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Effects of index selection on the carcass composition of sheep given either *ad libitum* or controlled amounts of food

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Abstract

Sheep of a line (S) selected on an index to increase lean weight and decrease fatness at an age, and a control line (C), were given a high quality food at different levels including *ad libitum*. Live performance 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 feeding did not affect the extent to which S was superior to C in either the level of fatness in the carcass (0.86 as much) or the ratio of lean to fat (1.28 as much). The lean to bone ratio was slightly greater in S (1.028 of the value of C; $P < 0.05$) and was higher on the lowest level of feeding compared with the two higher levels used ($P < 0.05$ in one experiment on females and $P < 0.001$ in another on males). On *ad libitum* feeding the S line grew 1.19 times as fast and was 1.17 times as efficient compared with C. These advantages to S decreased as level of feeding decreased to become virtually zero at the lowest level of feeding used, which allowed C to grow at only 0.53 of the rate seen on *ad libitum* feeding. On *ad libitum* feeding growth was well described by a Gompertz growth function of the form $W = (Z/B) \exp(-\exp(G_0 - B t))$. The maximum growth rate is (Z/e) . Line S had a value of Z that was 1.10 that of C averaged across the two sexes. A Spillman function $W = W_0 + (A - W_0)(1 - \exp(-k F))$ was used to describe weight, W, in terms of cumulative intake, F. It worked well for *ad libitum* feeding and for the two restricted regimes used. The value of the combined parameter (A/k) varied across treatments in the same way as efficiency did.

Keywords: carcass composition, feeding, genotype environment interaction, sheep.

Introduction

Lamb carcasses produced in the UK (Kempster, 1983; Woodward and Wheelock, 1990) and in other countries (Beauchemin, 1995; Fennessy, 1993) are considered to be excessively fat and this has contributed to a reduction in lamb consumption. A reduction in the fatness of lamb, through changes both in breeding and finishing systems, can help the sheep industry to better meet consumer requirements.

Having examined a wide range of techniques for estimating carcass composition in live sheep Simm (1987) concluded that ultrasonic scanning provided an acceptable compromise between accuracy and cost. A selection index that combined ultrasonic measures of fat and muscle depth and live weight was designed to improve the rate of lean growth

(Simm and Dingwall, 1989). The index was applied to a selection flock of Suffolk sheep starting in 1986 and substantial responses in each of the selection criteria have been achieved. After 9 years, the selection line sheep weighed 4.9 kg more, had 1.1 mm lower fat depth and 2.8 mm greater muscle depth at 150 days of age across sexes; these responses are between 7 and 15% of the overall means of the traits concerned (Simm *et al.*, 2002).

The genetic change created allows the consequences of index selection on carcass composition to be estimated. Although the lines have been compared on live predictors of carcass composition (Simm *et al.*, 2002) it is important to establish how these changes in live measures correspond with those in the carcass itself. It is also important to see if the ability of measurements on the live animal to predict carcass

characteristics applies across degrees of maturity and continues under selection.

In the UK, lambs in terminal sire flocks are usually reared intensively. One benefit of this is that genetic variation within a group of lambs in carcass composition may not be constrained by nutrition or maternal effects. The selection flock (Simm *et al.*, 2002) was given, *ad libitum*, a food with high energy and protein contents to allow genetic differences between animals for lean growth and fatness to be fully expressed. In commercial flocks, where terminal sire rams are used in crossbreeding, lambs are usually reared in more extensive grazing systems. It has been found that the use of high index Suffolk rams improves the carcass composition of crossbred lambs at grass (Lewis *et al.*, 1996; Simm and Murphy, 1996; Jones *et al.*, 1999). However, these benefits appeared to be lower than expected. It is important to test whether the advantage from selection for lean growth rate and less fat in terminal sires remains regardless of nutrition, or whether there is an interaction between the lines and their feeding environment.

The first objective of the work reported here was to test whether selection decisions based on the lean growth index have produced an improvement in carcass composition in purebred terminal sire sheep. The second was to test whether these changes persist when level of feeding and live weight at slaughter differ from those under which selection was carried out. The data collected were also used to explore the relationships between weight and time and between weight and cumulative food intake, as affected by line and level of feeding.

Material and methods

Suffolk selection experiment

In the early 1980s a Suffolk flock was established at the Scottish Agricultural College (SAC) and in 1986 a regimen to test performance was started with ram lambs and, from 1989 onward, also with ewe lambs. In this regimen lambs were offered a creep food from 1 week of age and gradually switched to *ad libitum* access to a complete pelleted ration by weaning at 56 days of age. The food used was high in energy and protein (Table 1).

