1999

Genetic relationships between visual and objective measures of carcass composition in crossbred lambs

H. E. Jones
Scottish Agricultural College, West Mains Road, Edinburgh

G. Simm
Scottish Agricultural College, West Mains Road, Edinburgh

W. S. Dingwall
Scottish Agricultural College, West Mains Road, Edinburgh

R. M. Lewis
Scottish Agricultural College, West Mains Road, Edinburgh, ron.lewis@unl.edu

Animal Science 1999, **69**: 553-561

1357-7298/99/96050553$20·00

Genetic relationships between visual and objective measures of carcass composition in crossbred lambs

H. E. Jones, G. Simm, W. S. Dingwall and R. M. Lewis

Genetics and Reproduction Department, Animal Biology Division, Scottish Agricultural College, King's Buildings, Edinburgh EH9 3JG

Abstract

The aim of this study was to estimate genetic and phenotypic (co)variances between objective measures and carcass visual scores, as a test of the potential value of visual scores in selection programmes to improve carcass composition in crossbred lambs. In each of 1986, 1987 and 1988, 22 Suffolk rams were chosen with either high or low scores on an index designed to increase lean growth rate. These rams were joined with 18 to 20 crossbred ewes each and their lambs were grown on grass to one of three target live weights (35·5, 41·5 and 47·0 kg) for slaughter. The carcasses of 1881 lambs were visually scored for overall conformation and fatness using the standard Meat and Livestock Commission methods. Additionally, a more detailed 15-point scale assessment of conformation and a direct visual score of subcutaneous fat on the carcass were taken on 1252 lambs during the latter 2 years of the study. Carcass composition was estimated by dissection of a shoulder joint into lean, fat and bone.

The possibility of combining data collected on lambs slaughtered at each of the three target live weights, for the estimation of genetic parameters was investigated. Results indicated that heritability estimates for a trait using data collected within each of the slaughter groups were homogeneous. Genetic correlations between records collected for a trait within each of the slaughter groups were not significantly different from one. These results indicated that data collected at each of the target slaughter weights could justifiably be combined.

Heritability estimates were generally higher for shoulder tissue proportions (0·3) than for visual scores (0·2). Genetic correlations between all conformation scores and tissue proportions were not significantly different from 0 and therefore of little or no value in predicting carcass composition. Genetic correlations between visual scores of fat and both tissue proportions and ratios were generally high (around 0·65). These results suggest that fat scores collected on crossbred animals could be valuable in purebred selection programmes where improving carcass composition of the crossbred generation is the underlying objective.

Keywords: *carcass composition, crossbreds, genetic parameters, sheep, visual grading.*

Introduction

The change in consumer attitudes to fat, particularly in red meats, has contributed to the steady decline in consumption of lamb over recent years (Woodward and Wheelock, 1990). The importance of reducing the fat content of lamb to arrest this decline is well established (Harrington and Kempster, 1989).

Genetic improvement has emerged as one of the preferred methods to reduce the fat content of lamb. With the development of techniques such as ultrasound to estimate carcass composition *in vivo* (Simm, 1987), the practicality and cost effectiveness of improving carcass composition within breeds through selection has been demonstrated in many studies (review by Simm, 1992). Within-breed improvement is now widely accepted as an effective method of achieving this goal, with selection programmes underway at a commercial level in many purebred terminal sire breeds in the UK (Guy and Croston, 1994) and elsewhere.

The majority of prime or market lamb in the UK is produced by crossing terminal sire rams with crossbred ewes. Several studies (Bennett *et al.*, 1988; Cameron, 1992; Lewis *et al.*, 1996) show that selection

of purebred terminal sires for improved carcass composition results in a correlated improvement in the carcass composition of their crossbred progeny. In each of these studies, the selection objective was to improve the carcass composition of the purebred. Where crossbreeding is important, Wei and van der Werf (1994) suggest that higher genetic responses in crossbred progeny could be achieved if breeding goals were defined at the crossbred levels and if information from these animals was used in the evaluation of purebred sires.

The feasibility of incorporating crossbred information into purebred selection programmes depends on the kinds of measurement that can be collected pragmatically on crossbred animals and the size of the genetic (co)variances among these. The costs of measuring carcass composition directly — typically by physical separation into lean, fat and bone or into saleable meat yields — prohibit its use as a routine procedure. Other carcass measures, such as visual scores, which can be made routinely, may provide an alternative source of information. Visual scores of fat and overall carcass conformation in particular are of interest since they are readily assessed and are used within the European Community to indicate the quality and value of lamb carcasses. However, the value of such assessments depends on how heritable they are.

