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Responses to selection for lean growth in sheep

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Abstract

This paper reports the selection responses achieved, and related results, following 9 years of index selection for lean growth in Suffolk sheep. The breeding goal of the index used comprised carcass lean weight and carcass fat weight at a constant age, with relative economic values of + 3 and –1 per kg. The selection criteria were live weight (LWT), ultrasonic fat depth (UFD) and ultrasonic muscle depth (UMD) adjusted to a constant age of 150 days. By year 9, responses in LWT, UFD and UMD in both sexes, as judged by the divergence between selection and control line performance, amounted to 4·88 kg, –1·1 mm and 2·8 mm respectively; these responses are between 7 and 15% of the overall means of the traits concerned. Although selection was originally on index scores based on phenotypic records, the retrospective analyses reported here used the mixed model applications of residual maximum likelihood to estimate parameters and best linear unbiased prediction to predict breeding values. The statistical model comprised fixed effects plus random effects accounting for direct additive, maternal additive and temporary environmental variation. Estimated genetic trends obtained by regressing estimated breeding values on year of birth were similar to annual responses estimated by comparing selection and control line means. Estimates of direct heritabilities were 0·054, 0·177, 0·286, 0·561 and 0·410 for birth weight (BWT), weaning weight (WWT), LWT, UFD and UMD respectively. Corresponding estimates of maternal heritabilities were 0·287, 0·205, 0·160, 0·083 and 0·164. Phenotypic correlations between all pairs of traits were positive and usually moderately high. There were low negative direct additive correlations between BWT and WWT, and between BWT and LWT, but higher positive maternal additive correlations between all other pairs of weight traits.

Keywords: *selection responses, sheep, ultrasonography.*

Introduction

In many western countries consumers have been expressing a strong preference for leaner meat (e.g. Kempster, 1983; Woodward and Wheelock, 1990). This has contributed to the decline in lamb consumption in several countries, including Britain, as lamb has a higher fat content than most other meats. Selection between and within breeds has been, and continues to be, practised in many countries to help to align the composition of lamb more closely with consumer preferences.

There have been several designed breed comparisons, involving terminal sire and other breeds, which provide objective information to help in the choice of breeds to improve carcass composition (e.g. McClelland *et al.*, 1976; More O'Ferrall and Timon, 1977; Wolf *et al.*, 1980; Kempster *et al.*, 1987; Leymaster and Jenkins, 1993). When breeds are compared at similar degrees of maturity in live weight, they tend to be similar in carcass composition (McClelland *et al.*, 1976; Taylor, 1980). However, at a constant level of fatness, lambs sired by breeds of larger mature size produce heavier carcasses. Alternatively, at a constant carcass weight, lambs sired by breeds of larger mature size are leaner.

Selection within breeds is somewhat more complex than selection between breeds. Perhaps for this reason it has been underutilized in the past. Even where there is good evidence for the superiority of one breed over another, there is usually substantial variation in growth and carcass characteristics within breeds, and hence overlap between the breeds. Consequently, it is important that there are tools available for both purebred and commercial sheep producers to select appropriate rams within the breed they choose to use.

Differences in mature size may also explain much of the within-breed variation in carcass composition at a given weight, though there is also evidence of variation in fatness at maturity and rate of maturing in fatness in laboratory animals and sheep (see review of Simm (1992)). Although these are biologically useful concepts when considering selection objectives, they are difficult to apply to within-breed selection in practice. Hence, more practical selection objectives are to alter the rate of gain of lean tissue to an immature weight, or to alter the proportion of lean in the carcass at an immature weight.

There has been substantial research effort to identify useful techniques for the *in vivo* measurement of carcass composition in sheep, and to define selection criteria incorporating these measurements, in pursuit of the breeding goals mentioned above (e.g. see reviews of Simm (1987, 1992 and 1994), Bennett (1990) and Banks (1999)). The *in vivo* measurements most widely used have been ultrasonic measurements of fat and muscle depths or areas. Selection experiments have been established to test these techniques, and selection criteria based on them, in a number of countries, particularly New Zealand and Britain. The purpose of this paper is to report the selection responses achieved in one of these experiments, and related results including estimates of heritabilities of, and correlations among, the selection criteria.

Material and methods

The experiment involved 9 years of index selection in Suffolk sheep at the East of Scotland College of Agriculture, now part of the Scottish Agricultural College (SAC). The breeding goal of the index comprised carcass lean weight and carcass fat weight at a constant age, with relative economic values of + 3 and –1 per kg, as proposed by Simm and Dingwall (1989). The selection criteria were live weight, ultrasonic fat depth and ultrasonic muscle depth adjusted to a constant age. The relative economic values were chosen to achieve 'desired gains' in the traits in the breeding goal, rather than being based on actual market returns and costs of production. This approach was chosen because of the weak relationship between carcass price and fatness in Britain at the time the index was derived. Selection on this index was expected to lead to close to maximum gains in lean weight, whilst restricting the correlated increase in fat weight to about 26% of that expected from selection on live weight alone (Simm and Dingwall, 1989).

Selection procedures

The flock was established in the early 1980s by purchasing females from around 50 pedigree Suffolk flocks throughout Britain. Some of the purchased females were pregnant already; the others were mated to purchased or hired rams. About 25 different rams were used during this establishment phase. The flock numbered about 140 ewes when selection began in 1985 but this was increased to about 250 by 1989. When selection began, ewes were allocated to selection and control lines, balanced for source flock, age, live weight and body condition score. The average coefficient of relationship between selection and control line females at this time was 0·03, which was not significantly different from the average relationship within the selection (0·04) and control (0·02) lines.

In the first year of selection, ram lambs with high and average predicted carcass lean weight were allocated to the selection and control lines respectively. For this initial selection, lean weight was predicted from live weight and ultrasonic muscle depth measurements (Simm, 1987); this criterion was very highly correlated with the index used in subsequent years. Thereafter, ram lambs from the two lines were performance tested together each year, and selected within line. Ewe lambs were performance tested from 1989 onwards.