When 150 days old, the lambs' live weights (LW) and ultrasonic measurements of their muscle (UMD) and fat depths (UFD) were recorded. Lambs were ultrasonically scanned at the level of the 13th rib and 3rd lumbar vertebra on two or three occasions spanning the 150 day target age, and the scan depths averaged. The measurements, after adjusting for the effects of dam age and birth rank, were then

Table 1 Composition of the food used

Ingredient (g/kg)	582.5
Barley	200.0
Dried grass	70.0
Hipro soya-bean meal	60.0
Fish meal	50.0
Molasses	37.5
Mineral and vitamin mix	
Chemical composition	881
Dry matter (DM; g/kg)	188
Crude protein (g/kg DM)	260
NDF (g/kg DM)†	30
AHEE (g/kg DM)†	86
Ash (g/kg DM)	781
NCGD (g/kg)†	11.7
Metabolizable energy (MJ/kg DM)‡	

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

‡ Predicted from $0.014 \text{ NCGD} + 0.025 \text{ AHEE}$ (Thomas *et al.*, 1988).

combined into a selection index constructed as $0.103\text{LW} + 0.257\text{UMD} - 0.406\text{UFD}$. The index was designed to increase the rate of lean deposition whilst restricting the rate of fat deposition (Simm and Dingwall, 1989). Lambs were selected on the basis of their index scores. The selection (S) line had high scores while the control (C) line were maintained at the flock's average index score at the start of selection experiment. Index scores were scaled such that the average of the C line was 100, and the standard deviation of the index was 40. Further details are given in Simm *et al.* (2002).

Lambs

Three experiments were conducted over 2 years. Multiple ovulation and embryo transfer (MOET) produced the S line lambs used in the 1994 experiment. This was an additional lambing to that of the main Suffolk flock. Scottish Mule (Bluefaced Leicester × Scottish Blackface) ewes were used as the surrogate dams for the MOET programme. No control line lambs were available for use in the 1994 experiment. The surrogate dams were approximately 1½ years of age at embryo transfer. The lambs were born over a period of 1 week in March from their surrogate dam. Genetically they were the progeny of seven rams and 34 mature ewes that contributed progeny only in this year. The MOET born lambs were either used in this experiment or sold once achieving market weight; none was retained as replacement animals in the Suffolk flock.

Starting in mid August of 1994, 195 S line and 112 C line ewes from the main SAC Suffolk flock were

mated over a period of 7 weeks to produce the lambs used in 1995. Within each line, ewes were separated into six paddocks and mated to a single ram. The rams used had been chosen from the 1994 lambing of the Suffolk flock at the end of the ninth performance test. At that time, across the two sexes, the S line differed from the C line by 4.88 kg in live weight, -1.1 mm in ultrasound fat depth and 2.8 mm in ultrasound muscle depth (Simm *et al.*, 2002).

Management

Following MOET or natural mating, the ewes were managed as a single flock. Ewes were 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. Triplet-born lambs were cross-fostered to ewes nursing a single lamb. Within a week of birth, lambs were offered free access to the same or a very similar food as that used in the performance test. From 2 weeks of age lambs were weighed on the same day (on a Monday in 1994 and on a Thursday in 1995) each week starting at 10:00 h.

Only those lambs reared by their birth dam were used. 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 food described in 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 its feeding treatment started. The mean starting weights were 22.6 (s.d. 1.25) kg for females and 25.2 (s.d. 1.40) kg males.

On the day when the lambs' live weights were taken, the residual food was also collected, weighed and discarded. For animals on feeding treatments M and L as described below, if food remained at the end of a week, this weight of food was added to their

allocation in subsequent weeks. Only a very few animals did not eat their entire food quota.

Carcass evaluation

Lambs were grown to three slaughter weights chosen as described below. On reaching their slaughter weight, animals were shorn. The following morning, they were weighed and transported for slaughter at the SAC Carcass Evaluation Unit. At slaughter the weight of the head, tail, feet, pelt, body organs and blood were recorded. The carcass was weighed after processing and chilling overnight to give the cold carcass weight, and then split, shrouded and frozen.

After defrosting, the left side of each carcass was weighed and then separated into eight joints (breast, chump, end-neck, leg, loin, mid-neck, scrag and shoulder) as described by Cuthbertson *et al.* (1972). Each joint was dissected into lean, fat (subcutaneous and intermuscular), bone (vertebral and other) and waste components.

Experimental design

Three levels of feeding (H, M and L) were used as described in Table 2. Level L was intended to give growth rates comparable to those seen in commercial systems and M was intermediate. Animals were given food twice daily (at 8:30 and 15:30 h). On treatment H, the level of food allowance 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 refused on H in both years had a lower DM content than that offered the difference was small (854 *v.* 885 g/kg in 1994, and 880 *v.* 898 g/kg in 1995). For this reason, intakes are reported on an as-fed basis. Starting part way through 1994, lambs were offered 150 g of poor quality hay (833 g/kg DM; 87 g/kg DM crude protein; 434 g/kg DM modified acid-detergent fibre; 56 g/kg DM ash) at each morning feeding. This was also done in 1995. Most animals ate all of their hay allowance in most weeks. The reported food intakes exclude hay.

