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Effects of index selection on the performance and carcass composition of sheep given foods of different protein concentrations *ad libitum*

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Abstract

Sheep of a line selected on an index to increase carcass lean content at 150 days of age (selected (S); no. = 90), and an unselected control line (control (C); no. = 90), were given *ad libitum* foods of three different protein concentrations (192, 141 and 120 g/kg dry matter). Growth was measured from about 21 to 114 kg live weight. The carcasses of each line were analysed for lean, fat and bone at three widely varying weights in both males and females. Level of protein did not affect the extent to which S was superior to C in the content of fat (0.86 as much) or lean (1.08 as much) in the carcass. The fat concentration of the carcass increased, and the lean concentration decreased, as dietary protein concentration was reduced ($P < 0.01$). On the highest level of protein used, the S line grew 1.17 times as fast and was 1.10 times as efficient compared with C. The extent to which growth rate in S exceeded that in C was greater on the highest level of protein used (92.3 g/day) than on the two lower protein diets (26.4 g/day). The difference of 65.9 (s.e. 18.4) g/day was significant ($P < 0.01$). On the diet of highest protein concentration, growth was well described by a Gompertz function. The S line had an estimated maximum growth rate 1.25 times that of the C when averaged across males and females. A Spillman function was used to describe weight in terms of cumulative intake. It worked well for all three levels of dietary protein concentration. S sheep performed better than unselected sheep on foods differing in protein concentration and over a wide range of live weights, suggesting benefits are likely within the diverse farming environments found in practice.

Keywords: carcass composition, dietary protein, genotype environment interaction, sheep.

Introduction

Excess fat in lamb carcasses produced in the United Kingdom (Kempster, 1983; Woodward and Wheelock, 1990) and in other countries (Fennessy *et al.*, 1993; Beauchemin *et al.*, 1995) has contributed to a reduction in lamb consumption. Changes to both breeding and finishing systems have the potential to bring about a reduction in the fatness of lamb, which could increase acceptability to consumers.

Simm and Dingwall (1989) suggested a genetic approach to redress the problem of over-fatness in lamb. They proposed a selection index designed to improve the rate of lean growth, which combined live weight and ultrasonic measures of fat and muscle depth. When the index was used in selection

in a flock of Suffolk sheep at the Scottish Agricultural College (SAC), substantial responses in each of the selection criteria were achieved after 9 years of selection (Simm *et al.*, 2002). As anticipated, these genetic changes produced consequential changes in the measured composition of the carcass (Lewis *et al.*, 2002b). In the selected line, carcass fatness was 0.86 and the ratio of lean to fat in the carcass was 1.28 of the values seen in the control line at a given live weight.

The selection flock was offered *ad libitum* a food with high concentrations of both protein and energy to allow any genetic differences between animals for lean growth and fatness to be manifested (Simm *et al.*, 2002). However, in commercial systems, lambs

are often reared on grass. Crossbred lambs sired by high index rams from the SAC Suffolk flock showed improved carcass composition when reared in this way (Lewis *et al.*, 1996; Simm and Murphy, 1996; Jones *et al.*, 1999). However, the observed improvement was lower than anticipated. Thus, there may be an interaction between the genetic lines of sheep and protein level.

Lewis *et al.* (2002b) investigated whether differences between Suffolk lines at SAC persisted across different levels of allowance of a food of high quality. They found that level of feeding did not affect the extent to which the selection line was superior to its control in either the level of fatness in the carcass, or the ratio of lean to fat. However, the advantages to the selection line in growth rate and efficiency showed an interaction with level of feeding such that they became virtually zero at the lowest level used. The purpose of the work reported here is to extend that investigation to the nutritional variable of dietary protein concentration on *ad libitum* feeding.

Fluharty and McClure (1997) found that a higher level of protein than that recommended for feeder lambs by National Research Council (1985) increased food intake, growth rate and food efficiency. Haddad *et al.* (2001) found that Awassi lambs given diets that contained below 160 g/kg of protein grew more slowly than those on higher levels, and that intake increased with increasing protein level. The effects of low dietary protein concentrations in lambs are thus expected to be lower growth rate, reduced rate of food intake and lower food efficiency. The expected effects on carcass composition are not so well defined in the literature. However, in monogastric animals a reduction in dietary protein concentration is expected to lead to a higher fat concentration in the gain (for example Kyriazakis and Emmans (1991) and Kyriazakis *et al.* (1991)).

The objective of the work reported here was to test whether selection decisions based on the lean growth index of Simm and Dingwall (1989) have produced changes in live and carcass characteristics that persist when the level of dietary protein is lower than that used during selection. The data collected were also used to explore the relationships between weight and time, and weight and cumulative food intake, as affected by line and level of dietary protein concentration.

