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Abstract

A progeny test was designed to test whether genetic superiority for lean growth in terminal sires is expressed in their crossbred progeny when reared in a different environment. In each of 1986, 1987 and 1988, 22 Suffolk rams were chosen at the conclusion of an indoor, intensive performance testing regime on an index score that rated their propensity for lean growth, while constraining fat growth, at 150 days of age. Half of these rams had high index scores and half had low index scores. In each year, around 400 crossbred ewes were mated and the resulting lambs were finished on grass to one of three target live weights (35·5, 41·5, and 47·0 kg). Shoulder joints were dissected on 1505 lambs whilst half carcasses were dissected on 372 lambs. Double sampling techniques were then used to combine the data from the shoulder and half carcass more precisely to predict the lean, fat and bone weight and content in the carcass.

With each increment in target live weight, the carcasses were heavier and had proportionally more fat. The progeny of high index rams consistently had 144 (s.e.d. 32) g more lean, 66 (s.e.d. 12) g more bone, and 186 (s.e.d. 32) g less fat in a 19·7 (s.e. 0·5) kg carcass than progeny of low index rams, from the double sampling procedure. This improved composition reflected a correlated response to ram selection on the index. One standard deviation increase in ram index score corresponded to 51 g more lean and 64 g less fat in the 20 kg carcass of their crossbred offspring. These results show that the use of rams with high lean index scores in a crossbreeding system will produce lambs with leaner carcasses. Visual appraisals of fat and conformation both increased as the weight and, consequently, the fatness of the carcass increased. Offspring of high index rams were consistently scored as less fat than offspring of low index rams. But, at the lighter weights (35·5 and 41·5 kg), they were also scored lower in conformation — in effect, a penalty for their higher genetic merit for lean growth.

Keywords: *carcass composition, genetic parameters, progeny testing, selection, sheep.*

Introduction

With concerns about the rôle of animal fats in human health, and the wastefulness of excess fat trim, consumers are discriminating against meats that they believe are too fat (Woodward and Wheelock, 1990). Lamb has typically been considered excessively fat and this belief has exacerbated its decline in competitiveness with other meats (Kempster, 1983). This view, combined with the energetic and processing inefficiencies of waste fat, means that it is important to reduce the fatness of lamb.

Carcass composition can be changed by selection as there is genetic variation both within and between breeds of sheep (Simm, 1992). Direct measurements of carcass traits have the difficulties of being costly and of requiring slaughter of the animal. With developments in real-time ultrasonics, indirect *in vivo* measures of carcass traits are available. When combined with live weight, ultrasound measures of fat and muscle depth provide a good indication of fat and lean in a carcass (Simm, 1987). With the incorporation of live weight and ultrasonic measures into selection indices to improve the rate of lean deposition (Simm and Dingwall, 1989), selection programmes to reduce fatness in lamb carcasses are now practicable.

Within the United Kingdom (UK), the sires of most lambs raised for meat production come from

terminal sire breeds. Genetic improvement schemes for lean meat production can therefore concentrate on those few breeds which have a great impact on the genotype of the national lamb crop (Meat and Livestock Commission, 1993). In many terminal sire flocks, lambs are 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. However, most crossbred lambs in the UK are reared in more extensive grazing systems. Thus it is important to test whether high ranking rams under intensive feeding produce lean crossbred progeny in grass-based systems.

In the UK, lamb carcasses are valued based on weight, and visual assessments of fatness and conformation. If genetic improvement focuses on reducing fat in lamb, the relationship of this selection goal on the evaluation system used to assess lamb carcasses is important.

The study reported here had two objectives: (i) to determine whether crossbred progeny of comparatively lean and fat Suffolk rams express this difference in their carcass under grass finishing; and, (ii) to investigate if such changes in carcass composition affects visual assessments of carcass fatness and conformation.

Material and methods

Suffolk flock

In the early 1980s a Suffolk flock was established at the East of Scotland College of Agriculture, now part of the Scottish Agricultural College (SAC). In 1986 a performance testing regime was started. Ram lambs were creep fed from 1 week of age and gradually switched to *ad libitum* access to a complete pelleted diet which was high in energy (12·3 MJ/kg dry matter (DM)) and protein (178 g crude protein per kg DM) content by weaning at 56 days from birth. When 150 days old, their live weights (*LW*), and their ultrasound measurements of muscle (*UMD*) and fat depth (*UFD*), were recorded. These measurements were then combined into a selection index constructed as 0·103 *LW* + 0·257 *UMD* – 0·406 *UFD*. The index was designed to increase the rate of lean deposition, with little change in the rate of fat deposition (Simm and Dingwall, 1989). Ram lambs were selected on index score to produce one line with high index scores and another line with average index scores as a control. Index scores were scaled such that the average of the control line was 100 points, and the standard deviation of the index was 40 points.