The principal aim of this study was to estimate genetic and phenotypic (co)variances between metric (objective) measures and visual scores of carcass composition in crossbred lambs. In the trial, lambs were grown to three fixed live weights that correspond with the range of carcass weights which are produced commercially in the UK. Testing whether records collected on lambs slaughtered at each of these end points can justifiably be combined and analysed jointly was central to the investigations.

Material and methods

Suffolk ram progeny test

Data were from a progeny test of Suffolk rams conducted in 1987, 1988 and 1989 at the East of Scotland College of Agriculture, now part of the Scottish Agricultural College (SAC). Ram lambs were performance tested and evaluated on the basis of an index designed to increase the rate of lean deposition whilst limiting the rate of fat deposition (Simm and Dingwall, 1989). Each year 11 high index and 11 low index rams were chosen from on average 86 candidates. An additional low index ram was used in the 1st year of the study (1986) due to the poor performance at mating of one ram. Therefore, in total, 67 rams were progeny tested.

Each selected ram was joined with 18 to 20 Scottish Mule (Bluefaced Leicester × Scottish Blackface) ewes in October of each year. Mating occurred over a 6-week period during which mating groups were maintained in separate paddocks. Over the 3 years 1999 lambs were reared from 1142 lambings of 481 ewes. Most lambs were reared as twins (90%) with the remainder reared as singles. Any additional lambs were either fostered or reared artificially.

Within sire families, lambs were allocated at random to one of three target live-weight groups for slaughter (35·5, 41·5 or 47·0 kg). These weights were chosen to represent the range of carcass weights typical in commercial lamb production (16·5, 20·0 and 23·5 kg respectively). Lambs, and their dams through weaning, were maintained on mixed grass sward of predominantly perennial ryegrass (*Lolium perenne* L.) until they reached slaughter weight. Lewis *et al.* (1996) describe in greater detail the characteristics of the SAC Suffolk selection flock and the design and management of the progeny test.

Table 1 *Means, standard deviations (s.d.) and abbreviations designated for carcass measures recorded*

Traits	Abbreviation	Mean	s.d.
Carcass visual scores			
MLC carcass conformation score†	MLCC	0·0	0·9
Leg conformation score‡§	LGCONF	9·6	2·4
Loin conformation score‡§	LNCONF	9·9	2·5
Shoulder conformation score‡§	SHCONF	9·5	2·5
Overall carcass conformation score‡§	OVCONF	9·7	2·5
MLC carcass subcutaneous fat score (%)	MLCF	12·0	3·2
Estimated subcutaneous fat proportion (%)‡	ESTF	11·6	3·1
KKCF score†‡	KKCF	0·0	0·9
Shoulder tissue proportions			
Lean content (g/kg)	LEAN	528	33
Subcutaneous fat content (g/kg)	SFAT	133	31
Intermuscular fat content (g/kg)	IFAT	165	23
Overall fat content (g/kg)	FAT	298	45
Bone content (g/kg)	BONE	174	18
Shoulder tissue ratios			
Lean to fat	LFR	1·8	0·4
Lean to bone	LBR	3·1	0·3

† Threshold values corresponding with the proportion of lambs categorized into each level of score. Larger values (more positive) indicate a higher visual conformation or heavier internal fat weight.
‡ Records only available in 1988 and 1989 (1252 records).
§ Scored 1 to 15, where 1 is poor conformation and 15 is excellent conformation.

Slaughter measurements

Details of the carcass measurements recorded are given in Table 1. A classifier from the Meat and Livestock Commission (MLC) visually scored subcutaneous and internal fat and conformation (as an indicator of muscularity) on all carcasses.

The MLC fat scores were intended to indicate the level of subcutaneous fat in the carcass. The scores (Un, 2, 3L, 3H, 4L, 4H and 5) therefore were replaced by their corresponding estimated subcutaneous fat percentages (4, 8, 11, 13, 15, 17 and 20%, respectively) for analysis (Kempster *et al.*, 1986).

The kidney knob and channel fat (KKCF) and MLC conformation score each have few categories. Both measures were therefore transformed to threshold values based on the proportion of lambs falling into each category. Threshold values for MLC conformation (corresponding conformation score shown in brackets) were 2·72 (E), 1·36 (U), 0·01 (R), –1·19 (O) and –2·07 (P). For internal fat score threshold values (corresponding KKCF weight per carcass shown in brackets) were –1·67 (0 to 110 g), –0·36 (120 to 230 g), 0·83 (240 to 340 g) and 2·00 (350 to 450 g). Larger more positive threshold values indicate better conformation and higher KKCF weight. Lewis *et al.* (1996) provide further details about the way threshold values were assigned to these scores.