Material and methods

Suffolk selection experiment

The Suffolk selection experiment at SAC has been fully described elsewhere (Simm *et al.*, 2002). Only a brief summary is given here. After weaning at 56

days of age, the sheep were given *ad libitum* access to a complete pelleted ration with high energy and protein concentrations (food H in Table 1). Measurements on live weight and ultrasonic muscle and fat depths, made at 150 days of age at the end of the performance test, were combined into a selection index. The index was designed to increase the rate of lean deposition whilst restricting the rate of fat deposition (Simm and Dingwall, 1989). The selection (S) line was chosen to have high index scores and the control (C) line to have average scores.

Lambs and management

The lambs used were produced by artificial insemination. About one-third of the 158 S and 129 C line ewes available were inseminated on each of three dates (21, 25 and 31 August 1995). The six rams used from each line had been chosen from the 1994 lambing of the Suffolk flock at the end of the ninth performance test.

Ewes were managed as a single flock and housed 6 weeks before lambing. Within 1 day of birth, the weight and sex of each lamb was recorded. All lambs were reared as singles or twins. Within a week of birth, lambs were offered free access to the same food as that used in the performance test. From 2 weeks of age, lambs were weighed on Thursday each week starting at 10:00 h.

Table 1 Composition of the diets used

	Diet		
	High	Medium	Low
Ingredient (g/kg)			
Barley	582.5	504.2	464.0
Dried grass	200.0	66.7	0.0
Oatfeed	0.0	31.0	46.7
Citrus pulp	0.0	233.0	350.0
Hipro soya-bean meal	70.0	34.4	16.7
Fish meal	60.0	20.0	0.0
Molasses	50.0	63.0	70.0
Protected fat	0.0	11.0	16.6
Mineral and vitamin mix	37.5	36.7	36.0
Chemical composition			
Dry matter (DM; g/kg)	880	882	878
Crude protein (g/kg DM)	192	141	120
NDF (g/kg DM)†	242	228	212
AHEE (g/kg DM)†	26	30	28
Ash (g/kg DM)	87	81	73
NCGD (g/kg)†	789	826	845
Metabolizable energy (MJ/kg DM)‡	11.7	12.3	12.5

† NDF = neutral-detergent fibre; AHEE = acid hydrolysed ether extract; NCGD = neutral cellulase gamanase digestibility.

‡ Predicted from 0.014 NCGD + 0.025 AHEE (Thomas *et al.*, 1988).

Only those lambs reared by their birth dam were included in the experiment. Once a female or male lamb reached a target weight of 19.0 or 22.0 kg, respectively, or a lamb was 8 weeks of age (whichever came first), it was weaned. All lambs were group penned and allowed free access to the high protein diet (Table 1). Once a lamb was 2 kg more than its target weaning weight, it was shifted to an individual pen (1.52 × 1.40 m) with slatted floors and, where prescribed, gradually shifted to a new diet (described latterly) over the next week. Weekly records of *ad libitum* intake were started at this time. The mean starting weights were 21.7 (s.d. 0.95) kg for females and 24.2 (s.d. 0.94) kg for males.

On the days when live weights were taken, the residual food was also collected, weighed and discarded.

Carcass evaluation

The details of carcass evaluation were presented by Lewis *et al.* (2002b). Lambs were grown to three slaughter weights chosen as described below. On reaching their target weight they were slaughtered and processed at the SAC Carcass Evaluation Unit. The carcasses were frozen. After defrosting, the left side of each carcass was dissected into lean, fat (subcutaneous and intermuscular), bone (vertebral and other) and waste components.

Experimental design

Three levels of dietary protein (high (H), medium (M) and low (L)) were used (Table 1). Animals were offered food twice daily (at 8:30 and 15:30 h). The level of food given was such that there were always food refusals. Samples of the food offered and bulked refusals were analysed for dry matter (DM) weekly. Although the food refusals had a lower DM concentration than that offered (873 v. 880 g/kg), the difference across foods was small. For this reason, intakes were reported on an as-fed basis. Lambs were also offered about 150 g of poor quality hay (794 g/kg DM; 108 g/kg DM crude protein; 407 g/kg DM modified acid-detergent fibre; 69 g/kg DM ash) at each morning feeding. Most animals ate all their hay allowance in most weeks. The reported food intakes excluded hay.

Experiment 1 was of a full factorial design with two lines (S and C), two sexes (ram and ewe lambs), two levels of dietary protein (high (H) and medium (M); Table 1) and three slaughter points (SP3, SP4 and SP5). The weights at SP4 approximated that at the selection age of 150 days: 66.0 kg for males and 57.5 kg for females. The weights at SP3 were 38.0 kg for males and 33.0 kg for females and at SP5 114.0 and 100.0 kg, respectively. The weights at SP3 and

SP5 were equidistant from SP4 on a logarithmic scale so that the proportional difference in weight between SP3 and SP4 was the same as that between SP4 and SP5. There were 5 replicates for each treatment at SP3 and SP5 and 10 at SP4 giving 160 animals in total.