Progeny test

In 1986, 1987 and 1988, in total 77, 94 and 88 Suffolk rams, respectively, were performance tested. At the end of each performance test, 22 of these rams with extreme index scores were chosen for progeny testing. Half of these rams had high index scores and half had low index scores (Table 1). In 1986 an additional low index ram was used due to the poor performance at mating of one ram. At the end of the performance test, these rams on average weighed 67·7 (s.d. 6·4) kg, and had an ultrasonic muscle depth of 28·8 (s.d. 2·4) mm and an ultrasonic fat depth of 7·9 (s.d. 1·4) mm. The rams selected as high index were on average 11·4 (s.e.d. 2·2) kg heavier, and had 4·8 (s.e.d. 2·3) mm more muscle depth and 1·2 (s.e.d. 1·0) mm less fat depth than their low index counterparts. The means of the two index categories differed by 121 index units. The selection differential (once accounting for the number of progeny produced by each ram) was 1·52 s.d. units of the

Table 1 *Numbers of sires and progeny by the year of the progeny test and index category*

	1987		1988		1989	
Category	High index	Low index	High index	Low index	High index	Low index
No. of sires	11	12	11	11	11	11
Mean no. of progeny per sire	25·3	24·8	29·1	31·1	29·9	28·3
s.d. half-sib (sire) family size†	5·0	9·2	7·9	11·5	10·1	10·0
No. of progeny by target slaughter weight category‡						
35·5 kg	94 (16)	101 (17)	95 (21)	119 (23)	107 (21)	102 (21)
41·5 kg	99 (17)	107 (17)	114 (23)	116 (26)	116 (26)	103 (25)
47·0 kg	85 (18)	89 (15)	111 (23)	107 (21)	106 (23)	106 (19)

† Expressed in s.d. units of index (s.d. of index was 40) accounting for rams alone being selected.
‡ Number of progeny with shoulder dissection data (number with full side dissection data shown in parentheses).

index. The number of rams used — proportionally, about the upper or lower 0·15 of those available — was chosen to minimize the variance of an offspring-parent regression given a trait with a heritability of 0·25, a genetic correlation of 0·75 between indoor and pastoral performance, and the fact that about 600 lambs could be evaluated each year (Hill and Thompson, 1977).

In 1986 around 400 Scottish Mule (Bluefaced Leicester × Scottish Blackface) ewes, 1½ and 2½ years of age, were purchased from three sources for use in the progeny test. In 1987 and in 1988 about 100 more 1½ year-old ewes were purchased from new sources. In each year, mating began in October and continued for 6 weeks. Between 18 and 20 ewes were assigned at random to each ram and joined in separate paddocks. Following mating, ewes were managed in a single flock. Ewes were housed in mid January. Within 1 day of birth, the weight and sex of each lamb was recorded. As a proportion, 0·94 of the ewes gave birth to two or more lambs. The extra lambs born in litters of three or more were either fostered or reared artificially. Ram lambs were castrated within 24 h of birth. By 1 week of age, lambs and ewes were shifted to one of three paddocks balanced for the lamb's sire. The specific paddocks grazed differed each year. Over the 3 years 2524 lambs were born and 1999 reared (90% as twins) from 1142 lambings of 481 ewes.

Within each sire progeny group, lambs were allocated at random to three target live weights for slaughter at 35·5, 41·5 and 47·0 kg. These live weights were chosen to achieve carcass weights of 16·5, 20·0 and 23·5 kg, which represent the range of carcass weights in commercial lamb production. Lambs, and their dams up to weaning, grazed swards of predominantly perennial ryegrass (*Lolium perenne L*) with an initial, target sward height of 8 cm. When swards were grazed to less than 4 cm (by October or November), lambs were supplemented with a diet based on barley, beet pulp and lucerne at rates of up to 150 g/day. Once near their slaughter weight, lambs were weighed weekly to ensure target slaughter weights were obtained. Across years, 41% of the lambs reached their target weight before weaning; of the remaining lambs, 60% reached their target weight on grass alone. All lambs were slaughtered by mid December. In total 1877 lambs were slaughtered so carcass measures on 28 (s.d. 9·1) lambs per sire were available for further analyses.

