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Selection for carcass quality in hill sheep measured by X-ray computer tomography

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This paper describes an investigation of the use of computer tomography (CT) to genetically improve carcass composition and conformation in Scottish Blackface sheep. After 5 years of selection on an index designed to improve both composition and conformation (the 'CT index'), a large response was observed in the CT index, with genetic progress equivalent to 0.11 phenotypic standard deviations per year. Heritabilities for the index and for the component traits of average CT-assessed muscle area, ultrasonic muscle depth and ultrasonic fat depth were 0.41 (s.e. 0.08), 0.38 (s.e. 0.07), 0.41 (s.e. 0.05) and 0.30 (s.e. 0.05), respectively. The index was positively genetically correlated with ultrasonic muscle depth and carcass weight and negatively genetically correlated with fat class. The genetic and phenotypic correlations among ultrasonic measurements were positive and moderate. However, many of the genetic correlations tended to have large standard errors. Selection on the CT index moderately improved conformation and was successful at decreasing fat class of the carcass. Equivalent selection on live weight at ultrasound scanning would improve carcass and slaughter weight, and total price received, but would have a slightly deleterious impact on conformation score. The results of this study demonstrate that genetic improvement of carcass quality can be achieved in hill sheep using CT assessed traits.

Introduction

Genetic improvement of hill sheep is an important objective within the UK sheep industry because of the importance of this sector in terms of maintaining the rural environment and its contribution of 34% of the genes to the slaughter generation (Meat and Livestock Commission, 1998). A particular issue in hill sheep is that they have been naturally selected primarily for their ability to survive and produce lambs in harsh environments. This is thought to have tended to favour the development of smaller and hardier breeds, which produce carcasses of small size and of moderate conformation.

Several options are available for assessing carcass composition *in vivo*. Ultrasonic scanning is widely used in commercial breeding programmes as it is a measurement that can be readily used on large numbers of animals (McEwan *et al.*, 1989; Cameron and Bracken, 1992; Fennessy *et al.*, 1993; Afonso and Thompson,

1996; Simm *et al.*, 2002). Computer tomography (CT) scanning has been demonstrated to improve prediction of carcass traits and genetic improvement over and above ultrasonic scanning (Jopson *et al.*, 1995; Young *et al.*, 1996 and 1999), albeit at a considerably higher cost. If suitable breeding structures are in place, CT has been shown to be cost effective (Simm *et al.*, 1987; Allen, 1990; Jopson *et al.*, 1997). Jones *et al.* (2002) showed that CT scanning also provides good *in vivo* measures of muscularity. Muscularity measures are of interest as they provide an objective description of the shape of a carcass independent of fatness. In the past, muscularity assessment could only be obtained either directly through carcass dissection after slaughter or by using ultrasound on live animals, as an indirect assessment of carcass tissue.

A long-term experiment at ADAS Redesdale was initiated in 1992 to improve carcass quality (weight and conformation) in hill sheep through genetic selection. Whereas good progress was made in increasing carcass

weights (Roden *et al.*, 2003), progress towards improving carcass conformation was hampered by inadequate live-animal measures of this trait. Thus, in 1997, a study was initiated in this population to explore the possibility of using CT measures to improve carcass quality. An index of CT traits was derived to predict carcass conformation and composition, and selection on this index commenced. The aim of the current study was to evaluate the impact of this CT index on carcass quality, when used as part of a breed improvement programme.

Material and methods

Flock establishment and experimental design
An open nucleus flock of 60 Scottish Blackface donor ewes was established in 1992 from a base population of approximately 1600 ewes that were maintained under hill conditions at ADAS Redesdale in Northumberland, England. The selection history of these base flocks was one of objective visual inspection to eliminate faults and to improve body size, conformation and breed characteristics (Roden *et al.*, 2003). The selection criterion used from 1992 until 1998 was a desired gains index designed to increase live weight at ultrasonic scanning and ultrasonic muscle width and depth, without changing ultrasonic fat depth, with the aim that this should also improve carcass conformation score and fat class (Roden *et al.*, 2003).

The flock was maintained and selection was performed using a multiple ovulation and embryo transfer (MOET) procedure. In mid November of each year, all nucleus donor and recipient ewes were initially transferred from open hill grazing to in-bye fields. They were then housed for a short period immediately before and during the mating period (a total of approx. 2 weeks) to facilitate the induction of superovulation, semen collection, AI, embryo collection and embryo transfer. Details of the treatment protocols for donor and recipient ewes and the methods for collecting and transferring embryos were provided in Bari *et al.* (1999 and 2000). The MOET design of the breeding project allows maternal environmental effects on lamb performance to be separated from direct genetic effects.

Each year from 1998 onwards, the flock comprised 60 donor ewes mated with six rams chosen on the basis of their carcass characteristics (described below), and *ca.* 300 recipient ewes (details in Roden *et al.* (2003)). Following the MOET procedure, these 60 ewes were then naturally mated to two further rams, also chosen on the basis of their carcass characteristics. Additionally, each year *ca.* 40 control ewes were naturally mated to four rams from the same sub-population to provide a control line. During the course of this study, donor ewes were selected from amongst those born to selected rams on the basis of their carcass characteristics and adherence to industry-accepted breed-type characteristics. Recipient ewes were generally unrelated sheep, born outside of the nucleus.

Husbandry and phenotypic measurements
Male lambs were reared entire and all lambs were weaned at 20 weeks of age. Each year, from 1993 to 2003, all lambs were ultrasound scanned on the same day; their average age varied between years from 20 to 29 weeks. CT measurements were taken on lambs at 26 weeks of age, from 1998 to 2003, with the exception of 2001 when the foot and mouth disease (FMD) epidemic and the subsequent livestock movement restrictions meant that CT measurements could not be taken on 2001-born lambs. In total the data set comprised 2562 lambs recorded at birth for 11 years (1993-2003). These lambs were the progeny of 123 sires, 348 donors and 1229 recipients. Additional pedigree information was available, and the complete pedigree comprised 3799 animals.