Experiment 2 used the rams of both lines given high (H), medium (M) and low (L) and taken to SP3 and SP4. There were five replicates of each of the 12 treatments except that there were 10 on the H and M dietary protein levels at SP4 giving a total of 80.

Derived variables

For consistency, the starting weight (actual weaning weight) of each lamb was called SP2 although none was slaughtered at this weight. For each animal present for an interval (SP2 to SP3, SP3 to SP4 and SP4 to SP5) gain in live weight (ADG; g/day), food intake (ADI; g/day), and the food efficiency (EFF = $1000 \cdot (\text{ADG}/\text{ADI})$; g/kg) were calculated. Live weight was related both to time and cumulative food intake from the starting weight. The data were edited so that the same animals contributed information at all weeks considered, to avoid bias. This was done by using data only up to the week that the first animal on a treatment reached slaughter.

The carcass yield (KO; expressed as % to be consistent with the industry norm) was calculated as the ratio of cold carcass weight to pre-shorn live weight. The weights of lean and total fat (the sum of subcutaneous and intermuscular fat) were expressed as proportions of the carcass side weight (g/kg). In addition, the proportion of total fat as subcutaneous fat (pSQFAT) and the ratio of lean to bone weight (LEAN : BONE) were calculated.

Statistical methods

In preliminary analyses, the residual maximum likelihood procedure (REML, Genstat 5 Committee, 1998) was used to fit a linear model to describe the derived variables. REML was used, as the data were unbalanced for some of the fixed effects tested. Initially, rearing type (as single or multiple), rearing category (weaned at target weaning weight or at 8 weeks of age) and genetic dam age (2, 3, 4 or 5 years of age), and the linear covariate of day of birth were included in the model in addition to treatment effects. None of these effects defined substantial variation in any of the measurements and significance at $P < 0.05$ was rare. The final model fitted therefore included only the treatment effects. These were line and level of diet protein concentration and, where appropriate, sex and slaughter point. All interactions between the treatment factors were also fitted.

Of the diets used in experiment 2 (H, M and L; Table 1) only H might allow maximum growth rate to be achieved by both lines. It was expected that on the two 'inadequate' diets (M and L) growth rate would not differ between the lines (Griminger and Scott, 1959) but that on an 'adequate' diet (H) the S line might well grow faster than the C. Data for the M and L diets were combined to contrast the lines on adequate and inadequate diets.

The experiments were analysed on the assumption that variances were homogeneous. While heterogeneity could be anticipated where controlled feeding was used, as was the case with Lewis *et al.* (2002b), this was not so with *ad libitum* feeding.

Weight by time and cumulative food intake. The values of the parameters of the Gompertz growth function were estimated for the H treatment using treatment mean data from the starting weight to SP5. The function used was

$$W = A \exp(-\exp(G_0 - Bt)) \quad (1)$$

where W is live weight (kg) and t is time (days), and the parameters A and B are the asymptotic weight (kg) and a rate parameter (per day). The third parameter, G_0 , is transformed initial weight given by $\ln(-\ln(W_0/A))$ and W_0 (kg) is the weight at $t = 0$. However, the estimates of A and B were found to be very highly correlated in agreement with Lewis *et al.* (2002 a and b). Using a second form of the Gompertz function, equation (2), reduced the problem of correlation.

$$W = (Z/B) \exp(-\exp(G_0 - Bt)) \quad (2)$$

The term (Z/B) is A . The lumped parameter Z , where $Z = (A/B)$, has a biological interpretation in that Z/B is the maximum daily growth rate (kg/day). As there is no *a priori* reason to expect the sheep on M and L to grow at a fixed proportion of their potential, the function was not used for their data.

Weight was plotted against cumulative food intake for all treatments and the values of the parameters of the Spillman function estimated. The function (see page 26 of Parks (1982)) is:

$$W = W_0 + (A - W_0) [1 - \exp(-kF)] \quad (3)$$

where F is cumulative food intake (kg) from the start of treatment, and A , k and W_0 are the parameters to be estimated. The parameter W_0 corresponds with the weight at which the food treatments began. It was found that the estimates of A and k were highly

correlated so the values of the lumped parameter (Ak) are also reported.

Environmental sensitivity

Genotypes may differ in their sensitivity to their environment. This can be tested by regression (Falconer, 1989). Following Lewis *et al.* (2002b) a least-squares procedure was used to obtain the mean performance across line on each dietary protein level, i.e. to estimate the environmental means across the two lines. The data used were ADG_{34} , ADI_{34} and EFF_{34} in experiment 2. The mean levels of performance of each line on the three levels of protein were also estimated. The line means, Y , were then regressed on the environmental (diet protein concentration) means, E , using the regression model:

$$Y = a + bL + (c + dL)E \quad (4)$$

where $L = 0$ for S line and 1 for C line, and E is environmental mean across lines. The difference of the value of the parameter d from zero tests whether the two lines differ in their environmental sensitivity.