Slaughter measurements
Lambs were weighed unshorn before transport for slaughter. The carcasses were chilled overnight and their weight recorded. All carcasses were scored for subcutaneous and internal fat, and for conformation, by the classifier on duty from the Meat and Livestock Commission (MLC). Fat classes were scored as Un, 2, 3L, 3H, 4L, 4H, and 5 which, on average, correspond with subcutaneous levels of fat of 4, 8, 11, 13, 15, 17 and 20% in the carcass (Kempster *et al.*, 1986). The recorded scores were replaced with the subcutaneous fat level before statistical analysis. In 1988 and 1989, the MLC classifier also made a direct visual estimate of proportion of subcutaneous fat on the carcass.

A kidney knob and channel fat (KKCF) score was used to categorize internal fat into four levels: 0 to 110, 120 to 230, 240 to 340 and 350 to 450 g per carcass. For the purpose of data analyses, it was assumed these scores were generated by an underlying normal distribution with mean zero and unit variance (Cameron, 1992). Based on the proportion of lambs falling into a category, a threshold value representing the average deviation (in s.d. units) from mean zero was determined. The proportion of lambs within each internal fat score category, and the corresponding threshold value, were 0·12 and –1·668 (0 to 110 g), 0·50 and –0·359 (120 to 230 g), 0·32 and 0·829 (240 to 340 g), and 0·06 and 2·004 (350 to 450 g). A larger (more positive) theshold value indicated more KKCF weight.

Carcass information was assessed as five categories (E, U, R, O, P) with 'E' indicating the best conformation. Since, as with internal fat score, there were few categories for conformation score, data were transformed to threshold values. The proportion of lambs scored E, U, R, O and P was 0·01, 0·18, 0·61, 0·15 and 0·05; these corresponded with threshold values of 2·72, 1·36, 0·01, –1·19 and –2·07. A larger (more positive) threshold value indicated better visual conformation. In 1988 and 1989, a 15-point scale assessment of leg, loin, shoulder and overall conformation also was used; larger scores indicated better conformation.

Tissue composition measurements
The left sides of about 20% of the carcasses in each sire family were separated into eight joints (breast, chump, end-neck, leg, loin, mid-neck, scrag and shoulder) as described by Cuthbertson *et al.* (1972). For the remainder, the shoulder joint alone was collected. Each joint was dissected into lean, fat (subcutaneous and intermuscular), bone, and waste components. KKCF weight was recorded in animals with half carcass dissections.

Statistical analyses
Model selection and fitting. Residual maximum likelihood procedure (REML; Patterson and Thompson, 1971) was used to fit a linear mixed model to describe measurements collected from

slaughter (age and carcass weight, yield and visual appraisal) and from tissue dissection (GENSTAT 5 Committee, 1993). Data for each target weight category were analysed separately. The fixed effects were index category, sex, dam age (2, 3, and 4 years of age and older), grazing location (three each year), rearing type and the interaction of rearing type and grazing location. For tissue weight (lean, fat and bone) and ratio (lean to fat and lean to bone) in the shoulder joint, and for visual appraisal of the carcass, a linear regression of the measurement on carcass weight was estimated. Sire (nested within index category) and residual were fitted as random effects.

The three target slaughter live weights were incorporated in the experiment to determine if differences in progeny carcass traits of high and low index rams were dependent on carcass weight. On the basis of shoulder joint dissection, the difference in carcass lean, fat and bone content between high and low index rams was the same for each target category (Table 2). Also, there were no differences in residual variances for shoulder joint lean, fat and bone content at each target slaughter weight (Table 2). Within each of the three target slaughter weight categories, regression coefficients for shoulder lean, fat and bone weight on carcass weight were similar for progeny from high and low index rams ($P > 0{\cdot}10$). Therefore, dissection data from the three target weight slaughter weights could be combined, based on the consistency of the difference in the shoulder joint composition between progeny of high and low index rams, the homogeneity of variances, and the lack of interaction between carcass weight and index category for the regression coefficients of weights of tissue in the shoulder joint on slaughter weight.

Shoulder joint and half carcass dissection data were combined across the three target slaughter weight categories, and described using a mixed linear model with the fixed and random terms defined earlier. Target slaughter weight (a fixed effect) and dam (a random effect) were added to the model. For tissue weight and ratio, a linear and quadratic regression of the measurement on carcass weight was also fitted.

Double sampling. Double sampling procedures were used to combine data from lambs with only shoulder dissections with those with half carcass dissections to more precisely estimate the difference in tissue composition between the high and low index groups. The proportion of lambs chosen (0·20) for half carcass dissections was based on a formula from Cook *et al.* (1983). The choice of the shoulder joint as the sample joint from all lambs to dissect was due to the high correlation (0·90) between the lean contents of the shoulder and the carcass (Cook *et al.*, 1983).

