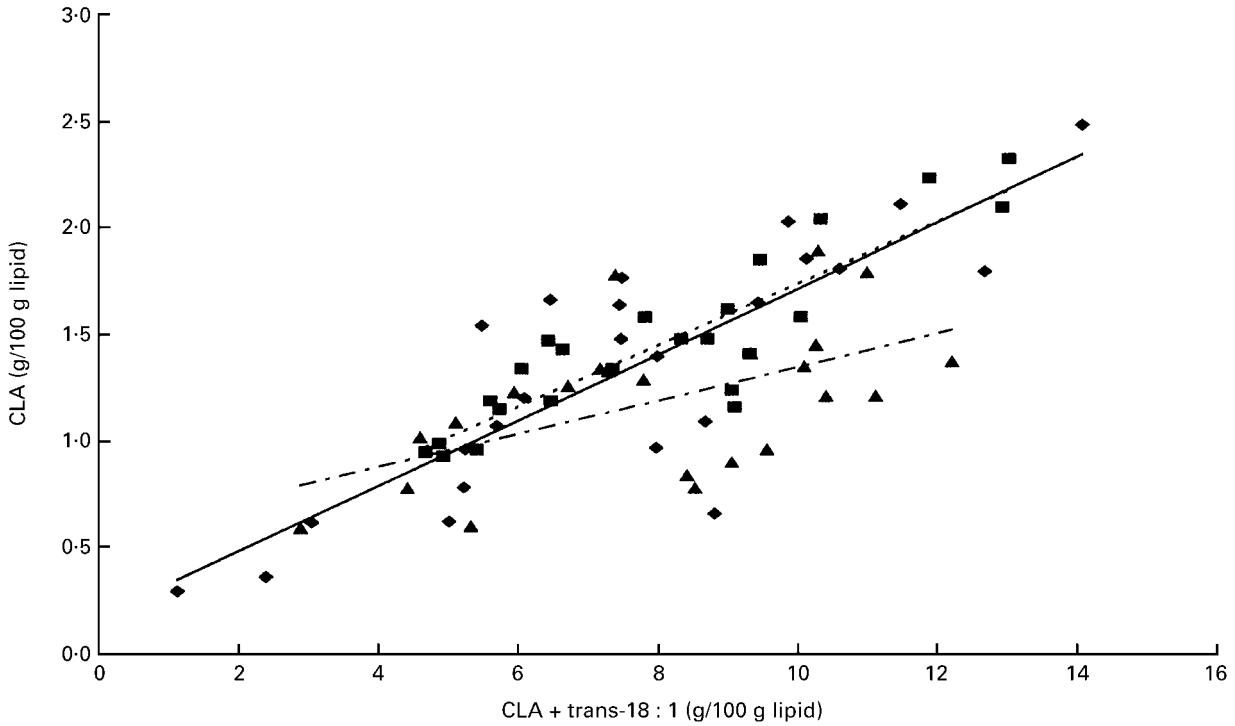

Fig. 1. Effect of breed of sheep on the relationship of muscle conjugated linoleic acid (CLA) (g/100 g lipid) to CLA + trans-18 : 1 (g/100 g lipid). For details of diets and procedures, see Table 1 and p. 698. (---■---), Soay lambs; (—◆—), Friesland lambs; (-–-▲-–-), Suffolk lambs.

of the subcutaneous adipose tissue are equivocal. In the current work, Soay lambs contained a lower proportion of both 18 : 2*n*-6 and 18 : 3*n*-3 in the subcutaneous adipose tissue than lambs from the other two breeds. In contrast, Cameron *et al.* (1994) found little difference in the subcutaneous fatty acid composition of Texel–Oxford or Scottish Blackface lambs, although within-breed selection for increased lean content was associated with a trend towards lower concentrations of 18 : 2*n*-6 and 18 : 3*n*-3. Webb & Casey (1995) reported differences in 14 : 0, 17 : 1 and 18 : 1 fatty acid composition of adipose tissue between Dorper and SA Mutton Merino wether lambs, although these differences largely disappeared when the two breeds were slaughtered at equal body fatness. By contrast, other workers have reported significant differences in the subcutaneous fat composition of cattle (e.g. Choi *et al.* 2000).