Ewes were housed 6 to 8 weeks prior to lambing, and lambs were reared indoors until the end of the performance test. Ewes that had triplet lambs, or were unable to rear twin lambs, had one or more lambs fostered off. Between 1 and 14 lambs were fostered annually. Lambs were given *ad libitum* access to a creep food from about 7 days of age. From 42 days of age this was gradually changed to a high

Table 1 *Index coefficients used in selection (from Simm and Dingwall, 1989). For ease of comparison of the relative emphasis given to each trait in this index, coefficients are also shown on a per phenotypic standard deviation (σ_p) basis, using the values of σ_p used in the derivation of the index*

Trait	Index coefficient (*b*)	σ_p	*b* per σ_p
Live weight at end of test (LWT)	+0·103 / kg	5·31 kg	+0·5478
Average ultrasonic muscle depth at end of test (UMD)	+0·257 / mm	2·08 mm	+0·5339
Average ultrasonic fat depth at end of test (UFD)	–0·406 / mm	1·25 mm	–0·5081

energy (12·4 MJ metabolizable energy per kg dry matter (DM)), high protein (178 g crude protein per kg DM) pelleted complete diet, based on dried grass, barley and sugar beet pulp, supplemented with protein, minerals and vitamins. At 56 (±2) days of age lambs were weaned abruptly and continued to have *ad libitum* access to the performance test diet until the end of test at 150 days of age. Relatively early weaning was adopted in an attempt to minimize maternal effects on performance. The relatively intensive feeding regime was chosen partly to increase variation in growth and carcass composition, and so make it easier to identify animals with high lean growth using *in vivo* measurements. It was also chosen to reflect the levels of performance achieved in most performance-recorded terminal sire flocks in the UK.

At the end of test, animals were weighed on 3 days consecutively (ram lambs), or on two occasions a few days apart, spanning the end of test (ewe lambs). Lambs were ultrasonically scanned at the level of the 13th rib and 3rd lumbar vertebra on either three or (from 1990 onwards) two occasions several days apart, spanning the end of test. (Repeated measurements were taken with the aim of increasing accuracy. However, subsequent analyses showed that there was only marginal benefit from this, and so the frequency of measurement was reduced. Sheep in industry flocks in most countries are scanned on a single occasion.) A Vetscan real-time B-mode ultrasonic scanner was used, as this ranked highly in an earlier comparison of *in vivo* measurement techniques (Simm, 1987). Four fat depths were measured on each scan-the first above the boundary between the *M. longissimus thoracis et lumborum* and the vertebral spinous process and the others at progressively lateral intervals of 1·88 cm. This resulted in depths that, for most animals, spanned the *longissimus* muscle. Muscle depth was measured vertically at the deepest point of the muscle.

Average fat depths, muscle depths and live weights were adjusted for the effects of birth rank (single, twin or triplet), dam age (2 years old or older) and covariates (age at scanning and age at weighing) as appropriate. These effects were identified as significantly affecting performance in an analysis of data collected up to, and including, the first year of selection. Rolling average estimates of these fixed effects were used until 1989. After this, dam age adjustments were no longer updated, to avoid confounding genetic and environmental effects of dam age, since younger dams are likely to be of higher genetic merit in a population under selection. Index scores were then calculated for each animal, using only the animal's own adjusted performance records (i.e. no information from relatives was used). The index coefficients used are shown in Table 1.

The six ram lambs with the highest index scores were selected for mating in the selection line, as long as they were functionally fit and met the minimum pedigree registration requirements. Typically one or two rams per line per annum were rejected for these reasons, which included jaw, foot or leg deformities or black wool. To limit inbreeding, no more than two rams per sire were selected. In the control line, a circular within-family selection scheme was practised across six families. The control ram lambs with index scores closest to their family average were selected for mating; this was expected to lead to less fluctuation in genetic merit of the control line over time than that following random selection within families. As in the selection line, control line rams were only used if they were functionally fit and met the minimum pedigree registration requirements. Control line rams selected from one family were used for mating in the next family, in the same sequence each year. These measures were intended to limit rates of inbreeding in the smaller control line to approximately those expected in the larger selection line.

In both lines, rams were used for one mating season only. Matings took place in August, in single-sire groups. Selection line ewes were allocated to mating groups according to age, and to avoid matings between close relatives. Ram lambs were replaced by reserves if they failed to mate, or when a high proportion of ewes in their mating group returned to oestrus. This resulted in more than six sires per line in some years. This was especially the case in the selection line, possibly as subfertile rams had more opportunity to leave offspring because of the larger mating groups. The initial mating period lasted for just over 5 weeks each year (two cycles). Ewes failing

Table 2 *Numbers of sires and candidates available for selection (i.e. completing performance test) by line, sex and year*

Year	Selection line			Control line		
	Sires	Candidates		Sires	Candidates	
		Males	Females		Males	Females
1986	8	53		6	22	
1987	6	68		6	26	
1988	6	61		6	26	
1989	9	68	81	7	39	40
1990	6	83	79	6	47	49
1991	6	94	99	6	52	49
1992	8	88	88	6	38	31
1993	7	103	86	6	42	37
1994	8	104	106	6	48	53

to conceive in this period were exposed to a ram two months later, but the resulting lambs were not performance tested. Table 2 gives details of the numbers of sires represented in each line in each year of the experiment, and of the number of lambs performance tested each year.

No selection was practised among potential female replacements in the early years of the experiment, as the flock was being expanded. From 1989, selection line ewe lambs were also selected on index scores. The proportion of ewe lambs selected and the ewe replacement rate were chosen to maximize predicted response to selection. Thus, the top 60% of animals in the selection line were selected as replacements, and ewes were kept for a maximum of three lamb crops prior to culling. The 60% of ewe lambs with index scores closest to their family mean were selected in the control line, in order to keep the age structure of the two lines the same. Lambs born in 1994 were the last to be performance tested, and no further selection was practised.