For each index category, a maximum likelihood estimate of the mean (and variance) of the weight and content of lean, fat and bone, and the ratio of lean to fat and lean to bone, in the half carcass was derived using procedures described by Conniffe and Moran (1972). A stepwise selection procedure was used to choose those regressors defining the most variation in each tissue evaluated to be included in the prediction equation. The covariates were the weight and content of lean, fat and bone, or their ratio, in the shoulder as appropriate. To determine if the regressions were index category specific, coefficients were estimated both within and between index categories. However, the difference between the within index group coefficients did not differ from zero ($P > 0{\cdot}10$) so the same prediction equation was used for both index categories.

Correlated response to selection. The effect of sire selection on progeny performance was characterized by the offspring-parent regression $0{\cdot}5\ [r_a h_x h_y (\sigma_{py}/\sigma_{px})]$ where y was the progeny trait measured, x was the sire index score, r_a was the genetic correlation between the progeny trait and the sire index score, h^2 was the heritability, and σ_p was the phenotypic standard deviation. The term $r_a h_x h_y$ is referred to as the co-heritability and quantifies the predicted genetic response from selection of rams on index score on the correlated slaughter and carcass traits expressed in their progeny.

The offspring-parent regression and co-heritability were estimated in two ways. Firstly REML methodology was used to estimate the offspring-parent regression coefficients concurrently with sire, dam and residual as random effects (Cameron, 1992). Sire index category was excluded. The parental record, sire index score, was repeated as a covariate for each record on its offspring. The underlying assumption in this model was that sires were unrelated and unselected — neither of which was true in this case. However, the experiment was conducted early in the development of the Suffolk flock (less than one generation of past selection) and any bias in the estimates was expected to be small. Co-heritabilities and their standard errors were estimated from the solutions for the regression coefficients.

The offspring-parent regression and co-heritability were also derived using bivariate REML (BIREML) methodology to consider the importance of past selection within the Suffolk flock, and any genetic relationships between animals, on these estimates. The performance test records on the 331 Suffolk rams tested between 1985 and 1989 were joined with the records collected in the progeny test. The index score on each Suffolk ram was now included only once in

the data. Pedigree information on all animals since the establishment of the Suffolk flock was combined with that from the progeny test (in total 4778 pedigree records). For each pair of sire (index score) and progeny trait, the genetic and residual variances, and the genetic covariance, were then estimated using the MTDFREML program (Boldman *et al.*, 1995). Since only one of the two traits was measured on each animal with performance information, there was no residual covariance between the traits. The model chosen to describe the performance of Suffolk rams included only birth year as a fixed term. All relationships between animals were considered in the analysis. Purebred Suffolks with unknown ancestries and the Scottish Mule ewes were assigned to separate genetic groups. With MTDFREML the maximum of the log likelihood function is found by the Simplex method. The convergence criterion chosen was that the variance of the Simplex function fall below 1×10^{-9}. The offspring-parent regressions and co-heritabilites where then calculated from the (co)variance components that maximized the likelihood (Cameron, 1992).

The standard error of a BIREML co-heritability was derived by fitting a quadratic regression to a grid of log likelihood values. A point on this grid or surface was obtained by solving the log likelihood for a co-heritability and sire index heritability at fixed increments from their converged values; for each point, the heritability of the progeny trait was kept the same (Cameron and Curran, 1995). A log likelihood surface contained 10 points. The co-heritability, and the sire index heritability, at the maximum of the log likelihood surface was found and the standard error estimated. In all cases, the quadratic regression explained as a proportion at least 0·98 of the variation in the log likelihood surface. Standard errors for the offspring-parent regressions were calculated from the standard errors for the co-heritabilities.