Results

Experiment 1

Growth, food intake and efficiency between slaughter weights. On average, female lambs grew at 0.808 of the rate of males, ate 0.849 as much food and were 0.954 as efficient (all $P < 0.01$). As shown in Table 2, the S line grew faster over the range of weights considered and was more efficient than C irrespective of dietary protein level. Food intake did not differ between the two lines ($P > 0.20$). On M, intake, growth rate and efficiency were all reduced compared with H in the first two periods ($P < 0.01$). In the final period the differences became small and

Table 2 Growth and food intake in experiment 1 between successive slaughter points 2, 3, 4 and 5 by line (selected (S) and control (C)) and protein level (high and medium)

	High		Medium		s.e.
	S	C	S	C	
Variable†					
ADG_{23} (g/day)	438.3	395.2	308.9	288.8	8.38
ADI_{23} (g/day)	1461	1445	1335	1340	17.9
EFF_{23} (g/kg)	300.1	272.8	230.9	215.6	5.52
ADG_{34} (g/day)	439.3	378.1	328.0	310.8	11.25
ADI_{34} (g/day)	2350	2274	2043	2039	30.2
EFF_{34} (g/kg)	185.5	165.2	159.4	151.8	3.94
ADG_{45} (g/day)	255.9	203.6	243.5	220.3	15.31
ADI_{45} (g/day)	2564	2256	2423	2251	84.0
EFF_{45} (g/kg)	98.5	90.5	100.2	97.5	3.62

† ADG = average daily gain; ADI = average daily intake; EFF = efficiency (1000 ADG/ADI).

Table 3 Values of the parameters of the Gompertz growth function $W = (Z/B) \exp(-\exp(G_0 - Bt))$ for lambs given the high protein diet in experiment 1†

Line	Sex	A (kg)‡	1000B (per day)	Z (kg/day)	G_0	Residual s.d. (kg)
Selected	Male	119.9	11.42	1.370	0.4297	0.258
	Female	102.0	10.86	1.108	0.4339	0.258
Control	Male	110.3	10.59	1.168	0.3934	1.583
	Female	98.4	8.45	0.831	0.3657	0.741

† s.e. values are not included as the estimates of the parameter values are highly correlated and thus their s.e. values are misleading.

‡ Estimated from equation (1) in text.

were not significant. The interaction between line and protein level was not significant for any variable ($P > 0.05$). However, across the three periods, the mean line difference for ADG was 52 g/day on food H whilst only 20 g/day on food M, a substantial difference that was significantly greater than zero ($P < 0.05$). Similarly the difference in efficiency between lines was consistently greater on H (18.2 points) than on M (8.5 points) although not significant ($P = 0.07$).

Live weight by time and cumulative food intake. For the H treatment, the parameters of the Gompertz growth function, equations 1 and 2, were estimated using mean data to SP5. The estimates are shown in Table 3 and the curves in Figure 1a and b. As expected, the estimates A and Z were greater for males than for females and for S compared with C. On H the predicted maximum growth rates, calculated as Z/e , were 504 and 430 g/day in males and 408 and 306 g/day in females, in the S and C lines, respectively.

The values of the parameters of the Spillman function, equation (3), are shown in Table 4 for both protein levels, again using mean data to SP5. The growth curves are shown in Figure 2a and b. The value of the lumped parameter (Ak) was lower in females than in males, in C compared with S and on M compared with H. All of these differences were consistent with the effects of these factors on food efficiency.

Carcass composition. The data on carcass characteristics are summarized by line and dietary protein level in Table 5. The effects of line on the carcass variables were clearly present at all slaughter points in both sexes ($P < 0.01$). Interactions between line and weight at slaughter were either absent or small. Where an effect was present it largely reflected scaling; proportional differences remained close to constant. The S animals had only 0.860 of the fat concentration of C and had 1.083 times the lean

Figure 1 Live weight against time to SP5 for (a) males and (b) females of the selected line on high (actual $\blacktriangle$, predicted —) and medium (actual $\bullet$), and of the control line on high (actual $\triangle$, predicted) and medium (actual $\circ$) protein diet. The data to SP4 for males on low protein diet are for the selected line (actual $\blacksquare$) and for the control line (actual $\square$).

concentration. The S line had a lean to bone ratio that was 1.032 of that of the C line ($P < 0.05$), a difference that was significant but small. The proportion of dissected fat (the sum of subcutaneous and

Table 4 Values of the parameters of the Spillman function $W = W_0 + (A - W_0)(1 - \exp(-kF))$ with W = weight and F = cumulative food intake for lambs taken to SP5 in experiment 1†