Experiment 1 in 1995 was of a full factorial design with two lines (S and C), two sexes (ram and ewe lambs), two levels of feeding (*ad libitum*, H, and the restricted regime M; Table 2) 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 are equidistant from SP4 on a logarithmic scale. There were five replicates for each treatment at SP3 and SP5 and 10 at SP4 giving 160 animals in total.

Table 2 The three levels of feeding used

Feeding treatment	Experiment food used in	Amount offered
H	1, 2, 3	<i>Ad libitum</i>
M	1, 2	600 g/day 1st week on treatment; 105 g/day increment each week thereafter to 2070 g/day
L	2, 3	400 g/day 1st week on treatment; 70 g/day increment each week thereafter to 2080 g/day

Experiment 2 used the rams of both lines in 1995 on H, M and 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 feeding treatments at SP4. An additional comparison, treated as experiment 3, was for females of the S line only in 1994 taken to SP4 on either H (no. 25) or L (no. 23).

Derived variables

For consistency the starting 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_{ij} ; g/day), food intake (ADI_{ij} ; g/day), and the food efficiency ($EFF_{ij} = 1000 \cdot (ADG_{ij}/ADI_{ij})$; g/kg) were calculated, where i and j are the slaughter point numbers that define the three intervals (SP2-SP3, SP3-SP4 and SP4-SP5). Live weight was related both to cumulative 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 sum of the weights of the eight dissected joints (g/kg). In addition, we calculated the proportion of total fat that was subcutaneous fat (pSQFAT), the ratio of lean to fat weight (LEAN:FAT) and the ratio of lean to bone weight (LEAN:BONE), all as g/kg.

Statistical methods

Heterogeneity of variance. We expected that on restricted feeding treatments that are time-based, such as those used here, there would be no variation in food intake between a pair of ages with no refusals. In this study, although food allowances were time-based (see Table 2), the start and end slaughter points were weight-based. As a consequence we expected some variation on the restricted feeding treatments, but that it would be less than on the *ad libitum* treatment. This was tested using Bartlett's test in Genstat (Genstat 5 Committee, 1998). There was marked and highly significant ($P < 0.01$ in eight of nine cases) heterogeneity of variance for the growth, intake and efficiency measures. The CVs were also higher on *ad libitum* than on the restricted treatments for both ADG (about 1.5 times) and EFF (about 1.2 times) showing that a logarithmic transformation of the data would not have removed the heterogeneity.

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 defined substantial variation in any of the measurements and significance at $P < 0.05$ was rare. As this could have been due to heterogeneous variance between the feeding treatments, the importance of these fixed effects was then tested within feeding levels. The conclusions drawn were the same as with the analyses across feeding treatments. The fixed effects were therefore excluded from the final models fitted. The experiments were analysed as factorial designs.

For growth rate and intake, there were the obvious expected effects of level of feeding. We were mainly interested in the effects of line (S *v.* C), and in particular in whether line differences within a sex interacted with level of feeding. Answering these questions was complicated by the presence of heterogeneous variances between levels of feeding. The s.e.s of differences were calculated after making allowance for the heterogeneous variances as described by Snedecor and Cochran (p. 96, 1980).

Weight by time and cumulative food intake. For the H treatment the values of the parameters of the Gompertz growth function (Winsor, 1932) were estimated using treatment mean data from the starting weight through to both SP4 and SP5. The function was fitted in two ways (Lewis *et al.*, 2002). The first was

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

where W is live weight (kg) and t is time (days), and the parameters A and B are the mature weight (kg) and a rate parameter (per day). The third parameter, G_0 , is a transformed initial weight given by $G_0 = \ln(-\ln(W_0/A))$ and W_0 (kg) is the weight at $t = 0$. However, the estimates of A and B were found to be very highly correlated (Lewis *et al.*, 1998 and 2002). One way to overcome this inevitable problem of estimating A and B as separate parameters is to consider them together by defining a variable Z as the product ($A B$). This lumped parameter Z has a lower error of estimation, and a distribution of values closer to normal than A and B separately. Thus, the second form of the Gompertz function fitted was

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

The parameter Z has a biological interpretation in that Z/e , where e is the exponential function, is the maximum daily growth rate (kg/day). As there was 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 also 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 and k are the parameters to be estimated. 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

Genotype by environment interactions may arise because some genotypes show a greater sensitivity to their environment than others. Regression procedures can illustrate the extent of this environmental sensitivity (Freeman, 1973; Jinks and Connolly, 1973; Falconer, 1989).