Results

Slaughter measurements

In Table 2, results for the measurements recorded at slaughter, and for the tissue content of the shoulder joint, are summarized for each target live-weight category. The extra live-weight gain of 11·5 kg from

Table 2 *Measures recorded at slaughter and tissue composition of the shoulder joint for each target weight category*

	Target weight									
	35·5 kg (no. = 618)			41·5 kg (no. = 655)			47·0 kg (no. = 604)			Between target weight
Measure	Mean	Difference high-low	s.e.d.	Mean	Difference high-low	s.e.d.	Mean	Difference high-low	s.e.d.	s.e.d.
Age at slaughter (day)	110·2	−2·8	2·9	140·9	−7·7	4·0	169·1	−1·0	2·6	1·8
Carcass weight (kg)	17·05	0·04	0·10	19·72	−0·14	0·11	22·40	−0·15	0·10	0·05
Carcass yield (g/kg)	471·7	−1·0	2·5	471·3	−2·8	2·2	476·0	−5·1	1·9	1·2
Visual appraisal†										
Fat score subcutaneous fat (%)	9·40	−0·66	0·20	12·24	−0·40	0·19	14·29	−0·64	0·22	0·12
Estimated subcutaneous fat (%)‡	9·30	−0·70	0·22	11·78	−0·29	0·21	13·79	−0·57	0·25	0·13
Internal fat score‡§	−0·62	−0·17	0·07	0·11	−0·11	0·07	0·63	−0·05	0·07	0·05
Conformation score§	−0·55	−0·30	0·08	0·06	−0·19	0·07	0·40	−0·03	0·08	0·04
Conformation‡‖										
Leg	7·83	−0·73	0·27	9·76	−0·29	0·20	10·78	0·02	0·25	0·13
Loin	7·90	−0·79	0·27	10·00	−0·35	0·20	11·34	−0·09	0·21	0·13
Shoulder	7·65	−0·75	0·25	9·68	−0·31	0·19	10·88	0·02	0·22	0·13
Overall	7·81	−0·75	0·27	9·73	−0·34	0·20	10·99	−0·04	0·23	0·13
Tissue composition (shoulder)										
Lean content (g/kg)	535	7	3	517	9	3	504	8	3	2
Fat content (g/kg)	275	−10	4	305	−11	4	328	−9	3	2
Bone content (g/kg)	183	3	1	171	2	1	161	2	1	1

† Regressed to the average weight of the carcass within the target weight category.
‡ Recorded in 1988 and 1989 only. Numbers were 416 (35·5 kg), 439 (41·5 kg) and 416 (47·0 kg).
§ Threshhold values corresponding with the proportion of lambs categorised into each level of score. Larger values (more positive) indicate a heavier internal fat weight or a higher visual conformation.
‖ Fifteen-point visual conformation score with larger values indicative of better conformation.

the lightest to the heaviest target weight category took about 60 days and produced a 5·4 kg heavier carcass. On average, a carcass weighed 19·7 (s.e. 0·5) kg. The progeny of the high index rams reached their pre-assigned target live weight more quickly than those of the low index rams, but the difference was significant only for the medium weight (41·5 kg). Although low index lambs had higher carcass yields than high index lambs at all weights, it was only at the heaviest live weight (47·0 kg) that the difference was significant.

On average, the carcasses were scored 3L-3H on the MLC fat class scale. For both the fat class score and the direct visual appraisal of subcutaneous fatness, offspring of high index rams had less subcutaneous fat than those of low index rams. The size of the difference in visual fatness between index categories was, in general, consistent across the target weight categories.

On average, the carcasses were scored 'R' on the EUROP conformation score. For both the EUROP and 15-point conformation score, visual conformation increased with live weight at slaughter. In general, progeny of high index rams were scored lower in conformation than progeny of low index rams; however, a significant difference between index categories was only detected for those lambs slaughtered at the lightest weight.

Tissue composition measurements

Shoulder joint. The lean and bone content of the shoulder joint decreased, whilst the fat content increased, with the increase in carcass weight at each target weight category ($P < 0·01$). However, within a target weight category, progeny of high index sires had a consistent advantage in terms of lean content (on average 8 g/kg) and fat content (on average –10 g/kg) in their shoulder joint. The amount of residual variation around the mean was the same for each target weight category.

In Table 3 results from the shoulder joint and half carcass dissections between target weight categories are shown. In terms of tissue weights, high index lambs had more lean and bone, and less fat than low index lambs although the absolute differences were small (less than 20 g). The reduction in fat weight in high index lambs was, as a proportion, 0·38 more than the increase in lean weight with much of that change occurring in the subcutaneous fatness.

Half carcass. On average, a half carcass contained 532 g/kg lean, 290 g/kg fat and 167 g/kg bone — a higher lean content than in the shoulder joint. The progeny of high index rams had proportionally more lean (6 g/kg) and less fat (–9 g/kg) in their carcass than progeny of low index rams — this difference corresponded with 154 g more lean and 146 g less fat in the carcass. Although the total weight of subcutaneous fat was less than that of fat elsewhere in the carcass (and shoulder), it changed proportionally more due to index category (0·32).