Line	Sex	Protein level	Parameters			Residual s.d. (kg)
			A (kg)	1000 k	A k	
Selected	Male	H	121.7	2.864	0.3485	0.836
		M	147.0	1.799	0.2645	0.395
	Female	H	108.7	3.045	0.3310	0.540
		M	118.9	2.267	0.2695	0.431
Control	Male	H	120.5	2.429	0.2927	1.654
		M	145.0	1.629	0.2360	0.939
	Female	H	110.9	2.280	0.2529	0.934
		M	139.3	1.461	0.2035	1.198

† The mean values for W_0 were 23.3 and 26.2 kg for females and males, respectively. H = high. M = medium.

intermuscular fat) in the intermuscular depot in the S line was 1.06 of that in the C line ($P < 0.001$). However, the absolute weight of intermuscular fat was less (4627 v. 5047 g; $P < 0.001$).

The effects of dietary protein concentration were consistent with those found in monogastric animals (Kyriazakis and Emmans, 1991). On H, fat concentration was less, and lean concentration more than on M ($P < 0.01$). There was no effect of diet on either the lean to bone ratio or pSQFAT ($P > 0.20$).

The large effects of slaughter weight and sex on carcass characteristics, and the interaction between them, are summarized in Table 6. The females at the same slaughter point were fatter than the males and also had a higher ratio of lean to bone. The extents to which lean concentration declined, and fat concentration increased, with slaughter weight were greater in females than in males. Similarly the increase in the proportion of fat that was in the subcutaneous depot as slaughter weight increased was more marked in females.

Experiment 2

Growth and food intake between slaughter weights. The results for live performance from experiment 2 are in Table 7. The main effect of dietary protein concentration on growth rate and efficiency was large ($P < 0.01$) and in agreement with that seen in experiment 1, as seen in Table 2. The rate of food intake and efficiency both declined as dietary protein concentration decreased. The S lambs grew faster than C lambs, which mainly reflected a difference in efficiency rather than a greater food intake.

In agreement with experiment 1, the extent to which S exceeded C in growth rate and efficiency was greater on H than on M (Table 7). The difference in

growth rate between S and C on L was similar to that on M. More specifically the extent to which growth rate in S exceeded that in C was greater on H (92.3 g/

Figure 2 Live weight against cumulative food intake to SP5 for (a) males and (b) females of the selected line on high (actual $\blacktriangle$, predicted —) and medium (actual $\bullet$, predicted ----), and of the control line on high (actual $\triangle$, predicted —) and medium (actual $\circ$, predicted ----) protein diet. The data to SP4 for males on low protein diet are for the selected line (actual $\blacksquare$, predicted), and for the control line (actual $\square$, predicted).

Table 5 Effect of line (selected (S) and control (C)) and dietary protein level (high (H) and medium (M)) on carcass composition in experiment 1†

Variable‡	H		M		s.e.d.	Significance	
	S	C	S	C		Line	Diet
Killing out (%)	48.85	49.34	49.44	49.96	0.341		**
Lean concentration (g/kg)	549.0	513.9	538.1	490.3	3.92	**	**
Fat concentration (g/kg)	286.9	329.5	303.1	356.7	4.83	**	**
pSQFAT (g/kg)	556.9	586.4	572.6	592.5	5.21	**	
Lean : bone	3.611	3.548	3.682	3.519	0.0517	**	

† There were no significant interactions between line and diet ($P > 0.10$).

‡ KO = killing out (carcass yield); pSQFAT = proportion of total fat in the subcutaneous depot; lean : bone = ratio of lean to bone weights.

Table 6 Carcass composition by sex and slaughter point (SP3, SP4 and SP5) in experiment 1 for lambs given the high protein diet

Variable†	Male			Female			s.e.d.‡
	SP3	SP4	SP5	SP3	SP4	SP5	
Cold carcass (kg)	16.855	31.402	61.312	14.867	28.103	55.262	0.3413
Killing out (%)	44.12	47.86	54.06	45.10	49.57	55.68	0.458
Lean concentration (g/kg)	609.2	539.5	449.4	604.0	515.5	419.6	5.26
Fat concentration (g/kg)	184.1	298.0	430.3	195.4	333.4	473.0	6.48
pSQFAT (g/kg)	522.2	587.3	590.9	533.8	606.3	622.0	6.99
Lean : bone	3.091	3.553	3.971	3.167	3.621	4.137	0.0693

† See Table 5 footnote.

‡ Sex and slaughter point were significant for all variables ($P < 0.01$), as were their interaction except for killing out and lean : bone ($P > 0.10$).

day) than on M and L combined (26.4 g/day). The difference of 65.9 (s.e. 18.4) g/day was significant ($P < 0.01$) indicating a line by dietary protein concentration interaction.