Ultrasonic scanning was performed at the level of the 3rd lumbar vertebra using a Dynamic Imaging real-time ultrasound scanner, with a 7.5 MHz 56-mm probe. Live weight at scanning (SWT) and three individual subcutaneous fat depth measurements were taken over the *longissimus dorsi* muscle, moving laterally between the vertical and transverse processes of the vertebra, from which the average fat depth was calculated (UFD). A single muscle depth (UMD) and a single muscle width (UMW) measurement were taken at the deepest and widest point on the muscle, respectively. Ultrasonic scanning data were available on 2018 of the lambs, representing 123 sires, 290 donors and 1071 recipients. Subjective conformation score was assessed on the live animal at the time of ultrasound scanning. The actual score was the average of assessments at the shoulder, leg and loin, scored from 1 (very lean) to 5 (very fat).

Carcass composition was assessed by CT techniques on 1266 lambs, representing 49 sires, 189 donors and 711 recipients. CT measurements provided areas of fat, bone and muscle at the 8th thoracic vertebra (TV8), at the 5th lumbar vertebra (LV5) and at the ischium (ISC). The traits were the CT assessed area of tissue at each anatomical site.

Carcass assessments were taken on male lambs that were not required for further breeding purposes. Lambs were selected for slaughter at a target fat class of 3 (EUROP, 1995) by the same person on all occasions. Measurements included slaughter weight and carcass weight, conformation score (EUROP, 1995) and fat class. Total price received for each animal was recorded. Carcass data were available for 1148 lambs, representing 79 sires, 124 donors and 799 recipients.

CT selection criteria
A 'desired gains' index was derived from available unpublished data from a CT calibration trial on Blackface lambs, unpublished data from the SAC/Roslin Hill Sheep Project and data collected on these sheep in 1998, with the aim of simultaneously improving both carcass composition and carcass conformation. The derived index, combining live weight (taken on the farm, prior to CT

scanning), subjective conformation, and the fat, muscle and bone areas at the ischium, the 5th lumbar vertebra, and 8th thoracic vertebra, was:

$$\text{CT index} = -216.6 \, (\text{Live weight})$$
$$+ \, 272.2 \, (\text{Subjective Conf.}) - 0.00\,596 \, (\text{ISC fat})$$
$$+ \, 0.1814 \, (\text{ISC muscle}) + 0.2838 \, (\text{ISC bone})$$
$$+ \, 0.0263 \, (\text{LV5 fat}) + 0.169 \, (\text{LV5 muscle})$$
$$+ \, 3.156 \, (\text{LV5 bone}) + 0.128 \, (\text{TV8 fat})$$
$$+ \, 0.139 \, (\text{TV8 muscle}) + 0.273 \, (\text{TV8 bone})$$

This index was derived with the following relative 'economic weightings': conformation $= 2$, fat $= -1$, muscle $= 2$. These weightings were chosen because, given the available data, they resulted in predicted gains in carcass characteristics that were close to perceived optimal responses, i.e. improved conformation and decreased fatness with minimal changes in live weight. Additionally, they reflected the economic weightings of fat $= -1$ and muscle $= 2$ advocated by Simm and Dingwall (1989) and now widely used in UK terminal sire selection indices. The negative index weighting on live weight ensures that live weight should not increase greatly with selection on the index.

The CT index was implemented in 1999, and the first cohort of lambs resulting from selection decisions made using the CT index were born and evaluated in 2000. Each year, BLUP estimated breeding values (EBVs) were calculated for the CT index for all animals, and sires were selected on the basis of their CT index EBV, along with adherence to industry-accepted breed-type characteristics. As described above, animals were not CT scanned in 2001. To enable selection to continue in 2001, lambs were ranked on an index comprising their parental average CT index EBV and their muscle width EBV. Based on data available at the time and using selection index methodology, this index had a relative efficiency of 0.75 compared with the CT index based on data from the selection candidates themselves.

Statistical analysis
Data summary and trait definition. Data analyses were performed using all available data but responses to selection are only presented for the years in which CT measurements were taken. Data were initially analysed by fixed linear model methods in order to identify significant fixed effects, covariates and two-way interactions, using Genstat 7 Committee (2003). The fixed effects subsequently included in analysis of slaughter and carcass traits were year of birth (11 classes), lamb sex (male or female), type of rearing (singles and twins), and flock (two classes). Recipient age (seven levels) was included as a fixed effect only in the analysis of live animal

measurements. Day of birth and weaning age were fitted as covariates for ultrasound scanning traits and CT traits. Analyses of traits measured post slaughter were performed with unadjusted data, or data adjusted to either a constant fat classification score or to a constant age at slaughter by fitting fat score as a linear covariate or age as linear and quadratic covariates. Fixed effects and covariates found to be significant in the multiple linear regression analysis were included in the variance component analysis of each trait. Day of birth was not found to be significant for the post slaughter traits.

To analyse post slaughter fat classification, i.e. the amount of fat on the outside of the carcass visible to an assessor, a new trait (fat class) was constructed as follows: fat classification 5 (very high)→5, 4H→4, 4L→3.5, 3H→3, 3L→2.5, 2 (low)→2 and 1 (very low)→1. Also, conformation score values were recoded as E (Excellent)→5, U (very good)→4, R (good)→3, O (medium)→2 and P (poor)→1. Thus, higher scores indicate better conformation and greater fatness. Conformation describes carcass shape in terms of convex/concave profiles and indicates the amount of flesh (muscle + fat) in relation to the length of bones.