Double sampling

When information from the half carcass and shoulder joint were combined using the double sampling procedure, the difference in tissue content between index categories was very similar to that

Table 3 *Differences between progeny of high and low index sires for tissue composition of shoulder and carcass*

	Shoulder joint (no. = 1877)			Carcass (no. = 372)			Predicted carcass from double sampling	
Measure	Mean	Difference high-low	s.e.d.	Mean	Difference high-low	s.e.d.	Difference high-low	s.e.d.
Joint (g)	1886	–3	5	19234	–31	103		
Tissue composition†								
Lean content (g/kg)	519	8	2	532	6	3	7	2
Fat content (g/kg)	301	–10	2	290	–9	4	–12	2
Bone content (g/kg)	172	3	1	167	3	1	4	1
Lean (g)	981	13	5	9692	154	78	144	32
Fat (g)‡	564	–18	6	5392	–146	70	–186	32
Subcutaneous fat (g)	254	–13	4	2414	–82	48	–106	20
Other fat (g)§	311	–5	3	2976	–62	32	–74	16
Bone (g)	327	3	2	3012	68	28	66	12
Lean to fat ratio (g/g)	1·82	0·09	0·02	1·88	0·07	0·04	0·10	0·02
Lean to bone ratio (g/g)	3·01	0·01	0·02	3·22	–0·02	0·03	–0·02	0·02

† Regressed to the average weight (across target weight categories) of the carcass.
‡ Subcutaneous and intermuscular fat. For carcass, includes kidney knob and channel fat (KKCF)
§ Intermuscular fat. For carcass, includes KKCF.

detected for the shoulder joint and half carcass dissections. However, the differences in the weight of lean decreased (144 g) whilst that of fat increased (–186 g) between the index categories with the double sampling procedure as compared with the half carcass dissections. This possibly was due to those lambs chosen for half carcass dissection tending to be leaner. Although the shoulder joint of these lambs had a similar weight (1888 g) and quantity of fat (567 g) to that of lambs for which only a shoulder was dissected, they had slightly more lean (991 g) and less bone (315 g) in their shoulder. Also, the difference in shoulder fat weight between the offspring of high and low index rams was smaller (–13 (s.e.d. 9) g).

The multiple regression equations used for prediction in the double sampling methodology explained, as a proportion, at least 0·83 of the variation in the weight and content of lean and fat, and the lean to fat ratio, in the carcass. For bone weight and content, and for the ratio of lean to bone, the predictions were somewhat poorer — the models fitted explained 0·79, 0·76 and 0·59 of the variation. The additional information provided by the shoulder joint dissections reduced the s.e.d. between the two index categories by at least one half in the double sampling procedure.

Correlated response to selection

Offspring-parent regression. In Table 4 the REML and BIREML estimates of the offspring-parent regression coefficients are shown. There was only a small reduction in the age at which lambs reached their target weight with an increase in ram index score ($P > 0{\cdot}10$). But, as index score increased, lambs deposited more lean, less fat and more bone in both the overall carcass and shoulder joint ($P < 0{\cdot}05$). Each point increase in the index score of the sire translated into about 1·3 g more lean and 1·6 g less fat in the carcass of their crossbred progeny. Regression coefficients for lean and fat weight deposition were approximately five times greater for the half carcass than for the shoulder, which corresponds with the shoulder joint comprising proportionally 0·2 of the total carcass weight. The estimates obtained for the regression coefficients by REML and BIREML were similar in magnitude.

Co-heritability. The REML and BIREML co-heritability estimates are shown in Table 5. The co-heritabilities based on shoulder and half carcass dissections were significantly different from zero, and similar in magnitude to one another, for all tissues considered except non-subcutaneous fat and lean to bone ratio. The co-heritabilities for lean and fat content, and their ratio, were as much as twice the size of those for other tissues. The low co-heritability for intermuscular fat in the shoulder, and for the intermuscular plus KKCF fat in the half carcass, is consistent with the small difference detected in these fat depots between the two index categories. As was found with the estimates of offspring-parent regression coefficients, the co-heritability estimates from REML and BIREML were generally in agreement. Across tissues, and between the shoulder

Table 4 *Offspring-parent regression coefficients (s.e.) of progeny age at slaughter, and of tissue composition of the shoulder and carcass, on sire index score, estimated by residual maximum likelihood (REML) and bivariate REML (BIREML)*