Live weight by time and cumulative food intake. The weight by time and weight by cumulative food curves for treatment L are shown in Figures 1a and 2a, respectively, for the males of the two lines. The data for treatment L only go to SP4 as no animals on this treatment were continued beyond this point. The

clear differences due to dietary protein concentration in the weight by time graph, Figure 1a, are difficult to distinguish in the weight by cumulative food graph, Figure 2a.

Carcass composition. Table 8 shows the effects of line and level of dietary protein concentration on carcass composition in males averaged across SP3 and SP4. There were effects of line on lean and fat concentrations ($P < 0.001$). The proportion of fat in the subcutaneous depot was less in S than in C

Table 7 Effects of line (selected (S) and control (C)) on gain (ADG_{34}), intake (ADI_{34}) and efficiency (EFF_{34}) from SP3 to SP4 for males given high, medium, and low protein diets in experiment 2†

Protein level	ADG_{34} (g/day)			ADI_{34} (g/day)			EFF_{34} (g/kg)		
	S	C	S-C‡	S	C	S-C‡	S	C	S-C‡
High	504.1	411.8	92.3	2563	2438	125	196.1	169.0	27.1
Medium	366.7	343.5	23.2	2195	2178	17	166.9	157.4	9.5
Low	301.7	265.6	36.1	1868	1821	47	160.2	145.0	15.2

† s.e.d.s are: for ADG_{34} 11.1 for high and medium, and 19.2 for low; for ADI_{34} 27.8 for high and medium, and 48.6 for low; for EFF_{34} 3.79 for high and medium, and 6.56 for low.

‡ Selected minus control.

Table 8 Effects of three protein levels (high (H), medium (M) and low (L)) in males of the selected (S) and control (C) lines in experiment 2 (means across SP3 and SP4)

Variable†	H		M		L		s.e.d.	Significance	
	S	C	S	C	S	C		Line	Diet
Killing out (%)	45.45	45.49	46.53	46.49	47.48	47.26	0.601		**
Lean concentration (g/kg)	597.0	568.6	582.8	548.9	550.6	506.6	7.48	***	***
Fat concentration (g/kg)	214.2	245.2	231.2	273.5	269.8	318.0	9.37	***	***
pSQFAT (g/kg)	540.6	568.2	544.8	565.4	537.6	571.4	9.92	***	
Lean:bone	3.353	3.254	3.363	3.317	3.257	3.142	0.0956		**

† See Table 5 footnote.

($P < 0.001$). As dietary protein concentration was reduced, lean concentration decreased and fat concentration increased. The lean to bone ratio declined as protein concentration decreased ($P < 0.01$). There was no evidence at all of any interaction between line and dietary protein concentration for any of the carcass traits ($P > 0.2$).

Environmental sensitivity

The regression coefficients (s.e.) for testing the environmental sensitivity of the S and C line rams for ADG_{34} , ADI_{34} and EFF_{34} were:

$$ADG_{34} = -38.1 (43.9) + 76.3 (62.0) L + (1.173 (0.118) - 0.347 (0.167) L) E$$

residual s.d. 14.6 g/day

$$ADI_{34} = -95 (136) + 189 (193) L + (1.058 (0.0622) - 0.1158 (0.0879) L) E$$

residual s.d. 28.8 g/day

$$EFF_{34} = -28.6 (18.7) + 57.3 (26.5) L + (1.1228 (0.113) - 0.456 (0.160) L) E$$

residual s.d. 2.47 g/kg

here $L = 0$ for S and 1 for C, and E is the environmental mean across lines. The interaction between line and environment was not significant for any of the three traits ($P > 0.1$). For ADG_{34} and EFF_{34} the negative coefficient for the interaction term suggests that the S line responded more favourably to an improving environment than did the C line.

Discussion

Carcass composition

In agreement with Lewis *et al.* (2002b), who used level of feeding as the nutritional variable, we found that the marked differences in carcass composition between the two lines persisted across the level of protein in the food. In the case of Lewis *et al.* (2002b) the nutritional variable caused a reduction in carcass

fatness while in this case the reduction in dietary protein level caused a marked increase. Again in agreement with Lewis *et al.* (2002b) the line differences in carcass fatness were seen over widely varying live weights. Together these findings give confidence that the lower fat concentrations of the carcasses resulting from selection will be seen across a broad range of finishing systems.

Selection had a large effect on carcass composition. Lambs of the S line had only 0.86 as much fat as those of its C line. A further effect of selection was a slight increase in the lean to bone ratio, which was 1.032 times as high in the S line. In the S line where muscle depth was part of the selection index, it increased by 2.8 mm over 9 years of selection whilst fat depth decreased by 1.1 mm (Simm *et al.*, 2002). Abdullah *et al.* (1998) found that selection for lower backfat depths alone led to lower muscle to bone ratios. These findings suggest that the weighting given to muscle depth in selection needs to be such that the ratio of muscle to bone continues to allow functional soundness. Selection for an excessive ratio of muscle to bone has been found in other species such as turkeys (Emmans, 1989) to reduce fitness.