Genetic parameters. Restricted maximum likelihood methods were used to estimate variance components with an animal model, fitting the complete pedigree structure (3799 animals), using the *ASReml* program (Gilmour *et al.*, 2004). All traits, except the CT traits, were initially analysed in three different univariate models. Model 1 fitted animal as the only random effect: $\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e}$. In model 2, the effect of maternal environment was included by fitting recipient as a second random effect, uncorrelated with the animal genetic effect: $\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wm} + \mathbf{e}$. In model 3, the effect of common environment was included by fitting litter as a third uncorrelated random effect: $\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wm} + \mathbf{Sc} + \mathbf{e}$. In these models, $\mathbf{y}$ is the vector of observations on the specific trait of the animal; $\mathbf{b}$ is the vector of fixed effects described before; $\mathbf{a}$ is the vector of additive random animal (genetic) effects, m is the vector of maternal (recipient) genetic effects, $\mathbf{c}$ is the vector of random common environmental effects (litters) and $\mathbf{e}$ is the vector of random residual effect. $\mathbf{X}$, $\mathbf{Z}$, $\mathbf{W}$ and $\mathbf{S}$ are the incidence matrices relating records to fixed, animal, maternal genetic and common environmental effects respectively. It was assumed that the expectations (E) of the variables were: $E(\mathbf{y}) = \mathbf{Xb}$ and expectations of all random effects and the residual were zero. Further, $\text{var}(\mathbf{a}) = \mathbf{A}\sigma_{\alpha}^2$; $\text{var}(\mathbf{m}) = \mathbf{A}\sigma_{m}^2$; $\text{var}(\mathbf{c}) = \mathbf{I}\sigma_{c}^2$; $\text{var}(\mathbf{e}) = \mathbf{I}\sigma_{e}^2$, where $\mathbf{A}$ is the numerator relationship matrix of animals in the model, $\mathbf{I}$ is the identity matrix, σ_{α}^2 is the additive genetic variance for direct effects (animal), σ_{m}^2 is the additive genetic variance for maternal effects, σ_{c}^2 is the variance due to common environmental effects and σ_{e}^2 is the residual error variance. Due to the fact that models were nested, the significance of the second and third random effects were tested using

log-likelihood ratio tests, to determine the most suitable model for each trait in univariate analyses.

Following univariate analyses, each combination of traits was analysed with a bivariate model using the most appropriate model for each trait. Estimates from the univariate analyses were used as starting values in the bivariate analyses. Approximate standard errors for heritabilities and correlations were constructed by ASReml from approximations to variances of ratios and products.

Genetic trends and selection differentials. Mean values for the selection line (S) and the control line (C) were calculated by two methods: (i) calculating the average CT index EBVs for S and C line animals each year when fitting model 1 (animal as the only random effect), and (ii) by fitting line x year as an additional fixed effect in the REML analysis. Genetic trends for the direct additive genetic values were then calculated by regressing the line difference (**S**-**C**) for each year on year of birth. The impact of selection on other traits was estimated from the difference between the estimates of selection and control line fixed effects, averaged across the 2002 and 2003 birth years. The average was taken across two years because the small size of the control line meant that comparisons made from any one year were imprecise. The standard errors of these estimated differences were constructed from the variance/covariance matrix of fixed effects.

Selection differentials were estimated to investigate the extent to which selection was truly performed using the CT index. The actual selection differential per year was calculated as the weighted average CT index EBV of sires against the mean EBV of the cohort from which they were selected, the weight given to each sire being his proportional contribution to the individuals that were measured in the next generation. The maximum potential selection differential was estimated by calculating the difference between the mean EBV of the six top ranking sires against and the mean EBV of the cohort from which they would have been selected, using the CT index as the sole ranking criterion and the same selection intensity as was achieved in practice. Comparing the selection differential achieved and the maximum potential provides an estimate of the proportion of the possible selection that was applied to the selection criterion in the selection line. The actual expected and maximum potential selection differentials were all estimated within year (Mrode *et al.*, 1990).

Results

Summary statistics
Means and standard deviations for the CT, ultrasonic and carcass measurements are in Table 1. Backfat depth in Blackface lambs was extremely variable, with a coefficient of variation of 0.61 compared with 0.11 for muscle depth. Also, the three fat areas (ISC, LV5, TV8) assessed by CT

Table 1 *Mean values and phenotypic standard deviations for CT, ultrasound and carcass traits*

| Trait	n	Mean	Phenotypic s.d.[‡]
CT index (units)	1074	4621	475
CT traits			
Live weight (kg)	1266	32.7	3.27
Fat area ISC (mm^2)	1266	3504	994
Muscle area ISC (mm^2)	1266	20 560	1613
Bone area ISC (mm^2)	1266	2887	269
Fat area LV5 (mm^2)	1266	1326	713
Muscle area LV5 (mm^2)	1266	7270	772
Bone area LV5 (mm^2)	1266	859	106
Fat area TV8 (mm^2)	1266	3511	1330
Muscle area TV8 (mm^2)	1266	9451	1095
Bone area TV8 (mm^2)	1266	3303	425
Ultrasound traits			
Muscle width (UMW) (mm)	2018	41.5	3.32
Muscle depth (UMD) (mm)	2018	20.8	2.21
Fat depth (UFD) (mm)	2018	1.70	1.04
Scan weight (SWT) (kg)	2554	32.7	3.50
Post-slaughter traits[†]			
Carcass weight (kg)	1148	18.3	1.98
Slaughter weight (kg)	1148	42.8	4.22
Conformation score (units)	1148	2.97	0.49
Fat class (units)	1148	2.75	0.50
Total price (£)	485	30.9	4.36

[†] Data not corrected to a predefined endpoint.
[‡] Phenotypic standard deviation obtained from REML analyses.

were moderately variable, with coefficient of variations of 0.28, 0.54 and 0.38, respectively.