	Shoulder				Carcass			
	REML		BIREML		REML		BIREML	
	Coefficient	s.e.	Coefficient	s.e.	Coefficient	s.e.	Coefficient	s.e.
Slaughter age (day)	–0·023	0·016	–0·015	0·041				
Tissue composition								
Lean content (g/kg)	0·063	0·017	0·069	0·019	0·053	0·024	0·065	0·031
Fat content (g/kg)	–0·084	0·019	–0·097	0·025	–0·076	0·030	–0·096	0·041
Bone content (g/kg)	0·021	0·007	0·023	0·013	0·026	0·011	0·031	0·018
Lean (g)†	0·110	0·037	0·115	0·046	1·250	0·597	1·272	0·619
Fat (g)†‡	–0·136	0·043	–0·146	0·075	–1·283	0·535	–1·602	0·704
Subcutaneous fat (g)†	–0·103	0·029	–0·106	0·033	–0·753	0·364	–0·847	0·373
Other fat (g)†§	–0·034	0·021	–0·039	0·023	–0·502	0·263	–0·599	0·406
Bone (g)†	0·027	0·013	0·024	0·025	0·489	0·219	0·516	0·306
Lean to fat ratio (g/g)†	0·693	0·186‖	0·784	0·355‖	0·603	0·285‖	0·714	0·327‖
Lean to bone ratio (g/g)†	0·077	0·150‖	0·138	0·204‖	–0·107	0·215‖	–0·053	0·227‖

† Regressed to the average weight (across target weight categories) of the carcass

‡ Subcutaneous and intermuscular fat. For carcass, includes kidney knob and channel fat (KKCF).

§ Intermuscular fat. For carcass, includes KKCF.

‖ Regression coefficients (and s.e.) × 1000.

Table 5 *The co-heritability (s.e.), estimated by REML and BIREML, for age at slaughter and the tissue composition of the shoulder and carcass*

	Shoulder				Carcass			
	REML		BIREML		REML		BIREML	
	Co-heritability	s.e.	Co-heritability	s.e.	Co-heritability	s.e.	Co-heritability	s.e.
Slaughter age (day)	−0·06	0·05	−0·03	0·09				
Tissue composition								
Lean content (g/kg)	0·25	0·07	0·18	0·05	0·23	0·11	0·20	0·09
Fat content (g/kg)	−0·25	0·06	−0·21	0·05	−0·24	0·09	−0·23	0·10
Bone content (g/kg)	0·15	0·05	0·12	0·07	0·20	0·09	0·18	0·11
Lean (g)†	0·12	0·04	0·14	0·05	0·13	0·06	0·17	0·08
Fat (g)†‡	−0·13	0·04	−0·16	0·08	−0·13	0·05	−0·21	0·09
Subcutaneous fat (g)†	−0·17	0·05	−0·18	0·05	−0·14	0·07	−0·19	0·08
Other fat (g)†§	−0·06	0·04	−0·07	0·04	−0·10	0·05	−0·15	0·10
Bone (g)†	0·10	0·05	0·07	0·08	0·19	0·09	0·17	0·10
Lean to fat ratio (g/g)†	0·23	0·06	0·19	0·09	0·21	0·10	0·19	0·09
Lean to bone ratio (g/g)†	0·03	0·07	0·04	0·06	−0·05	0·10	−0·02	0·08

† Regressed to the average weight (across target weight categories) of the carcass
‡ Subcutaneous and intermuscular fat. For carcass, includes kidney knob and channel fat (KKCF).
§ Intermuscular fat. For carcass, includes KKCF.

joint and half carcass dissections, there was no clear trend in the differences between the REML and BIREML estimates. Although the rams chosen for use within the Suffolk flock and progeny testing were related, there had apparently been little reduction in genetic variation within the flock due to past selection at the time of the experiment.

Discussion

The index category of a lamb affected its tissue composition at a fixed carcass weight. Lambs with high rather than low index sires produced a carcass with on average 7 g/kg more lean and 12 g/kg less fat. This improved composition reflected a correlated response to ram selection on the index. A 40-point increase in index score (one standard deviation) corresponded with more than 50 g of fat being replaced by lean in a 20-kg carcass. These results show that the use of rams with high lean index scores in a crossbreeding system will produce lambs with leaner carcasses.

The design of the experiment included three target live weights for slaughter, largely to ensure a range in carcass weights typical for the UK market. As expected, with each increment in target live weight, carcass weight increased, and the carcass became proportionally fatter. However, at each target weight considered in this study, the increase in lean content in progeny of high over low index rams remained the same. Importantly, this implies that across a range of live weights and levels of maturity, the response to selection for lean growth persists.