In agreement with Lewis *et al.* (2002b), in work on the same lines at the same weights, the females were fatter at the same slaughter point over the wide range of carcass weights used (Table 6). At the same slaughter point the live weights of the females were 0.87 of those of the males. At the same degree of maturity this ratio would be expected to be 0.76 of the weight of the males, the reciprocal of 1.3 (Hammond, 1932). Our sex comparisons were thus neither at the same weights nor at the same degree of maturity. McClelland *et al.* (1976) and Thompson *et al.* (1985) concluded that there were no sex differences in fatness at the same degree of maturity. In contradiction, Emmans (1988) and Taylor *et al.* (1989) estimated that mature females would have a higher proportion of fat than mature males. As our females

were both more mature and fatter than the males, our data cannot directly help to resolve this disagreement.

The Agricultural Research Council (1980) suggested that fat concentration would fall as growth rate was reduced. While this may be the case where growth rate is reduced by a lower level of feeding, as found by Lewis *et al.* (2002b) with the same lines as used here, it may not apply generally. Where the reduction in growth rate was caused by a low dietary protein concentration, as here, the reverse was the case. Reducing dietary protein concentration had a large effect on carcass fatness. For lambs given H, M and L protein levels the carcass fat concentration was 230, 252 and 294 g/kg, respectively ($P < 0.001$). An additional effect was that the lean to bone ratio declined as protein concentration decreased ($P < 0.01$). This probably reflects the relatively greater effect of a low protein diet on limiting the growth of muscle compared with the skeleton.

Growth and food intake

The S line grew faster and was more efficient than its C line to extents that were similar to those reported by Lewis *et al.* (2002b) on the same lines. In that work the advantage to the S line decreased as the level of food allowance decreased. As the level of dietary protein was decreased the same effect was seen as when food allowance was reduced, but the size of the effect was much smaller.

The regressions to test for environmental sensitivity failed to show any significant interaction between the lines and the level of protein in the food. However, in all cases the sign of the coefficient was such as to indicate that the S line was more sensitive than its C line for intake, growth rate and efficiency as protein concentration was reduced. In agreement with this, the difference between the lines in the extent to which growth rate was greater on H than on M and L (65.9 (s.e. 18.4) g/day) was significant ($P < 0.01$) indicating a line by dietary protein concentration interaction.

The data on weights collected over time on *ad libitum* feeding could be well described by a Gompertz growth function, as was expected (Lewis *et al.*, 2002a and b). The lumped parameter ($Z = A/B$) could be well estimated, where the maximum growth rate is Z/e . Since the Gompertz function tracked the data well, changes in the values of its parameters seem a suitable way to summarize the effects of selection on growth.

Weight as a function of the cumulative amount of food eaten was also of interest (described in Spillman

and Lang (1924) as quoted by Parks (1982)). The exponential functional form worked well, as seen in Figure 2a and b, for all three levels of protein used. There is a problem in separately estimating the values of the two parameters A and k but their product was much more stable and could be well estimated. The value of (Ak) was consistently greater in S than in C, in males than in females, and on H than on M, all of which reflected differences in efficiency (Table 4). To attain a given gain in live weight the amounts of both time (Figure 1a and b) and food (Figure 2a and b) increased as the level of protein in the food declined.

The use of an index designed to improve lean growth rate resulted in a higher lean concentration in the carcass of a selected as compared with unselected (C) line of Suffolk sheep. This benefit persisted over a wide range of live weights and for foods that differed appreciably in their protein concentration. Genetic selection appears to be both a useful and robust mechanism to affect the composition of the carcass and thereby its quality.

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References

- Abdullah, A. Y., Purchas, R. W. and Davies, A. S. 1998. Patterns of change with growth for muscularity and other composition characteristics of Southdown rams selected for high and low backfat depth. *New Zealand Journal of Agricultural Research* 41: 367-376.
- Agricultural Research Council. 1980. *The nutrient requirements of ruminants*. Commonwealth Agricultural Bureaux, Slough.
- Beauchemin, K. A., McClelland, L. A., Jones, S.D. M. and Kozub, G. C. 1995. Effects of crude protein-concentration, protein degradability and energy concentration of the diet on growth and carcass characteristics of market lambs fed high concentrate diets. *Canadian Journal of Animal Science* 75: 387-395.
- Emmans, G. C. 1988. Genetic components of potential and actual growth. In *Animal breeding opportunities* (ed. R. B. Land, G. Bulfield and W. G. Hill), *British Society of Animal Science occasional publication no. 12*, pp. 153-181.
- Emmans, G. C. 1989. The growth of turkeys. In *Recent advances in turkey science* (ed. C. Nixey and T. C. Grey), *Poultry Science symposium no. 21*, pp. 135-166. Butterworths, London.