Line differences and responses to selection
Mean values for the CT index for the S and C lines, from REML analyses fitting the line x year interaction, are in Figure 1 and responses to selection on the CT index, as estimated from the difference between the **S** and **C** lines, are in Figure 2. The estimated genetic trend was 52 (s.e. 38) units per year for the CT index, representing an annual genetic progress of 1.2% relative to the base year or 0.11 phenotypic standard deviation units per year. The genetic trend for the CT index estimated from the line mean EBV
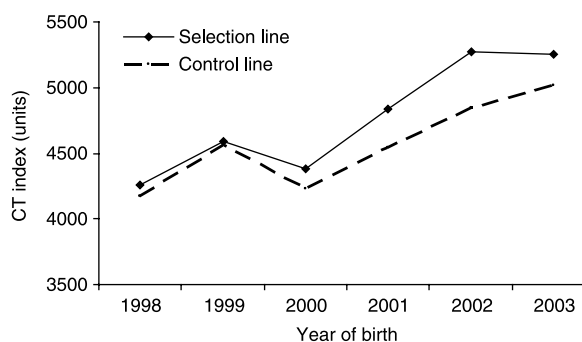
Figure 1 Line means for computer tomography (CT) index for the selection and control lines.

$$y = -26 + 52(x-1997)$$
$$s.e. = 38$$
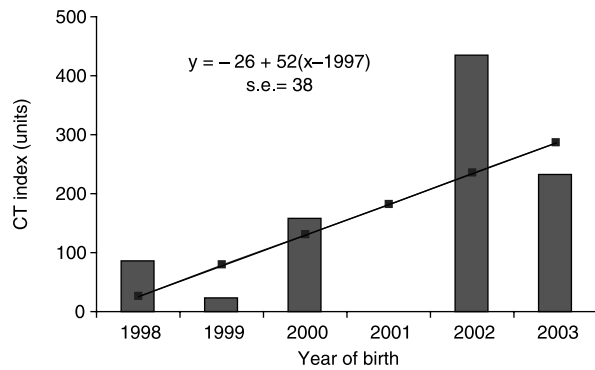
Figure 2 Direct genetic trends for the computer tomography (CT) index from 1998 to 2003, with the straight line showing the regression of line difference on year.

was 40 (s.e. 24) units per year. Although it appears from Figure 1 that the control line may also have drifted upwards with time, these year by line means do not disentangle genetic and environmental effects.

Line differences (S-C) for the CT and ultrasonic assessed traits are in Table 2, and line differences for carcass traits are in Table 3. The S line lambs had greater muscle and bone areas at the three sites (ISC, LV5, and TV8) and greater ultrasonic muscle width and depth. Furthermore, the S line lambs had higher conformation score and lower fat class score, both of which were in the desired direction. Non-significant trends were also seen for fat areas at the three sites (ISC, LV5, and TV8), with the S line having less fat than the C line. Line differences for carcass traits adjusted to a constant fat classification score and to a constant age were similar to those described above (results not shown).

Genetic parameters
Univariate heritability estimates for all live animal measurements are in Table 4. Maternal genetic effects were

significant, and therefore fitted, for some traits. The model containing common environmental effects (litter) was never significantly ($P > 0.05$) better than that with maternal genetic effects. Heritabilities for traits describing carcass composition (i.e. ultrasonic and CT measures) were all moderate, and their maternal genetic component was small or not significant ($P > 0.05$). In contrast, for live weight at scanning, the maternal genetic contribution and the contribution of the genes of the lamb were very similar (0.16 and 0.17, respectively). The CT index was highly heritable (0.41), which is in consistent with selection on the index being successful.

Heritabilities for post slaughter traits are in Table 5. Maternal genetic and litter effects were largely unimportant for these traits. The end-point adjustment (none, fat class or age) had no impact on the heritability estimates but did affect the standard errors of the estimates: they were lowest when a quadratic age correction was used and it is these estimates that are presented in Table 5. Almost all these traits were lowly heritable, except for carcass weight and slaughter age, which were both moderately heritable (0.21).

The estimated phenotypic and genetic correlations between the CT index and ultrasonic and carcass traits are in Table 6, with mean heritability estimates calculated from the bivariate models. Univariate estimates of heritability presented in Tables 4 and 5 and bivariate estimates in Table 6 were very similar. Estimates of phenotypic correlations were robust, with no standard errors greater than 0.06. However, several genetic correlations had large standard errors. This is particularly the case where one or both traits had low estimates of heritability and this limits the interpretation of many of the correlations presented.

The genetic correlations between the CT index and ultrasonic measurements were all positive and generally low to moderate. The estimated genetic correlations between the CT index and carcass traits were generally positive and low

Table 2 *Line means and differences for traits measured on the live animal, assessed using data collected in 2002 and 2003 (significant $P < 0.05$ line differences are indicated by an asterisk)*