Strategies to alter the composition of the carcass may be seen as acting in one of two ways: direct effects on the composition or the indirect effect of changing the size of the animal at maturity (Simm *et al.*, 1987; Thompson 1990; Cameron and Bracken, 1992). The two effects may be linked. Growth waves or gradients in the tissues of the body exist and follow a specified order — for example brain, bone, muscle and then fat (Hammond, 1940). At each stage of growth, each of these tissues will have matured to a different extent. If live weight at maturity is increased itself, at a given lighter weight the earlier maturing tissues will make up a greater proportion of the body.

With slaughter at an age rather than a weight, Bennett *et al.* (1988) and Cameron (1992) found that the carcass composition of a lamb depended on whether its sire originated in a lean or fat line. In both studies, rams were selected on live weight and *in vivo* measure of fat depth combined to achieve the goal of reduced fat with little change in live or carcass weight. Bennett *et al.* (1988) recorded the selection criteria repeatedly from weaning until selection at 18 months of age whilst the candidate rams grazed a mixed sward of ryegrass and clover. With lambs slaughtered at an early age (15 or 19 weeks) Bennett *et al.* (1988) found that progeny of lean rams had less fat weight; these lambs, however, did not differ in lean weight. At a later age (26 or 28 weeks), the initial difference in fat remained. It would appear that rates of fat deposition were changed, at least to the early age, with no change in lean growth. In the current study, the difference in lean, fat and bone was established by the lightest target weight (35·5 kg; about 16 weeks of age)

and remained through to the heaviest target weight (47·0 kg; about 24 weeks of age). At these weights (or aligning ages) these lambs would have reached, as a proportion, 0·3 to 0·5 of their mature weight. Between breeds, it has been reported that proportional differences in the tissue composition of the body may be established proportionally by 0·3 mature live weight, and then remain fairly constant thereafter to maturity (McClelland *et al.*, 1976; Wolf and Smith, 1983). This also appears to be the case among lines within a breed.

Cameron and Bracken (1992) recorded live weight and ultrasonic fat depth at 20 weeks of age at the end of a performance testing regime similar to that described here. At 16 weeks of age, Cameron (1992) found that the progeny of lean rams selected from this performance test had more lean weight and the same fat weight in their carcass. As in this study, the progeny of lean rams had higher carcass lean and lower carcass fat propotions. Cameron (1992) concluded that the two lines had different rates of lean growth but similar rates of fat growth. In each of these studies, carcass composition changed in line with sire genotype. What differed was how the change in composition was expressed.

What remains unclear is what changes in the genotype of the lambs in the current study led to the compositional characteristics of their carcass that were measured. Was the regulation of tissue composition of these lambs changed as well as their mature live weight? The index used in this study was designed to identify rams with higher rates of lean deposition and larger body size. Within a breed, heavier strains are larger at maturity (Butterfield *et al.*, 1983; Thompson, 1990) so weigh more when compared at the same age. When compared at the same weight, however, heavier strains have been shown to have more lean and bone and less fat in their body (Butterfield *et al.*, 1983; Thompson *et al.*, 1985) presumably due to a lower degree of maturity (Taylor, 1985).

In the current study, the high index Suffolk rams used weighed over 10 kg more than the low index rams at the same age at the end of their performance test. When compared at the same live weight, their progeny had more lean and bone, and less fat in their carcass. Both results could be explained, at least in part, by a change in mature size. Also, the rate of tissue deposition could have been altered. Further work is in progress in the SAC Suffolk flock which will provide information on body composition at a series of live weights; this research is designed to disentangle the effects of the selection using the described index on the rate of deposition of lean and fat, and on mature size.

The visual appraisals of fat and conformation both increased as the weight and, consequently, the fatness of the carcass increased. Reducing carcass fatness while at the same time improving visual conformation as it is currently defined thus appear to be contrary objectives, at least within the common breed type considered in this study. At every weight considered in this study, lambs with low index sires were appraised as having a fatter carcass than lambs with high index sires. The difference in fat score remained about the same at each target weight — the same pattern as found for the fat content of the shoulder joint. At the lightest target weight category, the progeny of low index rams were awarded significantly higher conformation scores for their carcass than progeny of high index rams. At the medium weight the difference in carcass conformation was smaller and, by the heaviest weight, no difference in carcass conformation was recorded. Firstly, differences in visual conformation appear to be more clearly discriminated at lighter carcass weights when lambs are less fat. More importantly, progeny of rams selected for high genetic merit for lean growth were penalized for their extra leanness. An unfortunate consequence of this coupling of conformation with fat score is that progress in reducing fat in market lambs will be slowed by the carcass assessment system in place.

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