Where there was an interaction between line and the three levels of feeding, a least-squares procedure was used to obtain the mean performance across line on each feeding treatment i.e. to estimate the environmental means across the two lines. The mean performance of each line on each feeding treatment was also estimated. The line means were regressed on the environmental means with a test for a line difference in the slope of the regression for the two lines. This was used as a measure of environmental sensitivity (Jinks and Connolly, 1973; Falconer, 1989).

The regression model used for testing the environmental sensitivity of the S and C line rams was:

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

where $L = 0$ for S and 1 for C, and E is the 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

Live performance between slaughter weights. On average female lambs on feeding level H grew at 0.76 of the rate of males, ate 0.83 as much food and were 0.93 as

Table 3 Live performance in experiment 1 between successive slaughter points 2, 3, 4 and 5†

Variable	Feeding treatment				s.e.d.‡
	H		M		
	S line	C line	S line	C line	
ADG ₂₃ (g/day)	460.8	436.3	226.4	215.1	12.35
ADI ₂₃ (g/day)	1467	1524	932	956	19.6
EFF ₂₃ (g/kg)	311.1	284.7	243.6	226.2	8.69
ADG ₃₄ (g/day)	463.4	392.6	317.2	287.7	10.09
ADI ₃₄ (g/day)	2374	2331	1828	1871	23.5
EFF ₃₄ (g/kg)	193.7	167.8	173.8	154.0	4.41
ADG ₄₅ (g/day)	270.8	197.5	210.3	193.6	7.06
ADI ₄₅ (g/day)	2627	2276	2048	2003	45.6
EFF ₄₅ (g/kg)	102.8	86.8	102.7	96.4	2.29

† The variables are ADG = average daily gain, ADI = average daily intake and EFF = 1000 ADG/ADI. Feeding treatments are H = *ad libitum* and M = restricted. S = selected line; C = control line.

‡ s.e.d. from ANOVA assuming homogeneity of variances.

efficient (all $P < 0.01$). On feeding level M, where intakes were essentially the same, the females grew at 0.94 the rate of the males, a difference that is less than that on H. The difference is consistent with the difference in efficiency on H. As shown in Table 3, the S line grew faster throughout and was more efficient than C irrespective of level of feeding. Variances were significantly heterogeneous between feeding levels for ADG and ADI but not for EFF. The interaction between line and feeding treatment was not significant for EFF₂₃ or EFF₃₄ ($P > 0.05$) but was for EFF₄₅ ($P < 0.01$). The greater variance for gain on H than on M meant that the testing of an interaction between line and feeding level was not straightforward. However, across the three periods, the mean line difference for ADG was 56 g/day on food H whilst only 19 g/day on M, a substantial difference that was significant ($P < 0.05$).

Live weight by time and cumulative food intake. For the H treatments the parameters of the Gompertz growth function were estimated using mean data to SP5. The estimates are shown in Table 4 (year 1995) and the curves as lines in Figure 1. The latter also shows points of live weight against time for lambs on the M as well as the H feeding level. The values of the parameters of the Spillman function, equation (3), are shown in Table 5 for both H and M feeding treatments, again using mean data to SP5. The growth curves are shown in Figure 2. The effect of the decrease in the value of the parameter k as the level of feeding is decreased can be seen clearly in Figure 2.

Table 4 Values of the parameters of the Gompertz growth function $W = (Z/B) \exp(-\exp(G_0 - Bt))$ for lambs in 2 years on feeding treatment H†

Year	Line	Sex	A (kg)	1000 B (per day)	Z (kg/day)	G_0	Residual s.d. (kg)
1994	S	Male	111.3	9.65	1.074	0.404	0.277
	S	Female	65.3	15.70	1.025	0.028	0.386
1995	S	Male	116.2	13.36	1.552	0.442	0.285
	S	Female	90.9	12.11	1.101	0.338	0.155
	C	Male	90.7	14.90	1.351	0.234	0.200
	C	Female	85.0	12.43	1.056	0.283	0.180

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

Table 5 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 on feeding treatments H and M†

Line	Sex	Feeding treatment	Parameters			Residual s.d. (kg)
			A(kg)	1000 k	Ak	
S	Male	H	119.8	3.124	0.3743	0.942
		M	140.7	1.957	0.2754	1.422
	Female	H	105.8	3.015	0.3190	0.993
		M	121.0	2.201	0.2663	1.214
C	Male	H	115.6	2.970	0.3433	1.055
		M	145.5	1.696	0.2468	1.609
	Female	H	108.0	2.563	0.2768	1.105
		M	121.1	1.981	0.2399	1.315

† The data are for animals taken to SP5 only.