Trait	Selection line (S)	s.e. (S)	Control line (C)	s.e. (C)	Line differences (S-C)	s.e.d.
Live weight (kg)	28.66	0.24	27.54	0.44	1.12*	0.49
Fat area ISC (mm^2)	2933	72.0	3010	135	-76.8	147
Muscle area ISC (mm^2)	20 040	116	18 888	217	1153*	237
Bone area ISC (mm^2)	2666	19.4	2569	36.3	97.3*	39.7
Fat area LV5 (mm^2)	712	52.3	738	97.9	-26.3	106
Muscle area LV5 (mm^2)	6929	55.4	6393	103	537*	113
Bone area LV5 (mm^2)	838	7.69	807	14.4	30.8*	15.7
Fat area TV8 (mm^2)	2497	97.0	2640	181	-142	198.3
Muscle area TV8 (mm^2)	9687	79.1	8919	148	768*	161.7
Bone area TV8 (mm^2)	2888	31.2	2714	58.4	175*	63.8
Muscle width (UMW) (mm)	40.33	0.22	38.50	0.44	1.83*	0.48
Muscle depth (UMD) (mm)	19.74	0.14	18.87	0.29	0.87*	0.32
Fat depth (UFD) (mm)	1.12	0.07	1.06	0.13	0.06	0.15
Scan weight (SWT) (kg)	25.49	0.23	24.17	0.46	1.32*	0.50

Table 3 *Line means and differences for carcass and slaughter traits[†], assessed using data collected in 2002 and 2003 (significant P < 0.05 line differences are indicated by an asterisk)*

Trait	Selection line (S)	s.e (S)	Control line (C)	s.e. (C)	Line differences (S-C)	s.e.d.
Carcass weight (kg)	16.3	0.23	16.8	0.37	− 0.58	0.41
Slaughter weight (kg)	37.1	0.48	38.1	0.80	− 1.00	0.87
Conformation score (units)	2.96	0.06	2.74	0.09	0.22*	0.10
Fat class (units)	2.49	0.06	2.78	0.10	− 0.28*	0.10
Total price (£)	28.1	0.60	28.3	1.02	− 0.29	1.12

[†] Data not corrected to a predefined endpoint.

to moderate, except that with fat class which was negative. The genetic correlations between ultrasonic measurements were positive and low to moderate but with large standard errors, and in the case of backfat depth, not significantly different from zero. In addition, carcass traits were moderately positively correlated, with a very high genetic correlation for carcass and slaughter weight (0.91). Genetic correlations between ultrasonic and carcass traits were variable. Live weight at scanning had a high positive genetic correlation with slaughter and carcass weight.

The genetic correlation between total price and carcass weight was positive and very strong (0.90) and the genetic correlation between price per kg and carcass weight was also positive and strong (0.52) (result not shown). The genetic correlation between total price and slaughter age was positive and very strong (0.90). Additionally, the estimated genetic correlations of total price with live weight at scanning and slaughter weight were positive and moderate (both 0.63). Slaughter age was positively genetically correlated with slaughter (0.44) and carcass weight (0.71).

Selection differentials
The ratio of the actual selection differential achieved to the maximum potential selection differential for the CT index

was calculated to evaluate how effective actual selection was relative to the intended selection. In the **S** line, the selection differential achieved for the CT index across all years was proportionately 0.89 of the maximum potential. The selection differential achieved for CT index was proportionately 0.90 for 2000, 0.87 for 2001, 0.88 for 2002 and 0.88 for 2003, all relative to the maximum potential for that year. The value achieved in 2001, when indirect selection had to be practised, was only marginally lower than that achieved in other years.

Discussion

Inheritance of traits
Estimates of heritability for CT traits, i.e. both the CT index and the CT tissue areas, on the live animal were moderate, indicating that CT provides a quick and reliable means of genetically changing carcass composition in sheep. In another study, on a different population of Blackface sheep at 24 weeks of age (Karamichou *et al.*, 2006), heritability estimates of CT tissue areas traits were moderate to high and were very similar for bone (average $h^2 = 0.36$) and muscle areas (average $h^2 = 0.33$), but somewhat higher than the current study for the three fat areas (average $h^2 = 0.64$).

The ultrasonic measures of post-weaning body composition were moderately to highly heritable. Our estimate of heritability for fat depth was lower than that reported by Roden *et al.* (2003) on a subset of this data ($h^2 = 0.44$), by Puntila *et al.* (2002) for Finnsheep ($h^2 = 0.39$), by Bishop *et al.* (1996) for Scottish Blackface sheep kept in an intensive environment ($h^2 = 0.39$), by Saatci *et al.* (1998) for Welsh Mountain sheep ($h^2 = 0.40$), by Thorsteinsson

Table 4 *Univariate estimates of heritabilities of direct (h^2) and maternal effects (m^2), and their standard errors (s.e.), for traits[†] measured in the live animal*

Trait	h^2	s.e. (h^2)	h_m^2	s.e.(h_m^2)
CT index (units)	0.41	0.08	—	—
Live weight (kg)	0.19	0.06	0.14	0.04
Fat area ISC (mm²)	0.34	0.07	—	—
Muscle area ISC (mm²)	0.38	0.07	0.12	0.04
Bone area ISC (mm²)	0.37	0.08	—	—
Fat area LV5 (mm²)	0.30	0.07	—	—
Muscle area LV5 (mm²)	0.38	0.07	0.11	0.04
Bone area LV5 (mm²)	0.35	0.07		
Fat area TV8 (mm²)	0.26	0.07	0.10	0.04
Muscle area TV8 (mm²)	0.39	0.07	—	—
Bone area TV8 (mm²)	0.29	0.07	—	—
Muscle width (UMW) (mm)	0.14	0.04	—	—
Muscle depth (UMD) (mm)	0.41	0.05	—	—
Fat depth (UFD) (mm)	0.30	0.05	0.06	0.03
Scan weight (SWT) (kg)	0.16	0.03	0.17	0.03

[†] Data not corrected to any endpoint.

Table 5 *Univariate estimates of heritabilities (h^2), with standard errors (s.e.), for carcass and slaughter traits at a constant age*

Trait	h^2	s.e.
Carcass weight (kg)	0.21	0.06
Slaughter weight (kg)	0.15	0.05
Conformation score (units)	0.14	0.05
Fat class (units)	0.19	0.05
Slaughter age (days)[†]	0.21	0.05
Total price (£)	0.19	0.06

[†] Not adjusted to a constant age.