- Falconer, D. S. 1989. *Introduction to quantitative genetics, third edition*. Longman Scientific and Technical, England.
- Fennessy, P. F., Greer, G. J., Bain, W. E. and Johnstone, P. D. 1993. Progeny test of ram lambs selected for low ultrasonic backfat thickness or high post-weaning growth-rate. *Livestock Production Science* 33: 105-118.
- Fluharty, F. L. and McClure, K. E. 1997. Effects of dietary energy intake and protein concentration on performance and visceral organ mass in lambs. *Journal of Animal Science* 75: 604-610.
- Genstat 5 Committee. 1998. *Genstat 5 release 4.1 (PC/Windows NT)*. Lawes Agricultural Trust, Rothamsted Experimental Station, Harpenden.
- Griminger, P. and Scott, H. M. 1959. Growth rate and lysine requirement of the chick. *Journal of Nutrition* 68: 429-442.
- Haddad, S. G., Nasr, R. E. and Muwalla, M. M. 2001. Optimum dietary crude protein level for finishing Awassi lambs. *Small Ruminant Research* 39: 41-46.
- Hammond, J. 1932. *Growth and development of mutton qualities in the sheep*. Oliver and Boyd, Edinburgh.
- Jones, H. E., Simm, G., Dingwall, W. S. and Lewis, R. M. 1999. Genetic relationships between visual and objective measures of carcass composition in crossbred lambs. *Animal Science* 69: 553-561.
- Kempster, A. J. 1983. Carcass quality and its measurement in sheep. In *Sheep production* (ed. W. Haresign), pp. 59-74. Butterworths, London.
- Kyriazakis, I. and Emmans, G. C. 1991. Diet selection in pigs: dietary choices made by growing pigs following a period of underfeeding with protein. *Animal Production* 52: 337-346.
- Kyriazakis, I., Stamataris, C., Emmans, G. C. and Whittemore, C. T. 1991. The effects of food protein content on the performance of pigs previously given foods with low or moderate protein contents. *Animal Production* 52: 165-173.
- Lewis, R. M., Emmans, G. C., Dingwall, W. S. and Simm, G. 2002a. A description of the growth of sheep and its genetic analysis. *Animal Science* 74: 51-62.
- Lewis, R. M., Emmans, G. C. and Simm, G. 2002b. Effects of index selection on the carcass composition of sheep given either *ad libitum* or controlled amounts of food. *Animal Science* 75: 185-195.
- Lewis, R. M., Simm, G., Dingwall, W. S. and Murphy, S. V. 1996. Selection for lean growth in terminal sire sheep to produce leaner crossbred progeny. *Animal Science* 63: 133-142.
- McClelland, T. H., Bonatti, B. and Taylor, St C. S. 1976. Breed differences in body composition of equally mature sheep. *Animal Production* 23: 281-294.
- National Research Council. 1985. *Nutrient requirements of sheep, sixth revised edition*. National Academy Press, Washington, DC.
- Parks, J. R. 1982. *A theory of feeding and growth of animals*. Springer Verlag, Berlin.
- Simm, G. and Dingwall, W. S. 1989. Selection indices for lean meat production in sheep. *Livestock Production Science* 21: 223-233.
- Simm, G., Lewis, R. M., Grundy, B. and Dingwall, W. S. 2002. Responses to selection for lean growth in sheep. *Animal Science* 74: 39-50.
- Simm, G. and Murphy, S. V. 1996. The effects of selection for lean growth in Suffolk sires on the saleable meat yield of their crossbred progeny. *Animal Science* 62: 255-263.
- Spillman, W. J. and Lang, E. 1924. *The law of diminishing increment*. World, Yonkers.
- Taylor, St C. S., Murray, J. I. and Thonney, M. L. 1989. Breed and sex-differences among equally mature sheep and goats. 4. Carcass muscle, fat and bone. *Animal Production* 49: 385-409.
- Thomas, P. C., Robertson, S., Chamberlain, D. G., Livingstone, R. M., Garthwaite, P. H., Dewey, P. J. S., Smart, R. and Whyte, C. 1988. Predicting the metabolizable energy (ME) concentration of compound feeds for ruminants. In *Recent advances in animal nutrition* (ed. W. Haresign and D. J. A. Cole), pp. 127-146. Butterworths, London.
- Thompson, J. M., Butterfield, R. M. and Perry, D. 1985. Food intake, growth and body composition in Australian Merino sheep selected for high and low weaning weight. 2. Chemical and dissectible body composition. *Animal Production* 40: 71-84.
- Woodward, J. and Wheelock, V. 1990. Consumer attitudes to fat in meat. In *Reducing fat in meat animals* (ed. J. D. Wood and A. V. Fisher), pp. 66-100. Elsevier, London.

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