Carcass composition. The data on carcass characteristics are summarized by line and feeding treatment in Table 6. Clear effects of line on the carcass variables were present at all slaughter points and for both sexes. Interactions between line and weight at slaughter and between line and sex were either absent or small. The S animals had only 0.859 of the fat content of C and had 1.080 times the lean content. The difference in the lean to fat ratio was present on both feeding treatments across which the value for the S line was 1.28 that of the C line. The S line had a lean to bone ratio that was 1.028 of that of the C line ($P < 0.05$), a difference that was significant but small. Although the proportion of fat in the intermuscular depot was greater in the S than in the C line ($P < 0.001$), the absolute weight of intermuscular fat was less (4543 v. 4996 g; $P < 0.001$).

The large effects of slaughter weight and sex, and the interaction between them, on carcass characteristics are summarized in Table 7. The females, at the same degree of maturity in weight, were fatter but also had a higher ratio of lean to bone. The extents to which lean content declined, and fat content

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.

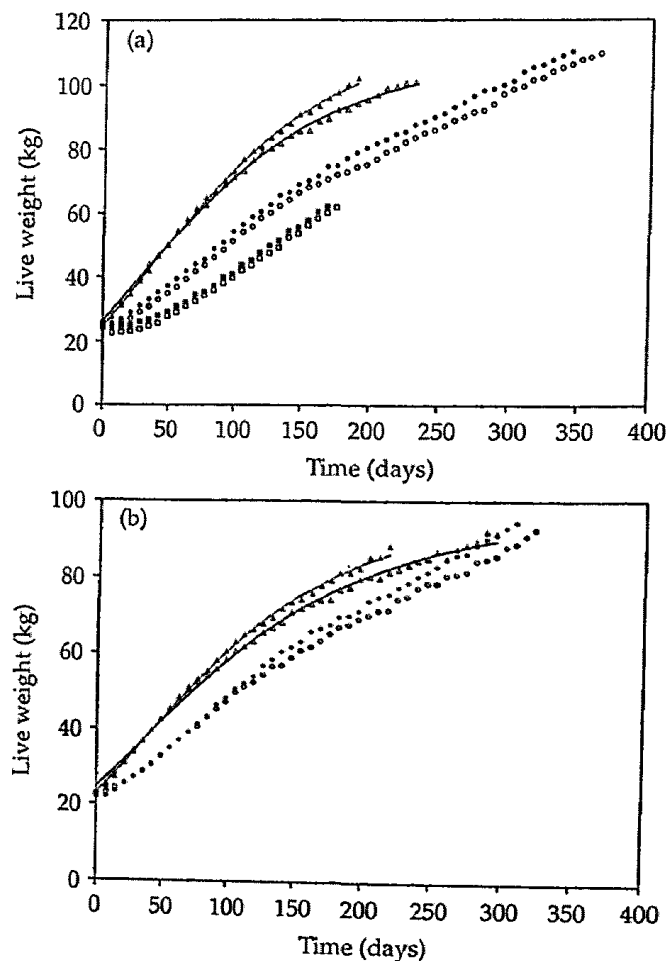


Figure 1 Live weight against time for (a) males and (b) females of the selected line on H (actual ▲, predicted —), M (actual ●) and L (actual ■), and the control line on H (actual △, predicted —), M (actual ○) and L (actual □).