The values for CLA found here are greater than those in beef muscle reported by Enser *et al.* (1999) (0·3–0·8 g/100 g fatty acids). The work of Enser *et al.* (1999) showed, as here, that adding *n*-3 PUFA to the diet increased CLA levels in tissues. This could occur as the result of impaired biohydrogenation of linoleic acid in the rumen, leading to increased CLA itself or increased production of *trans*-11–18 : 1 from which CLA can be produced in tissues (Griinari *et al.* 2000; Santora *et al.* 2000). The adipose tissue content of *trans*-18 : 1 follows the pattern we have reported previously for the duodenal concentrations in lambs fed the same diets (Wachira *et al.* 2000). The higher concentration of CLA after feeding linseed compared with the control diet fits a product–precursor pattern and strong linear correlations between *trans*-18 : 1 and CLA have been reported (Jiang *et al.* 1996; Jahreis *et al.* 1997; Enser *et al.* 1999). However, mixing linseed and fish oil in the feed gave the highest concentrations of *trans*-18 : 1 in the adipose tissue, but the amounts of CLA were similar to those in lambs fed the linseed diet. Adipose tissue *trans*-18 : 1 was also much higher in animals fed the fish oil alone compared with the control diet, yet the CLA levels were comparable. Thus, fish oil appeared to depress the level of CLA relative to *trans*-18 : 1. Since fish oil also decreased 18 : 1*n*-9, an inhibition of Δ^9-desaturase could be responsible for both effects. The results for breed showed that the Soay lambs had higher concentrations of CLA than Suffolk or Friesland lambs although the concentration of *trans*-18 : 1 was not significantly different. This breed effect on CLA is therefore difficult to explain.

Human nutrition

There are three factors that are generally considered to be important when judging the nutritional value of fatty foods: total fat content, the PUFA:saturated fatty acid ratio and the *n*-6:*n*-3 ratio (Department of Health, 1994). In the current work, although Soay lambs were shown to have a considerably lower carcass fat score, the content of fat in the *longissimus dorsi* was not significantly affected by either breed or diet. Similarly, there was little difference between breeds in the PUFA:saturated fatty acid ratio. Although feeding linseed was observed to increase the PUFA:saturated fatty acid ratio to a value closer to that of 0·45 recommended by the Department of Health (1994), the inclusion of fish oil was observed to depress it. However, even in

lambs fed the fish oil diet the PUFA:saturated fatty acid ratio was similar to the 0·12 reported in the *longissimus* of grass-finished Suffolk-cross lambs (Enser *et al.* 1998). The greatest effect of including dietary PUFA sources was on the 18:2*n*-6 : 18:3*n*-3 and *n*-6:*n*-3 ratios. The values reported are considerably lower than the ratio of 4·0 recommended by the Department of Health (1994), with linseed diets in particular reducing the former, and fish oil diets reducing the latter. It can be argued that these beneficial changes offset the low PUFA:saturated fatty acid ratio because ruminant animal products and oily fish represent the only significant sources of preformed *n*-3 fatty acids, particularly 20*n*-3 and 22*n*-3 fatty acids, in the diet of man (Gregory *et al.* 1990; Enser *et al.* 1996). Indeed, if it is assumed that an average portion of lamb is 100 g (Ministry of Agriculture, Fisheries and Food, 1994) then, as part of a balanced diet, muscle from lambs fed the fish oil diet would increase the daily intake of eicosapentaenoic acid and docosahexaenoic acid by 105 mg, half the recommended daily level of 200 mg long-chain *n*-3 PUFA recommended by the Department of Health (1994).

Compared with lambs fed the control diet, lambs fed diets high in PUFA had significantly higher levels of *trans* fatty acids in the *longissimus dorsi*, particularly in those fed the linseed plus fish oil diet. In man, *trans* fatty acids may have an undesirable effect not only on plasma low-density and high-density cholesterol, but also on lipoprotein(a) and CHD mortality (Department of Health, 1994). However, as part of a complete diet, the intake of *trans* fatty acids from a daily serving of lamb from animals finished on the linseed plus fish oil diet would contribute less than 0·14 % to daily energy intake, a value considerably less than the daily limit of 2 % recommended by the Department of Health (1994). In addition, epidemiological evidence (Willett *et al.* 1993) suggests that rumen-derived *trans* unsaturates (mainly vaccenic) are not risk factors for cardiovascular disease. The increased tissue levels of CLA that accompany the *trans*-18 : 1 may make a positive contribution to human health, but optimal dietary intakes remain to be established and at present there are wide variations in the suggested effective levels (Knecht *et al.* 1996; Finnegan & Williams, 2001).

In conclusion, the inclusion of fish oil in the diet depressed food intake and growth rate, but did not affect food conversion ratio. Compared with the control diet, the levels of 18 : 3*n*-3 in the *longissimus dorsi* were doubled by the addition of whole linseed, whilst 20 : 5*n*-3 and 22 : 6*n*-3 levels were increased threefold by the inclusion of fish oil, with proportional increases in the mixed diets. While there were large differences between breeds in their performance, the effects of breed on fatty acid composition were relatively small in comparison with the effects of diet. The deposition of CLA in muscle and adipose tissue of lambs was affected by both breed and dietary lipid source.

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