In the 1992 and 1993 breeding seasons respectively 33 and 36 selection line ewes with high index scores were superovulated and used as embryo donors, as part of a wider study on the rôle of multiple ovulation and embryo transfer in genetic improvement of sheep. Embryos were transferred to crossbred recipients of either 50% or 75% Suffolk ancestry. Averages of 4·2 and 4·6 progeny per donor ewe were born in 1993 and 1994 (Dingwall *et al.*, 1993 and 1994). A total of 118 and 120 embryo transfer (ET) lambs from the selection line were performance tested in 1993 and 1994 respectively (about 60% of the total number of selection line lambs tested in those years). Type of birth (natural or ET) and breed type of surrogate dam were accounted for in selection of the 1993-born lambs; no selection was practised in 1994-born animals. Otherwise, management of recipients and ET lambs was identical to that of the experimental flock in earlier years.

Data

The following data were analysed for selection and control line animals completing performance test between 1985 and 1994: birth weight (BWT), weaning weight (WWT), live weight at the end of test (LWT), average ultrasonic muscle depth at the end of test (UMD) and average ultrasonic fat depth at the end of test (UFD). For this analysis, index scores were calculated retrospectively for each animal from the measured traits, LWT, UMD and UFD, following adjustment for the relevant fixed effects. The index coefficients shown in Table 1 were applied to the measured traits. To allow ready comparison of results, the index scores were expressed on the scale widely used in UK sheep industry breeding schemes. This was achieved separately for each sex by (i) subtracting the mean index score of control line animals in that year, (ii) dividing by the average within-year standard deviation of index scores in selection line animals, (iii) multiplying by 40, and (iv) adding 100. This sets the average index score for control line animals of each sex to 100 each year, and creates an s.d. of 40 index points in the selection line.

Statistical methods

The data were initially analysed using the residual maximum likelihood procedure (REML; Patterson and Thompson, 1971) in GENSTAT (Genstat 5 Committee, 1993) to identify appropriate fixed effects and covariates. Sires were fitted as a random effect, and the following fixed effects were identified as being significant in the statistical model for most or all traits : dam age (two levels; 2 years old or older), birth type / dam breed (three levels; natural born lambs with 100% Suffolk dams or ET lambs with 50% or 75% Suffolk recipient dams), birth rank (three levels; single, twin or triplet), sex of lamb and year of birth. Recipient or foster dam age was fitted for ET and fostered lambs respectively. There was no significant improvement in the model from fitting rearing rank in addition to birth rank, or from fitting the interaction between them. Age at scanning (for UMD and UFD), age at weighing (for WWT and LWT) and date of birth were significant when fitted as linear covariates.

Selection was originally on index scores based on phenotypic records for the candidates alone (i.e. no records from relatives). However, the retrospective analyses reported here used the mixed model applications of REML to estimate parameters and best linear unbiased prediction (BLUP; Henderson, 1988) to predict breeding values, using full information from relatives. The genetic model used in the analyses was established by testing the improvement in the likelihood value after fitting additional variance components for each trait. This was done separately for each trait under a univariate animal model, using the ASREML program of Gilmour (1996), which uses an average information REML algorithm (Gilmour *et al.*, 1995). The following variance components were tested for significance : direct additive (σ^2_d), maternal additive (σ^2_m), covariance between direct additive and maternal additive (σ_{dm}), permanent environment (σ^2_c; environmental variation within ewes across litters) and temporary environment (σ^2_t; environmental variation within a litter). To test for significantly better fit when including an additional

Table 3 *Example of the procedure used to select (co)variances to be included in the statistical model, and the estimates of (co)variances and corresponding ratios obtained for live weight at the end of test (LWT). Models were fitted using ASREML (standard errors are shown in parenthesis)*

	(Co)variances fitted in model				
Parameter†	d	d, t	d, t, m	d, t, m, dm	d, t, m, dm, c
σ^2_p (kg^2)	36·92	36·57	36·71	36·76	36·62
h^2	0·408	0·364	0·277	0·314	0·318
	(0·037)	(0·049)	(0·054)	(0·072)	(0·073)
m^2			0·104	0·136	0·117
			(0·031)	(0·047)	(0·054)
r_{dm}				–0·047	–0·048
				(0·050)	(0·050)
c^2					0·020
					(0·034)
t^2		0·156	0·099	0·097	0·091
		(0·032)	(0·034)	(0·034)	(0·035)
h^2_t	0·408	0·364	0·329	0·311	0·305
	(0·037)	(0·049)	(0·048)	(0·053)	(0·054)
Difference‡		–23·28	–14·82	–0·96	–0·34
Significance		***	***		

† $h^2 = \sigma^2_d / \sigma^2_p$; $m^2 = \sigma^2_m / \sigma^2_p$; $r_{dm} = \sigma_{dm} / \sigma_d\sigma_m$; $c^2 = \sigma^2_c / \sigma^2_p$; $t^2 = \sigma^2_t / \sigma^2_p$; $h^2_t = (\sigma^2_d + 0.5\sigma^2_m + 1.5\sigma_{dm}) / \sigma^2_p$.
‡ – twice difference in likelihood between this and the previous model.

random term, minus twice the difference in maximum log-likelihood of the two models was compared to a chi-square distribution with one degree of freedom.

For ET and fostered lambs the estimates of permanent and temporary environmental variance were ascribed to the surrogate dam. However, in all cases the estimates of maternal genetic variation were ascribed to genetic dams. This is not strictly correct when lambs have been fostered or are the result of ET. However, in this study including data from fostered or ET animals in the analysis had only a minor effect on estimates of maternal genetic variation, so these data were retained.