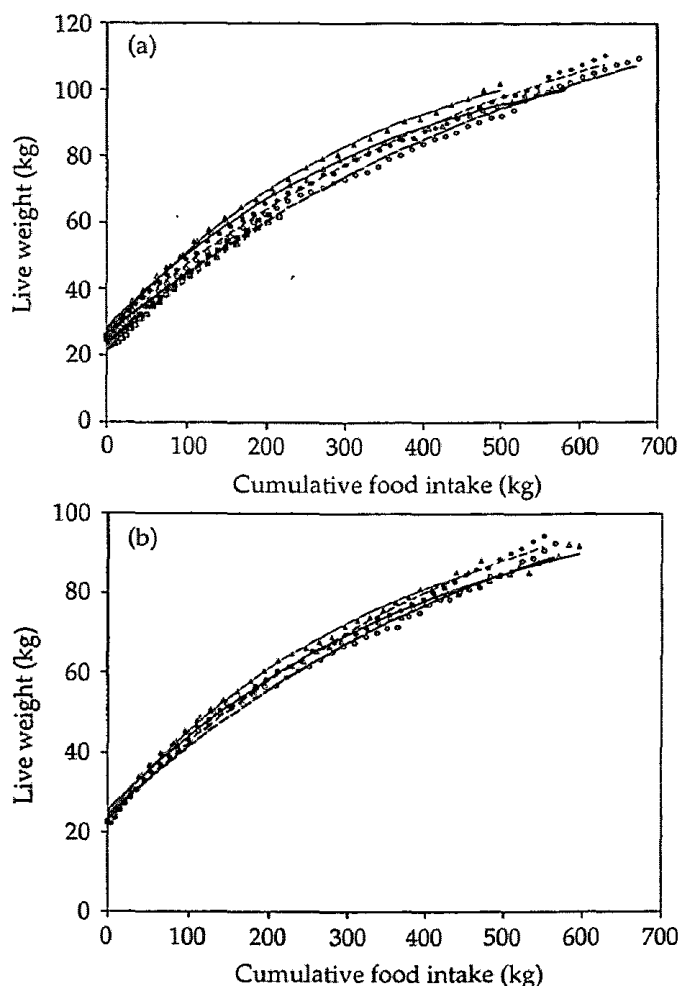


Figure 2 Live weight against cumulative food intake to SP5 for (a) males and (b) females of the selected line on H (actual \blacktriangle , predicted —) and M (actual \bullet , predicted ----) and the control line on H (actual \triangle , predicted —) and M (actual \circ , predicted ----). In (a) the data to SP4 for males on L are for the selected line (actual \blacksquare , predicted ----) and for the control line (actual \square , predicted ----).

Experiment 2

Live performance between slaughter weights. In experiment 1 it was found that the difference in ADG between the lines was lower on M than on H. To see if a further reduction in the difference between lines occurred when level of feeding was further reduced, the data for ADG and EFF between SP3 and SP4 were considered using the data shown in Table 8. The difference between the lines in both growth rate and efficiency decreased as level of feeding decreased. Indeed on L the difference between the lines in both ADG and EFF were negligible and no longer significant.

Live weight by time and cumulative food intake. The weight by time and weight by cumulative food curves for treatment L are shown by square symbols in Figures 1a and 2a, respectively, for the males of the two lines. The clear differences due to level of feeding in the weight by time graph, Figure 1, are difficult to distinguish in the weight by cumulative food graph, Figure 2.

Carcass composition. The level of feeding did not significantly affect the size of the line difference for lean and fat content, the proportion of total fat in the subcutaneous depot, and the ratios of lean to both fat and bone. This is shown by the absence of any interaction between the two factors (Table 9).

Fat content was no lower on L than on M and the lean to bone ratio was higher on L than on either H or M. The reduced fat content in rams on L as compared with H at equal weights through 66.0 kg meant that sheep on L had greater fat-free body weights. Their higher lean to bone ratio would be expected as a consequence of the increased degree of maturity.

Table 6 Effect of line and feeding treatment on carcass composition in experiment 1

Variable†	H		M		s.e.d.	Effect‡	
	S	C	S	C		Line	Feeding treatment
KO (%)	48.08	49.36	47.84	47.73	0.315		**
Lean content (g/kg)	534.5	489.8	550.7	515.5	4.50	***	***
Fat content (g/kg)	299.2	351.8	278.0	320.7	5.43	***	***
pSQFAT (g/kg)	551.9	579.0	558.5	575.7	5.25	***	
LEAN : FAT	2.113	1.624	2.391	1.890	0.0633	***	***
LEAN : BONE	3.508	3.397	3.505	3.428	0.0490	*	

† KO = killing out; pSQFAT = proportion of total fat in the subcutaneous depot; LEAN : FAT = ratio of lean to fat weights; LEAN : BONE = ratio of lean to bone weights.

‡ There were no significant interactions between line and feeding treatment ($P > 0.10$).

Table 7 Carcass composition by sex and slaughter point in experiment 1 (feeding treatment H)

Variable†	Male			Female			Max. s.e.d.‡
	SP3	SP4	SP5	SP3	SP4	SP5	
Cold carcass (kg)	16.22	30.97	59.99	14.81	27.57	54.04	0.388
KO (%)	42.78	46.76	53.16	44.37	48.02	54.43	0.422
Lean content (g/kg)	595.2	533.0	472.7	594.3	517.2	423.2	6.04
Fat content (g/kg)	187.3	298.3	398.4	200.1	324.4	466.1	7.28
pSQFAT (g/kg)	516.8	578.1	565.2	512.0	609.0	616.5	7.05
LEAN : FAT	3.310	1.828	1.234	3.098	1.637	0.922	0.0850
LEAN : BONE	2.915	3.316	3.891	3.071	3.454	4.110	0.0657

† See Table 6 footnote.

‡ Sex and slaughter point were significant for all variables ($P < 0.001$), as was their interaction except for KO, LEAN : FAT and LEAN : BONE ($P > 0.10$).