Table 6 *Estimates of heritabilities (using the average of the bivariate heritability estimates) and of phenotypic and genetic correlations (with standard errors) for CT, ultrasound and carcass traits[†‡]*

Trait	CT Index	SWT	UMW	UMD	UFD	Slaughter weight	Slaughter age	Carcass weight	Conformation score	Fat class	Total price
CT Index	**0.41 (0.07)**	0.14	0.16	0.35	0.15	0.12	−0.08	0.12	0.00	−0.07	0.04
SWT	0.32 (0.16)	**0.20 (0.04)**	0.34	0.34	0.33	0.52	−0.08	0.41	0.05	0.07	0.02
UMW	0.18 (0.18)	0.24 (0.16)	**0.14 (0.04)**	0.36	0.20	0.18	−0.06	0.17	0.05	0.05	0.01
UMD	0.50 (0.10)	0.23 (0.12)	0.30 (0.12)	**0.40 (0.05)**	0.32	0.16	−0.07	0.17	0.15	0.12	−0.11
UFD	0.10 (0.15)	0.10 (0.13)	−0.05 (0.15)	0.17 (0.10)	**0.41 (0.08)**	0.16	−0.14	0.20	0.10	0.20	−0.16
Slaughter weight	0.19 (0.22)	0.95 (0.07)	0.12 (0.21)	0.09 (0.15)	−0.02 (0.17)	**0.12 (0.09)**	0.36	0.84	0.09	0.18	0.61
Slaughter age	−0.10 (0.22)	−0.04 (0.19)	−0.25 (0.21)	−0.01 (0.16)	−0.33 (0.16)	0.44 (0.15)	**0.21 (0.06)**	0.42	−0.06	−0.04	0.40
Carcass weight	0.40 (0.26)	0.87 (0.16)	0.06 (0.26)	0.24 (0.18)	0.09 (0.21)	0.91 (0.13)	0.71 (0.15)	**0.17 (0.09)**	0.13	0.26	0.74
Conformation score	0.13 (0.28)	−0.17 (0.24)	−0.01 (0.26)	0.30 (0.19)	−0.08 (0.22)	0.11 (0.45)	−0.02 (0.27)	0.01 (0.37)	**0.22 (0.10)**	0.21	0.06
Fat class	−0.49 (0.25)	0.16 (0.20)	−0.02 (0.24)	0.20 (0.17)	0.97 (0.17)	0.20 (0.42)	−0.01 (0.23)	0.20 (0.35)	0.19 (0.28)	**0.25 (0.13)**	0.09
Total price	0.35 (0.34)	0.63 (0.32)	−0.37 (0.36)	0.11 (0.26)	0.13 (0.30)	0.63 (0.23)	0.90 (0.20)	0.90 (0.34)	−0.32 (0.51)	−0.22 (0.48)	**0.16 (0.08)**

[†] Heritabilities on diagonal, phenotypic correlations above and genetic correlations below diagonal.
[‡] Data not corrected to a predefined endpoint.

and Eythorsdottir (1998) for Icelandic sheep ($h^2 = 0.42$), and by Cameron and Bracken (1992) for a terminal sire breed ($h^2 = 0.35$). Our estimate for fat depth is almost the same as that summarised by Fogarty (1995) for dual-purpose sheep (a mean of 0.28 for fat depth, from 30 studies). The heritability estimate for muscle depth is similar to that reported by Puntila *et al.* (2002) for Finnsheep ($h^2 = 0.46$) and by Cameron and Bracken (1992) for a terminal sire breed ($h^2 = 0.46$). However, when considering other studies, the heritability of muscle depth in this study is high; Roden *et al.* (2003) reported a heritability of 0.26; Fogarty *et al.* (2003) of 0.27; Bishop et al. (1996) of 0.25); and Saatci et al. (1998) a heritability of 0.19. Lauridsen (1998) found 25 literature estimates of heritability ranged from 0.13 to 0.57 (average of 0.32) for muscle depth and from 0.07 to 0.62 (average of 0.31) for fat depth. Usually, fat depths have been reported to have medium to high heritabilities. Our results suggest that the potential for genetic progress for body composition traits in hill sheep maintained under extensive conditions may be higher than previously thought, however expected progress may vary greatly between populations.

Our estimate of the heritability of ultrasonic muscle width was considerably lower than that of muscle depth, which is in agreement with Fogarty *et al.* (2003), who estimated the heritability for muscle width in 19-month-old Merino rams to be 0.15. This most probably reflects the fact that muscle width is more difficult to measure accurately than muscle depth. Our estimates of heritabilities for fat and muscle measures from CT were almost the same as those from ultrasound, whereas in the study by Karami-chou *et al.* (2006), heritabilities were higher for CT measures than for ultrasound measures, particularly for fat measurements.

The estimate of heritability for live weight at ultrasound scanning was lower in this study than the estimates reported by Cameron and Bracken (1992) for a terminal sire breed ($h^2 = 0.20$), by Bishop (1993) for Scottish Blackface sheep ($h^2 = 0.23$) and by Puntila *et al.* (2002) for Finnsheep ($h^2 = 0.44$). However, a substantial maternal genetic component was also observed in our study.

Heritability estimates for carcass and slaughter traits were moderate. The estimate for carcass weight ($h^2 = 0.21$) was in agreement with results of Bennett et al. (1991) ($h^2 = 0.22$), which was done in crossbred lambs from Southdown sires and Romney ewes. Also, Henniñgs-son and Malmfors (1995) reported an estimate of 0.17 for Swedish Pelt sheep and Conington *et al.* (2001) reported an estimate of 0.33 for Blackface sheep.