As an example, the results of the model selection procedure for LWT are given in Table 3. This table shows that the terms for permanent environmental variance and for covariance between direct and maternal additive genetic effects can be dropped from the model with no significant decline in the maximum log-likelihood value. However, further simplifications of the genetic model do lead to a significant reduction in the maximum log-likelihood. Similar patterns were found for all traits (see Table 4) and therefore the model that comprised direct additive, maternal additive and temporary environment effects was adopted. All the available performance data and pedigree information were then analysed under the following multivariate linear mixed model:

Table 4 *Improvements in the fit of the model associated with adding an additional random effect. The effects considered are direct additive (d), temporary environment (t), maternal additive (m), direct maternal covariance (dm), and permanent environment (c). The improvements are expressed as minus twice the difference between the maximum log-likelihood figures. Where deviances are greater than 3·84, adding the random term improved the fit* ($P < 0{\cdot}05$)

Trait	d	d, t	d, t, m	d, t, m, dm	d, t, m, dm, c
LWT		–23·28	–14·82	–0·96	–0·34
UMD		–18·62	–3·16	–1·78	0·00
UFD		–10·42	–0·76	0·00	–1·36

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Z_d a_d} + \mathbf{Z_m a_m} + \mathbf{Z_t e_t} + \mathbf{e_e}$$

where **y** is a vector of observations, **b** is a vector of fixed environmental effects with incidence matrix **X**, $\mathbf{a_d}$ and $\mathbf{a_m}$ are vectors of random direct additive and maternal additive effects with incidence matrices $\mathbf{Z_d}$ and $\mathbf{Z_m}$ respectively, $\mathbf{e_t}$ is a vector of random temporary environmental effects with incidence matrix $\mathbf{Z_t}$, and $\mathbf{e_e}$ is a vector of random residuals. All five traits were included in a multivariate animal model analysis to estimate parameters for index traits plus BWT and WWT. A second analysis was restricted to the three index traits only. This was done to estimate parameters and predict breeding values for these traits without any influence from BWT and WWT, since the latter were not used in selection.

Table 5 *Simple means and phenotypic standard deviations for each of the traits analysed for animals with full performance test records (1932 records for each trait)*

Trait	Mean	s. d.
Birth weight (BWT) (kg)	4·66	0·98
Weaning weight (WWT) (kg)	23·27	4·39
Live weight at end of test (LWT) (kg)	63·22	8·50
Ultrasonic muscle depth (UMD) (mm)	30·04	2·63
Ultrasonic fat depth (UFD) (mm)	7·45	1·61

Results

The numbers of records available for each trait, and the mean and phenotypic standard deviation of these traits, are shown in Table 5. In total 1932 animals were performance tested over the 9 years of the selection experiment. Phenotypic standard deviations of index traits were somewhat larger than those assumed in the derivation of the index (Table 1) but those presented here are unadjusted for fixed effects.

Table 6 shows the selection intensities achieved by line, sex and year of performance test. The values shown are not weighted by progeny numbers. After weighting, female selection intensities in the selection line were higher than those shown here, as a result of the additional selection applied to embryo donors in the 1992 and 1993 breeding seasons. The average unweighted selection intensity achieved

Table 6 *Selection intensities achieved by line, sex and year of performance test (unweighted)*

Year	Selection line		Control line	
	Males	Females†	Males	Females
1986	1·41		–0·17	
1987	1·61		0·20	
1988	1·30		–0·12	
1989	1·48	0·37	0·11	0·16
1990	1·58	0·09	–0·46	0·12
1991	1·59	0·26	–0·02	0·08
1992	1·37	0·60	–0·12	–0·18
1993	1·52		0·02	
Average	1·48	0·33	–0·07	0·05

† After weighting by number of progeny, female selection intensities in the selection line were higher than those shown here, as a result of the additional selection applied to embryo donors in the 1992 and 1993 breeding seasons.

Table 7 *Direct and maternal heritabilities, temporary environmental variance as a proportion of total phenotypic variance (all on the diagonal), phenotypic, direct additive genetic, maternal additive genetic and temporary environmental correlations between birth weight (BWT), weaning weight (WWT), live weight at scanning (LWT), ultrasonic muscle depth (UMD) and ultrasonic fat depth (UFD). The results shown are from a multivariate analysis of all five traits†*

		BWT	WWT	LWT	UMD	UFD
Phenotypic	BWT	–	0·532	0·447	0·197	0·049
	WWT		–	0·687	0·333	0·333
	LWT			–	0·426	0·466
	UMD				–	0·169
	UFD					–
Direct	BWT	0·054	–0·326	–0·271	–0·084	–0·076
	WWT		0·177	0·528	0·487	0·164
	LWT			0·286	0·307	0·416
	UMD				0·410	0·142
	UFD					0·561
Maternal	BWT	0·287	0·705	0·669	0·388	0·006
	WWT		0·205	0·856	0·658	0·325
	LWT			0·160	0·802	0·502
	UMD				0·164	0·663
	UFD					0·083
Temporary environmental	BWT	0·111	–0·033	–0·172	0·125	–0·108
	WWT		0·026	0·516	0·630	0·260
	LWT			0·054	0·897	0·465
	UMD				0·074	0·478
	UFD					0·111

† Average standard errors are: 0·024 (phenotypic correlations), 0·020 (direct heritabilities), 0·110 (direct additive genetic correlations), 0·026 (maternal heritabilities), 0·395 (maternal additive genetic correlations), 0·032 (temporary environmental variance as a proportion of total phenotypic variance) and 0·198 (temporary environmental correlations).

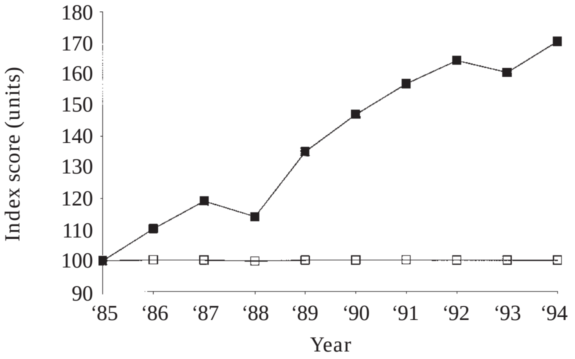

Figure 1 Phenotypic trend in scaled index score; ■ = selection; □ = control.