Table 8 Effects of line on gain and efficiency from SP3 to SP4 on three feeding treatments in males in 1995 in experiment 2

Feeding treatment †	ADG ₃₄ (g/day)			EFF ₃₄ (g/kg)		
	S	C	S-C (s.e.d.)‡	S	C	S-C (s.e.d.)‡
H	542.7	432.6	110.1 (14.4)	209.3	172.2	37.1 (4.50)
M	333.7	306.1	27.6 (9.5)	180.0	160.8	19.2 (5.82)
L	285.7	288.3	-2.6 (12.0)	170.3	165.2	5.1 (7.27)

† Treatments are described in Table 2.

‡ s.e.d.s are estimated from average line variances within a feeding treatment.

Experiment 3

To check the findings from experiment 2, the data from the S line females that were grown to SP4 on treatments H and L were used. The animals on L (Table 10) had higher lean and lower fat contents than those on H, and a higher ratio of lean to fat ($P < 0.01$), as expected. They also had the higher ($P < 0.05$) lean to bone ratio in agreement with the results seen in experiment 2.

Environmental sensitivity

The regression coefficients (s.e.) for testing the environmental sensitivity of the S and C line rams for ADG₃₄ and EFF₃₄ were:

$$\text{ADG}_{34} = -75.8 (11.0) + 151.6 (15.6) L + (1.270 (0.0293) - 0.5389 (0.0415) L) E$$

residual s.d. 4.46 g/day

Table 9 Effects of three levels of feeding (H, M and L) in males of the S and C lines in 1995 at SP3 and SP4 in experiment 2

Variable†	H		M		L		Max s.e.d.	Effect‡
	S	C	S	C	S	C		
KO (%)	44.45	45.84	44.50	44.28	45.12	44.02	0.450	F*, G×F*
Lean content (g/kg)	571.8	536.3	586.2	562.1	597.5	562.2	7.57	G***, F***
Fat content (g/kg)	233.9	275.2	215.0	247.1	221.5	256.9	9.53	G***, F***
pSQFAT (g/kg)	537.4	560.7	545.1	546.6	529.3	548.0	10.26	G*
LEAN : FAT	2.716	2.126	2.973	2.462	2.904	2.466	0.1369	G**, F***
LEAN : BONE	3.127	3.042	3.157	3.135	3.480	3.295	0.0709	F***

† See Table 6 footnote.

‡ G = line effect; F = feeding treatment effect; G×F = line by feeding treatment interaction effect.

Table 10 Carcass composition on two levels of feeding (H and L) in S line females in 1994 at SP4 in experiment 3

Variable†	H	L	s.e.d.	Effect
KO (%)	48.15	48.67	0.342	
Lean content (g/kg)	493.2	518.5	4.67	***
Fat content (g/kg)	349.0	325.4	5.98	**
pSQFAT (g/kg)	604.2	593.0	5.42	
LEAN : FAT	1.437	1.604	0.0408	***
LEAN : BONE	3.342	3.498	0.0518	*

† See Table 6 footnote.

$EFF_{34} = -95.3 (38.6) + 190.6 (54.5) L + (1.599 (0.218) - 1.197 (0.309) L) E$
residual s.d. 3.88 g/kg

where $L = 0$ for S and 1 for C, and E is the environmental mean across lines. The interaction between line and environment was significant for ADG_{34} ($P < 0.01$) and just failed to be so ($P = 0.06$) for EFF_{34} .

Discussion

During the selection phase of the flock from 1985 to 1994 (Simm and Dingwall, 1989; Simm *et al.*, 2002), lambs from both lines were offered *ad libitum* access to the food in Table 1 from weaning to 150 days of age. By the end of this selection phase the rams and ewes weighed about 66.0 and 57.5 kg, respectively, when averaged across lines. In the experiments reported here the S line sheep produced a substantially leaner carcass at these weights with a 0.23 proportional increase in the lean to fat ratio as compared with the C line. Rams of the S line grew proportionately 0.19 faster and were 0.17 more efficient than rams of the C line. The S line animals showed substantially higher lean to fat ratios in their carcasses over the whole, very wide, range of carcass weights used.

Different strategies have been used to affect the composition of the carcass. Cameron and Bracken (1992) divergently selected a Texel-Oxford composite at 20-weeks of age on an index composed of ultrasonic fat depth and live weight. The index was designed to restrict change in live weight. After 3 years of selection, they predicted an advantage of 13.5 g/kg in lean content and -13.8 g/kg in fat content for the high over the low index line. That difference is less than one-third the one observed in the current study where selection had continued for three times as long. Fennessy *et al.* (1993) also found that selection on the basis of live-weight adjusted ultrasonic backfat thickness could be expected to result in leaner lamb carcasses. Abdullah *et al.* (1998)

found that selection for lower weight-adjusted backfat depths alone in Southdown rams over five generations led to lower muscle to bone ratios particularly at higher live weights. The index used in the current study included ultrasound muscle depth as an additional selection criteria with no constraint on live weight. With approximately one generation less of selection, lean to bone ratio in high index lambs was on average 1.03 times that of low index lambs across the wide range of live weights considered in this study. Including muscle depth as a selection criteria, and allowing live weight to increase, appears to have compensated for the potential reduction in lean to bone ratio described by Abdullah *et al.* (1998) as an artefact of selection for lean growth rate.