Heritability estimates for fat class and conformation score were low, as expected, given that they are subjectively scored. There are very few estimates on genetic parameters for visually assessed muscling on live animals, such as conformation score. Bradford and Spurlock (1972) reported a heritability estimate of 0.32 (s.e. 0.25) for live conformation, and Schrooten and Visscher (1987) obtained

a relatively high heritability estimate for live muscling score (0.44, s.e. 0.09) in the Texel breed. Van Heelsum *et al.* (1999) reported a heritability estimate of 0.20 (s.e. 0.04) for scores of gigot conformation in the Bluefaced Leicester and Puntila *et al.* (2002) reported an estimate of 0.27 for Finnsheep. Also, Conington *et al.* (2001) reported a heritability estimate of 0.09 for conformation and 0.17 for fat class score in Blackface sheep. Their estimate for fat class score was in close agreement with our estimate. The estimated heritabilities for live animal conformation score suggest that there is scope for genetic improvement in breeds with low subcutaneous fat cover. It is known that conformation strongly depends on fatness and muscling (having moderate heritabilities) but it is scored in a subjective manner.

Relationships between traits
Our data set was large enough to allow estimation of genetic correlations between the CT index and ultrasonic and carcass measurements; they were low to moderate, albeit with large standard errors. Genetic change in any of these attributes is feasible in principle, and correlated responses in other traits predictable from genetic theory. Relationships of the CT index with live weight at scanning and muscle depth were moderately strong, indicating that selection on the index should moderately increase both these traits. Also, the CT index was strongly genetically correlated with carcass weight and fat class score, again indicating that selection on the CT index should increase carcass weight, but decrease fatness score.

A high genetic correlation of live weight at scanning with slaughter and carcass weight was found, indicating that selection for heavier lambs at weaning will increase slaughter and carcass weights. These results contradict the study made in Blackface sheep by Conington *et al.* (1998), who estimated genetic correlations of 0.18 and 0.07, respectively. Also, the very strong genetic correlation between ultrasonic fat depth and fat class indicates that selection for reduced fat depth could lower fatness scores, which is in the expected direction. In addition, carcass weight and slaughter weight were strongly genetically correlated, indicating that they are essentially expressions of the same trait, which is in agreement with the study of Conington *et al.* (1998) for Blackface sheep. The correlations between live animal and slaughter measurements are likely to change with the production environment, and hence the mean time between weaning and slaughter. Moreover, variation between animals in the length of time from live animal assessment to slaughter will change with production environment, and this will also impact on correlations between live animal and slaughter measurements.

The genetic correlation between total price and carcass weight was positive and very strong, indicating that heavier lambs made more money, as expected. The estimates of genetic correlations of total price with slaughter and carcass weight were in close agreement with those reported by Conington *et al.* (1998), who found estimates of 0.92

and 0.89, respectively. However, these relationships are stronger than can simply be explained by the fact that bigger carcasses fetch higher prices, because price per kg was also genetically positively correlated with carcass weight. In other words, larger carcasses are favoured, financially. Also, estimates of genetic correlations of slaughter age with total price, and with slaughter and carcass weight were in agreement with results of Conington *et al.* (1998), who reported estimates of 0.84, 0.67 and 0.67, respectively. The relationship between slaughter age and total price suggests a trend in prices through the season that is counter to most selection goals, as it indicates that genetically slower growing animals will return more money to the producer, under the pricing structure encountered in this study.

Selection responses
Selection differentials provide a convenient description of the selection pressure that has been applied. Comparison of actual and maximum selection differentials indicate that selection was largely on the CT index, but that other criteria were also included in the selection decisions. Moreover, selection was not markedly hindered by the absence of CT measurements for one year. Selection on the index was successful in increasing live weight and traits describing muscle dimensions, but reductions in fat dimensions assessed on the live animal were not significant. At slaughter, this corresponded to a small increase in conformation score and a small decrease in fatness.

Conclusions
This study has confirmed that CT and ultrasonic measurements provide an effective means of selecting for improved carcass composition. The ultrasonic and CT measured traits were more highly heritable than the subjectively assessed traits. Many of traits were also affected by the maternal environment, as expected. The ultrasonic and CT traits also showed high levels of genetic variation, which is the second requirement for making genetic progress.

Judging by the genetic correlations, selection on the CT index should achieve a moderate improvement in conformation, price and slaughter weight, and a decrease in fat class. These changes were in fact seen for fat class, conformation and live weight. Conversely, selection on live weight at scanning would be expected to improve carcass and slaughter weight, and total price received, but have slightly deleterious impacts on carcass conformation score.

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References

Afonso J and Thompson JM 1996. Fat distribution in sheep selected for/against backfat depth, during growth on ad libitum feeding. Livestock Production Science 46, 97-106.

Allen P 1990. Reducing fat in meat animals. In New approaches to measuring body composition in live animals (eds JD Wood and AV Fisher), pp. 201-254. Elsevier, London.

Bari F, Khalid M, Haresign W, Merrell B, Murray A and Richards RIW 1999. An evaluation of the success of MOET in two breeds of hill sheep maintained under normal systems of hill flock management. Animal Science 69, 367-376.

Bari F, Khalid M, Haresign W, Murray A and Merrell B 2000. Effect of mating system, flushing procedure, progesterone dose and donor ewe age on the yield and quality of embryos within a MOET program in sheep. Theriogenology 53, 727-742.

Bennett GL, Johnson DL, Kirton AH and Carter AH 1991. Genetic and environmental effects on carcass characteristics of Southdown × Romney lambs. II. Genetic and phenotypic variation. Journal of Animal Science 69, 1864-1874.

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

Bishop SC, Conington J, Waterhouse A and Simm G 1996. Genotype × environment interactions for early growth and ultrasonic measurements in hill sheep. Animal Science 62, 271-277.