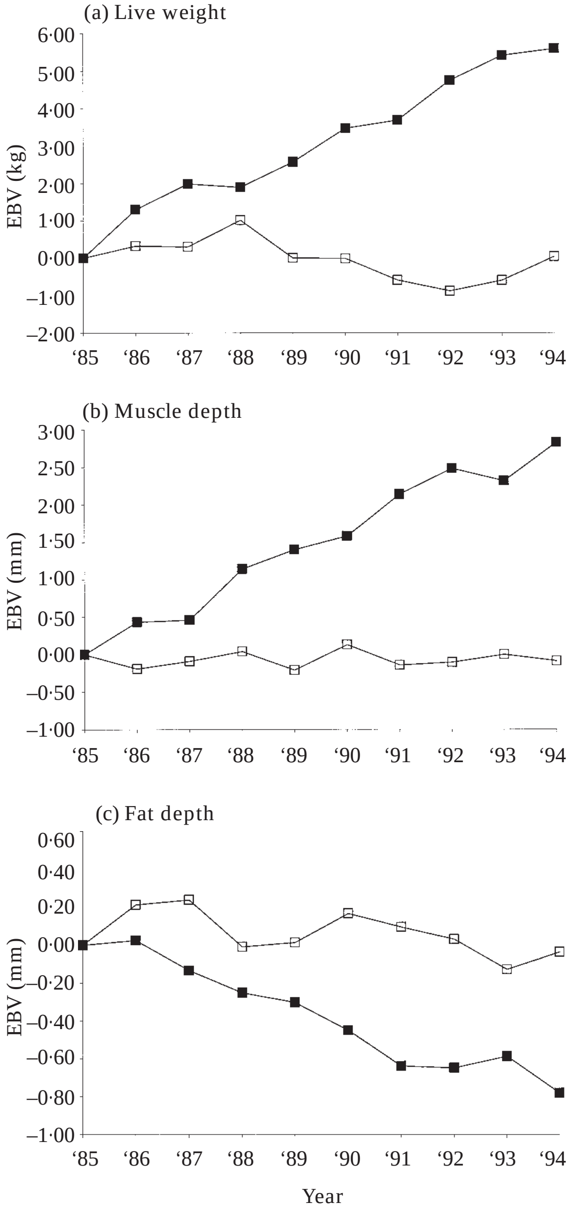

Figure 2 Estimated genetic trend in (a) live weight, (b) muscle depth and (c) fat depth (i.e. mean estimated breeding value (EBV) for animals in each line, by year of birth); ■ = selection; □ = control.

across sexes (0·94) was slightly lower than that expected (a selection intensity of 1·0 to 1·2 was thought to be achievable; Simm and Dingwall (1989)). This was probably mainly due to the lack of selection among females during the early years of the experiment, and the use of extra males to limit inbreeding.

Table 7 shows the estimates of phenotypic and genetic parameters for live weights and ultrasonic measurements from the multivariate analysis of all measured traits. Phenotypic correlations between all pairs of traits were positive and usually moderately high. The correlations between index traits were close to those assumed in the original index calculations. As expected, the direct heritabilities of weight traits increased steadily with age, from the low value of 0·05 for birth weight, to 0·29 for weight at the end of test. Conversely, the maternal heritabilities declined with increasing age at measurement, from 0·29 for birth weight to 0·16 for LWT. The direct heritability for LWT was slightly higher than the heritability assumed in the index calculations (0·29 *v.* 0·24). This is despite the fact that the heritabilities assumed in the index calculations were total heritabilities (i.e. not partitioned into direct and maternal components). The direct heritabilities of UFD and UMD were substantially higher than those for weight traits, whilst the maternal heritabilities for ultrasonic measurements were similar to, or lower than, those for weight traits. The direct heritabilities for ultrasonic measurements estimated here were substantially higher than the total heritabilities assumed in the original index calculations (0·56 *v.* 0·23 for UFD and 0·41 *v.* 0·22 for UMD). There were low negative direct additive correlations between BWT and WWT, and between BWT and LWT, but higher positive maternal additive correlations between all pairs of weight traits. There were low to moderate temporary environmental effects on all traits, accounting for between 3 and 11% of the total phenotypic variation.

Substantial responses to selection were achieved in each of the three index traits, as judged by the divergence between selection and control line

Table 8 *The regression of estimated breeding value on year of birth for selection line animals (Annual gain), its standard error (s.e.), and the mean EBV for selection line animals (Response) measured at year 9 (1994) for the three measured traits*

Trait	Annual gain	s.e.	Response at year 9
LWT (kg)	0·586	0·027	5·60
UMD (mm)	0·301	0·012	2·83
UFD (mm)	–0·090	0·008	–0·78

performance over time. By year 9, responses in LWT, UFD and UMD in both sexes amounted to between 7 and 15% of the overall mean of the trait concerned (results not shown). Phenotypic trends in index scores, calculated following adjustment for the fixed effects described earlier, are shown in Figure 1. Figure 2 shows the estimated genetic trends in the three measured traits, LWT, UMD and UFD, expressed as mean EBVs for animals in each line, by year of birth. Corresponding regressions of EBVs on year of birth for selection line animals are given in Table 8. The EBVs used in Figures 2 and Table 8 were from the trivariate analysis of the measured traits used in the index.

Table 9 shows the inbreeding coefficients of animals born each year in each line over the duration of the selection experiment. Within the limits of the pedigree information available, the results show that measures to control inbreeding were effective, as average inbreeding coefficients in each line were less than 5% at the end of the experiment. The objective of achieving similar levels of inbreeding in the two lines was also met.