Restricting food intake reduced the extent to which growth rate and efficiency in S exceeded that in C. When given food at about half of the *ad libitum* intake at a given live weight, with a consequent 0.47 proportional reduction in growth rate, there were virtually no differences in growth rate or efficiency between the lines. Thus live performance in the S line, expressed as growth rate and efficiency, was more sensitive to level of feeding than was the C line. However, the advantage to the S line in the lean to fat ratio in the carcass persisted to a similar extent at all levels of feeding. This suggests that the use of progeny from the S line will yield leaner carcasses across a wide range of finishing systems, even where these systems themselves affect the fatness of the carcass. Although the producer may not always see the benefit of the improved genotypes in terms of live performance, the consumer will probably see the benefit of reduced carcass fatness. Selection decisions based on an index of live weight and ultrasonic measures of fat and muscle depth have thus led to large improvements in carcass quality in terminal sire sheep that are expressed across a range of nutritional levels.

At the same estimated degree of maturity in weight, females were fatter over the wide range of carcass weights used (Table 7). McClelland *et al.* (1976) concluded that there were no sex differences in fatness at the same degree of maturity, as did Thompson *et al.* (1985). In disagreement with this Wylie *et al.* (1997) found that ewe lambs were fatter at common slaughter weights compared with their ram and wether siblings. The extent appeared to be greater than could be accounted for by a difference in degree of maturity. In general fatness is higher in female mammals at maturity and so would be expected to be so at all degrees of maturity (Emmans, 1988). In agreement with this Taylor *et al.* (1989) estimated that mature females would have a higher

proportion of fat than mature males using data from sheep and goats. Our results are consistent with this expectation.

In both lines the lean to fat ratio was somewhat increased by the levels of food restriction used. Beauchemin *et al.* (1995) also found that treating lambs in such a way that their growth rate was reduced by food restriction led to leaner carcasses. Lambs growing faster were found to be fatter at the same carcass weight than others growing more slowly (Hall *et al.*, 2001). The Agricultural Research Council (1980) suggested that fat content 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 in the cases quoted, it may not apply generally. Where the reduction is caused by, for example, a low food protein content, the reverse may be the case (R. M. Lewis *et al.*, unpublished).

The data on weights collected over time on *ad libitum* feeding could be described well by a Gompertz growth function, as expected (Lewis *et al.*, 2002). The high correlation between the estimated values of the two main parameters A , mature size, and B , the rate parameter, meant that little confidence could be placed in their estimated values separately, but together, in the form of their product $Z = AB$, a good estimate could be attained. The maximum rate of growth is given by Z/e . The function tracked the data well and changes in the values of its parameters can be seen as a suitable way of summarizing the effects of selection on growth.

Expressing weight as a function of the cumulative amount of food eaten, an approach that goes back at least to Spillman (in Spillman and Lang (1924), as quoted by Parks (1982)) was also of interest. The exponential functional form worked well as seen in Figure 2, both for *ad libitum* feeding and for the restricted regimes used here. As with the Gompertz function there is a problem in separately estimating the values of the two parameters A and k , but again their product is much more stable. The value of (Ak) was consistently greater in males than in females, on H than on M, and in S than in C, all of which differences reflected those in efficiency (Tables 3 and 5). Our lumped parameter (Ak) is equivalent to the efficiency parameter of Parks (1982). He found (his Table 4.2, p. 64) that the value of this parameter varied only between 0.30 and 0.62 in experiments on mice, rats, chickens and pigs. Parks (1970) had found that with rats the value of the efficiency parameter was proportional to the level of dietary energy content. Our slightly lower values found for sheep, Table 5, are likely to reflect the lower energy value of the food used due, in part, to the fermentation losses

that occur in ruminants and perhaps also the high fat content of sheep.

As cumulative food intake approximates to the cost of feeding and cumulative weight to the value of the animal, a good description of the relationship between the two has merit. Parks (1982) combined the Spillman function with another, presumed to describe the way in which *ad libitum* intake changed with time, to develop a system of growth and intake equations. The system depends on the intake function being of the correct form. The data on intake collected here suggest that the form used by Parks (1982) does not apply to sheep (R. M. Lewis *et al.*, unpublished).

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