Bradford GE and Spurlock GM 1972. Selection for meat production in sheep—results of a progeny test. Journal of Animal Science 34, 737-745.

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

Conington J, Bishop SC, Grundy B, Waterhouse A and Simm G 2001. Multi-trait selection indexes for sustainable UK hill sheep production. Animal Science 73, 413-423.

Conington J, Bishop SC, 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.

EUROP 1995. Community scale for the classification of carcasses of ovines. Office for Official Publications of the European Communities (EUROP), Luxemburg.

Fennessy PF, Greer GJ, Bain WE and Johnstone PD 1993. Progeny test of ram lambs selected for low ultrasonic backfat thickness or high post-weaning growth rate. Livestock Production Science 33, 105-118.

Fogarty NM 1995. Genetic parameters for live weight, fat and muscle measurements, wool production and reproduction in sheep: a review. Animal Breeding Abstracts 63, 101-143.

Fogarty NM, Safari E, Taylor PJ and Murray W 2003. Genetic parameters for meat quality and carcass traits and their correlation with wool traits in Australian Merino sheep. Australian Journal of Agricultural Research 54, 715-722.

GenStat 7 Committee 2003. Reference manual. Oxford University Press, Oxford.

Gilmour AR, Cullis BR, Welham SJ and Thompson R 2004. ASREML: program user manual. VSN International Ltd, Hemel Hempstead, UK.

Henniñgsson T and Malmfors G 1995. The relationship between live weight of Swedish lambs at 120 days of age and carcass traits. Proceedings of the Scandinavian Association of Agricultural Scientists. p. 256.

Jones HE, Lewis RM, Young MJ and Wolf BT 2002. The use of X-ray computer tomography for measuring the muscularity of live sheep. Animal Science 75, 387-399.

Jopson NB, McEwan JC, Dodds KG and Young MJ 1995. Economic benefits of including computer tomography measurements in sheep breeding programmes. Proceedings of Australian Association for Animal Breeding and Genetics, vol. 11, pp. 194-197.

Jopson NB, McEwan JC, Fennessy PF, Dodds KG, Nicoll GB and Wade CM 1997. Economic benefits of including computed tomography measurements in a large terminal sire breeding programme. Proceedings of the Australian Association for the Advancement of Animal Breeding and Genetics, vol. 12, pp. 72-76.

Karamichou E, Richardson RI, Nute GR, McLean KA and Bishop SC 2006. Genetic analyses of carcass composition, as assessed by X-ray computer tomography and meat quality traits in Scottish Blackface sheep. Animal Science 82, 151-162.

Lauridsen J (1998) Stochastic simulation of alternative breeding schemes for Danish meat type sheep and ultrasonic eyemuscle and backfat measurements on lambs Copenhagen.

McEwan JC, Fennessy PF, Greer GJ, Bruce GD and Bain WE 1989. Selection for carcass composition: effects on the development of subcutaneous and internal fat depots. Proceedings of the Nutrition Society of New Zealand, vol. 14, pp. 163-164.

Meat and Livestock Commission. 1998. Sheep yearbook. Meat and Livestock Commission, Milton Keynes, UK.

Mrode RA, Smith C and Thompson R 1990. Selection for rate and efficiency of lean gain in Hereford cattle 1. Selection pressure applied and direct responses. Animal Production 51, 23-34.

Puntila ML, Mäki K and Rintala O 2002. Assessment of carcass composition based on ultrasonic measurements and EUROP conformation class of live lambs. Journal of Animal Breeding and Genetics 119, 367-378.

Roden JA, Merrell BG, Murray AW and Haresign W 2003. Genetic analysis of live weight and ultrasonic fat and muscle traits in a hill sheep flock undergoing breed improvement utilizing an embryo transfer programme. Animal Science 76, 367-373.

Saatci M, Ap Dewi I and Ulutas Z 1998. Correlations between weaning weight, carcass traits and ultrasonic body measurements in Welsh Mountain sheep. Proceedings of the British Society of Animal Science, p. 84.

Schrooten C and Visscher AH 1987. Genetic parameters for growth and slaughter quality. IVO-DLO Report B-283. Instituut voor Veeteeltkundig Onderzoek 'Schoonoord' Zeist, The Netherlands.

Simm G and Dingwall WS 1989. Selection indices for lean meat production in sheep. Livestock Production Science 21, 223-233.

Simm G, Lewis RM, Grundy B and Dingwall WS 2002. Responses to selection for lean growth in sheep. Animal Science 74, 39-50.

Simm G, Young MJ and Beatson PR 1987. An economical selection index for lean meat production in New Zealand sheep. Animal Production 45, 465-475.

Thorsteinsson S and Eythorsdottir E 1998. Genetic parameters of ultrasonic and carcass cross-sectional measurements and muscle and fat weight of Icelandic lambs. Proceedings of the sixth world congress on genetics applied to livestock production, Armidale, vol. 24, pp. 149-152.

Van Heelsum AM, Lewis RM, Jones DW, Haresign W and Davies MH 1999. Genetic parameters for live weight, ultrasonic measurements and conformation in Bluefaced Leicester sheep. Proceedings of the British Society of Animal Science, p. 122.

Young MJ, Lewis RM, McLean KA, Robson NA. A, Fraser J, Fitzsimons J, Donbavand J and Simm G 1996. Prediction of carcass composition in meat breeds of sheep using computer tomography. Proceedings of the British Society of Animal Science, p. 43.

Young MJ, Logan CM, Beatson PR and Nsoso SJ 1999. Prediction of carcass tissue weight in vivo using live weight, ultrasound or X-ray CT measurements. Proceedings of the New Zealand Society of Animal Production 56, 205-211.