Discussion

The main aim of the selection experiment reported here was to test whether or not the expected direction and magnitude of responses to index selection for lean growth were achieved, and to estimate genetic parameters for the component traits of the index. Substantial responses to selection were achieved in the index and its components, as judged by the divergence in performance of the selection and control line animals of both sexes. Also, the response in each of the components was in the expected direction.

As in several other studies (see Lewis and Beatson (1999)), there were important direct and maternal additive genetic influences on performance. As expected, maternal genetic influences tended to decline with age, while direct genetic influences tended to increase in importance. These tendencies may have been reinforced in the present study by the management practices of creep feeding and relatively early weaning. In the present study, there was no evidence of important covariation between direct and maternal additive genetic effects. There is conflicting evidence in the literature on the magnitude and direction of this covariation, and some concern that it can arise as a result of the structure of the data available, rather than being a true biological effect (Lewis and Beatson, 1999). In a study of equivalent measurements from UK industry Suffolk flocks, Mercer *et al.* (1994) found that the most appropriate statistical model included terms for direct and maternal additive genetic variance, permanent environmental variance and the covariance between direct and maternal additive genetic effects. However, the permanent environmental variation accounted for by their model (0·07 to 0·16) was of similar magnitude to the temporary environmental variation accounted for here (the authors do not mention whether or not they tested for the significance of a temporary environmental term). Also, the correlations they found between direct and maternal additive genetic

Table 9 *Numbers of animals (No.) and mean, minimum (Min.) and maximum (Max.) inbreeding coefficients (%) by line and year of birth†*

	Selection line				Control line			
	No.	Mean	Min.	Max. ‡	No.	Mean	Min.	Max.
1986	53	0·06	0	3·13	22	0·14	0	3·13
1987	68	0·46	0	3·13	26	0·50	0	3·13
1988	61	1·40	0	6·64	26	1·32	0	6·25
1989	149	1·91	0	6·25	79	2·34	0	7·03
1990	162	2·58	0	5·66	96	2·07	0	8·06
1991	193	2·70	0·32	16·75	101	2·89	0·05	7·63
1992	176	3·33	0·42	6·68	69	3·58	0·65	8·34
1993	189	4·50	2·48	8·48	79	4·51	1·03	9·28
1994	210	4·86	3·18	7·67	101	4·84	1·03	8·50

† Prior to 1985 the inbreeding coefficient in the base flock was 0·03%.
‡ The value of 16·75 results from the mating of two individuals that shared a common grandparent.

effects were relatively low (–0·08 to –0·15). The modest differences between these models may be a result of sampling, or of differences in the management practices employed in this experimental flock and the industry flocks concerned (e.g. age at weaning may affect the size and persistence of maternal effects). However, the results of both studies indicate that a more comprehensive genetic model ought to be considered in national genetic evaluations in the UK.

The direct heritabilities for weight traits reported here tend to be similar to the (usually total) heritabilities for equivalent weights in meat or dual-purpose breeds reported elsewhere. The direct heritabilities for ultrasonic measurements reported are substantially higher than most other published estimates of total heritabilities (Solis-Ramirez *et al.*, 1993; Fogarty, 1995; Morris *et al.*, 1997; Conington *et al.*, 1998). This result is in line with the general trend for heritability estimates to increase when more comprehensive genetic models are used. The study of UK industry Suffolk flocks mentioned earlier (Mercer *et al.*, 1994) produced very similar estimates of direct and maternal heritabilities to those reported here. Exceptions were the direct heritabilities of WWT and UMD and the maternal heritability of UFD, which were all higher in industry flocks than those reported here (0·41 *v.* 0·18 for WWT, 0·52 *v.* 0·41 for UMD, and 0·22 *v.* 0·08 for UFD). In the case of the ultrasonic measurements, the heritabilities reported here might be expected to be higher also as a result of the measurement protocol (e.g. there were more scanning locations and measurement occasions here than in some other published studies, which reduced the error variance). However, the heritabilities of UFD and UMD reported by Mercer *et al.* (1994) were from measurements made on a single occasion for each animal.

Experimental sheep lines selected for various carcass composition traits have been established in a number of locations, particularly New Zealand and the UK (see reviews of Simm (1992 and 1994)). The earlier New Zealand experiments involved selection for divergent liveweight-adjusted ultrasonic backfat depth (McEwan *et al.*, 1989; Solis-Ramirez *et al.*, 1993; Morris *et al.*, 1997). Similarly, two UK experiments involved selection on an index designed to alter body composition at a constant live weight (Cameron and Bracken, 1992; Bishop, 1993). More recently, lines were established in New Zealand where selection was on an economic index similar to the index used here (Simm *et al.*, 1987; Nsoso, 1995). In most cases substantial responses have been achieved. In those reports where conversion of results is possible, approximate annual rates of change in overall index score, or in weight-adjusted backfat depth, are usually about 2% per annum. This is close to the maximum expected values for the traits and flock sizes concerned. The rates of change in the present study correspond closely with most of those published to date.

The index described here has been used in terminal sire flocks in Britain since 1988, in the performance-recording scheme formerly operated by the Meat and Livestock Commission (MLC), and now operated by Signet. Many of these flocks have also joined sire referencing schemes (SRS). These are co-operative breeding schemes that use teams of elite rams across flocks and years, to create genetic links among them. This permits across-flock genetic evaluations, and estimation of genetic trends. So, results are now available from large industry populations with which the responses reported here can be compared. Annual responses in lean growth index in the larger terminal sire breed SRS in Britain range from about 6 to about 14 index points (MLC, 1999; Simm *et al.*, 2001) — spanning the annual rate of response achieved in this study. Because of the much larger size of the industry schemes, they can achieve equivalent responses in the index of objectively measured traits, while simultaneously taking account of additional criteria such as visually assessed breed characteristics and conformation. There are strong positive genetic trends in live weight and muscle depth in these industry schemes, as in the experiment reported here. However, trends in fat in some of the industry schemes appear much smaller than in the present study. This is perhaps because of deliberate selection of high index animals with intermediate fat estimated breeding values, because fat levels are perceived to be low enough already in some of these breeds, or because of additional selection on conformation, which is usually positively associated with fatness.

Whilst measuring trends in components of an index is informative, it is achieving responses in the selection objectives which is the ultimate goal. Based on the genetic parameters presented here, and assumed genetic (co)variances for carcass lean and fat weights, the responses in selection criteria described here are expected to be associated with changes of +233 g carcass lean and +96 g carcass fat per annum. These estimated responses are higher than those predicted by Simm and Dingwall (1989; +194 g lean and +67 g fat per annum). This is largely a result of the revised genetic parameters, as the average selection intensity achieved was slightly lower than expected.

At the end of this experiment, selection and control line lambs were produced to investigate responses in carcass composition at a range of degrees of maturity spanning that at which selection took place, and on a range of feeding regimes, including the test regime. Results from this series of experiments indicate that there are significant improvements in the lean to fat ratio in the carcasses of selection line animals compared to control animals, at each of these stages of maturity, and on each of the feeding regimes. For example, following rearing on the test diet to target slaughter weights of 33 to 114 kg, selection line lambs had, on average, 40 g/kg more carcass lean and 48 g/kg less carcass fat than controls (Lewis *et al.*, 1999).

In other experiments where carcass composition has been measured directly (Bennett *et al.*, 1988; Lord *et al.*, 1988; Kadim *et al.*, 1989; McEwan *et al.*, 1989), selection for reduced ultrasonically measured backfat depth has resulted in reduced subcutaneous fat depth in the carcass. This has been accompanied usually by reduced proportions or weights of fat in other depots, as expected from the fairly strong genetic correlations between fat proportions in different depots (Wolf *et al.*, 1981; Bennett, 1990) and by increased proportions or weights of lean tissue. Equivalent results for chemical composition of carcasses from divergently selected Coopworth sheep were reported by McEwan *et al.* (1990). Nsoso (1995) estimated, using computed tomography (CT), that responses of + 72 g lean per year and –40 g fat per year had been achieved in an experimental line of Dorset Down sheep selected on an economic index very similar to the one used here (Simm *et al.*, 1987).

Often pedigree animals are reared under more favourable conditions than their commercial counterparts. The experiment reported here involved *ad libitum* feeding of a high energy, high protein diet. However, the majority of lambs slaughtered for meat production in Britain are reared at grass. Two experiments have been conducted, using sires from the lines described here, to investigate correlated responses to selection in crossbred lambs reared at grass.

The first of these experiments involved 66 high or low index Suffolk rams from the second, third and fourth years of performance testing (1986 to 1988). These were mated to Scottish Mule (Bluefaced Leicester × Scottish Blackface) ewes. Their lambs were reared at grass to target live weights of 35·5, 41·5 and 47·0 kg. At an average carcass weight of 19·7 kg, the progeny of high index sires had 144 g more lean and 186 g less fat than the progeny of low index sires (sires differed by 100 index points, or 2·5 standard deviations in index score; Lewis *et al.*, 1996). A more recent experiment involved the 12 selection and control line rams chosen for mating from the 1991 performance test. Again, these were mated to Scottish Mule ewes. Carcasses from progeny of selection line sires had significantly higher saleable meat yield than those from progeny of control line sires, both at a constant carcass weight (+ 0·10 kg) and a constant level of fatness (+ 0·25 kg). On average, carcasses from selection line sires achieved prices about £1·50 higher than those for controls, and were slaughtered 11 days sooner (Simm and Murphy, 1996). This financial advantage, together with estimated savings in grazing costs, was estimated at prevailing prices to be worth up to £600 over the working life of a ram.

The experimental results reported here show that substantial responses can be achieved by selecting sheep on an index of live weight and ultrasonic measurements of fat and muscle. The results from SRS, show that the same techniques are being applied very effectively in industry flocks. The selection responses being achieved are expected to lead to increased carcass leanness in both purebred and crossbred lambs, at a range of degrees of maturity, and in a range of feeding systems (Lewis *et al.*, 1996; Simm and Murphy, 1996, Lewis *et al.*, 1999).

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References

Banks, R. G. 1999. Genetics of lamb and meat production. In *The genetics of sheep* (ed. L. Piper and A. Ruvinsky), pp. 505-522. CAB International, Wallingford.

Bennett, G. L. 1990. Selection for growth and carcass composition in sheep. *Proceedings of the fourth world congress on genetics applied to livestock production, Edinburgh, vol. XV,* pp. 27-36.

Bennett, G. L., Meyer, H. H. and Kirton, A. H. 1988. Effects of selection for divergent ultrasonic fat depth in rams on progeny fatness. *Animal Production* **47:** 379-386.

Bishop, S. C. 1993. Selection for predicted carcass lean content in Scottish Blackface sheep. *Animal Production* **56:** 379-386.

Cameron, N. D. and Bracken, J. 1992. Selection for carcass lean content in a terminal sire breed of sheep. *Animal Production* **54:** 367-377.

Conington, J., Bishop, S. C., Waterhouse, A. and Simm, G. 1998. A comparison of growth and carcass traits in Scottish

Blackface lambs sired by genetically lean or fat rams. *Animal Science* **67:** 299-309.

Dingwall, W. S., McKelvey, W. A. C., Mylne, M. J. A. and Simm, G. 1994. A protocol for MOET in Suffolk sheep. *Programme and abstracts of the 45th annual meeting of the European Association for Animal Production, Edinburgh*, p. 256 (abstr.).

Dingwall, W. S., McKelvey, W. A. C., Mylne, J. and Simm, G. 1993. An evaluation of MOET in Suffolk sheep. *Animal Production* **56:** 444 (abstr.).

Fogarty, N. M. 1995. Genetic parameters for liveweight, fat and muscle measurements, wool production and reproduction in sheep: a review. *Animal Breeding Abstracts* **63:** 101-143. (Also, see Erratum preceding p. 935, vol. 63.)

Genstat 5 Committee. 1993. *Genstat 5 release 3 reference manual.* Oxford University Press, Oxford.

Gilmour, A. R. 1996. *ASREML, a spatial REML program.* NSW Agriculture, Orange, Australia.

Gilmour, A. R., Thompson, R. and Cullis, B. R. 1995. Average information REML, an efficient algorithm for variance estimation in linear mixed models. *Biometrics* **51:** 1440-1450.

Henderson, C. R. 1988. Theoretical basis and computational methods for a number of different animal models. *Journal of Dairy Science* **71:** (suppl.) 1-16.

Kadim, I. T., Purchas, R. W., Rae, A. L. and Barton, R. A. 1989. Carcass characteristics of Southdown rams from high and low backfat selection lines. *New Zealand Journal of Agricultural Research* **32:** 181-191.

Kempster, A. J. 1983. Carcass quality and its measurement in sheep. In *Sheep production* (ed. W. Haresign), pp. 59-74. Butterworths, London.

Kempster, A. J., Croston, D., Guy, D. R. and Jones, D. W. 1987. Growth and carcass characteristics of crossbred lambs by ten sire breeds, compared at the same estimated subcutaneous fat proportion. *Animal Production* **44:** 83-98.

Lewis, R. M. and Beatson, P. R. 1999. Choosing maternal-effect models to estimate (co)variances for live and fleece weight in New Zealand Coopworth sheep. *Livestock Production Science* **58:** 137-150.

Lewis, R. M., Emmans, G. C., Simm, G., Dingwall, W. S., FitzSimons, J., Fraser, J. C. and Donbavand, J. E. 1999. The consequences of index selection on carcass composition in Suffolk sheep. *Proceedings of the British Society of Animal Science, 1999,* p. 46.

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.

Leymaster, K. A. and Jenkins, T. G. 1993. Comparison of Texel- and Suffolk-sired crossbred lambs for survival, growth and compositional traits. *Journal of Animal Science* **71:** 859-869.

Lord, E. A., Fennessy, P. F. and Littlejohn, R. P. 1988. Comparison of genotype and nutritional effects on body and carcass characteristics of lambs. *New Zealand Journal of Agricultural Research* **31:** 13-19.

McClelland, T. H., Bonaiti, B. and Taylor, St C. S. 1976. Breed differences in body composition of equally mature sheep. *Animal Production* **23:** 281-293.

McEwan, J. C., Fennessy, P. F., Greer, G. J., Bain, W. E. and Bruce, G. D. 1990. Effects of selection for ultrasonic backfat depth on carcass growth and composition in sheep. *Proceedings of the Australian Association of Animal Breeding and Genetics* **8:** 323-326.

McEwan, J. C., Fennessy, P. F., Greer, G. J., Bruce, G. D. and Bain, W. E. 1989. Selection for carcass composition: effects on the development of subcutaneous and internal fat depots. *Proceedings of the Nutrition Society of New Zealand* **14:** 163-164.

Meat and Livestock Commission. 1999. *Sheep yearbook 1999.* Meat and Livestock Commission, PO Box 44, Winterhill House, Snowdon Drive, Milton Keynes, MK6 1AX.

Mercer, J. T., Brotherstone, S., Bradfield, M. J. and Guy, D. R. 1994. Estimation of genetic parameters for use in sheep sire referencing schemes. *Proceedings of the fifth world congress on genetics applied to livestock production, Guelph, vol. 18,* pp. 39-42.

More O'Ferrall, G. J. and Timon, Y. M. 1977. A comparison of eight sire breeds for lamb production. 1. Lamb growth and carcass measurements. *Irish Journal of Agricultural Research* **16:** 267-275.

Morris, C. A., McEwan, J. C., Fennessy, P. F., Bain, W. E., Greer, G. J. and Hickey, S. M. 1997. Selection for high or low backfat depth in Coopworth sheep: juvenile traits. *Animal Science* **65:** 93-103.

Nsoso, S. J. 1995. Genetic control of lean tissue growth rate in sheep: genetic parameters and responses to selection. *Ph.D. thesis, Lincoln University, New Zealand.*

Patterson, H. D. and Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrica* **58:** 454-544.

Simm, G. 1987. Carcass evaluation in sheep breeding programmes. In *New techniques in sheep production* (ed. I. F. M. Marai and J. B. Owen), pp. 125-144. Butterworths, London.

Simm, G. 1992. Selection for lean meat production in sheep. In *Progress in sheep and goat research* (ed. A. W. Speedy), pp. 193-215. CAB International, Wallingford.

Simm, G. 1994. Developments in improvement of meat sheep. *Proceedings of the fifth world congress on genetics applied to livestock production, Guelph, vol. 18,* pp. 3-10.

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., Collins, J. E. and Nieuwhof, G. J. 2001. Use of sire referencing schemes to select for improved carcass composition in sheep. *Journal of Animal Science* In press.

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.

Simm, G., Young, M. J. and Beatson, P. R. 1987. An economic selection index for lean meat production in New Zealand sheep. *Animal Production* **45:** 465-475.

Solis-Ramirez, J., Blair, H. T. and Purchas, R. W. 1993. Direct and correlated responses to selection for high or low ultrasonic backfat depth in Southdown sheep. *New Zealand Journal of Agricultural Research* **36:** 133-141.

Taylor, St C. S. 1980. Genetic size-scaling rules in animal growth. *Animal Production* **30:** 161-165.

Wolf, B. T., Smith, C., King, J. W. B. and Nicholson, D. 1981. Genetic parameters of growth and carcass composition in crossbred lambs. *Animal Production* **32:** 1-7.

Wolf, B. T., Smith, C. and Sales, D. I. 1980. Growth and carcass composition in the crossbred progeny of six terminal sire breeds of sheep. *Animal Production* **31:** 307-313.

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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