The shoulder joint from the left side of each carcass was physically separated into lean, fat (subcutaneous and intermuscular), bone and waste. For analysis tissue weights were expressed as proportions of the joint weight (g/kg). The ratios of lean to fat and lean to bone (g/g) were also calculated. The tissue proportions within the shoulder joint were chosen as representative of the whole carcass. The choice of this sample joint was based on the high correlation (0·9) between shoulder and carcass lean proportions found in earlier studies (Cook *et al.*, 1983). Subsequent studies by Cameron (1992) and Lewis *et al.* (1996) substantiate that shoulder dissections provide an unbiased prediction of carcass tissue composition.

Statistical analysis

Model selection. The residual maximum likelihood procedure (REML; Patterson and Thompson, 1971) was used to identify those fixed effects in a linear mixed model which were important to describe the carcass measurements within slaughter groups. The fixed effects investigated were sire index category (high or low), sex (wether or ewe), dam age (2, 3 or 4 years of age and older), grazing location (three per year), birth and rearing rank (e.g. single, twin), and the interaction between grazing location and both birth and rearing rank. The linear, quadratic and cubic regressions of the response variable on carcass weight were also considered.

Sire, common environment (effects specific to litters of a dam) and residual terms were included as random effects. The ancestry of Mule dams was unknown and therefore a maternal genetic effect could not be explicitly fitted. The common environmental effect therefore captured all sources of maternal random variation, both environmental and genetic.

Fitting both birth rank and rearing rank accounted for little additional variation ($P > 0{\cdot}05$) than that accounted for by fitting either effect separately. Rearing rank and its interaction with grazing location were included in the final model in preference to birth rank, due to the limited number of animals in some levels of the birth rank and grazing location interaction. Based on these preliminary investigations, sire index category, sex, dam age, rearing rank, grazing location, the interaction of rearing rank and grazing location, and the linear, quadratic and cubic regressions on carcass weight, were included as fixed effects in the mixed model fitted.

Heterogeneity of variance. Each slaughter group contained approximately one third of the data. Parameters estimated within slaughter groups were therefore expected to be less reliable than those based on all of the data. Three null hypotheses were tested as justification for combining data across slaughter groups for each trait. These hypotheses were: (i) the within-group phenotypic variance was equal to the across-group phenotypic variance for each slaughter group; (ii) as a ratio of the within-group phenotypic variance, the proportion of genetic and common environmental variance was equal across slaughter groups; and, (iii) the genetic correlation for a trait between all pairs of slaughter groups was equal to one. Failure to reject this set of hypotheses implies that the variances are not heterogeneous across slaughter groups and that the data may be combined and analysed jointly.

The tests of the homogeneity of phenotypic variance, and ratios of genetic (h^2) and common environmental (c^2) to phenotypic variance (hypotheses (i) and (ii) above) required that analyses were conducted both within and across slaughter groups. For the across group analyses, slaughter group category (35·5, 41·5 and 47·0 kg) was included as an additional fixed effect. An individual animal model was fitted that, besides the relevant fixed effects, included as random effects, genetic (direct additive), common

environment and residual terms. Estimates of variances were obtained using the variance component and estimation (VCE) REML program written by Groeneveld (1996).

For the test of hypothesis (i), within-group genetic, common environmental and residual variances (which together equal the total phenotypic variance) were fixed at values obtained from the converged across-group analyses. For the test of hypothesis (ii), the genetic and common environmental variances as proportions of the within-group phenotypic variance were fixed at values of the across-group estimates of h^2 and c^2. Log-likelihood values were calculated at these fixed parameter values for each slaughter group. A log-likelihood ratio test (see, for example, Mood *et al.*, 1973) was constructed as twice the difference in log-likelihood values between analyses where parameters were fixed or estimated (the converged value) and compared with a chi-square distribution with three degrees of freedom. For this part of the analysis the MTDFREML program (Boldman *et al.*, 1995) was used, since it allowed individual variances to be fixed at predetermined values. For these analyses the convergence criterion chosen was that the variance of the Simplex function falls below 1×10^{-8}. MTDFREML was not used for parameter estimation, since the version of the package available did not provide standard errors for parameter estimates.

To investigate if a measure recorded at each slaughter weight represented the same or different traits (hypothesis (iii) above), the records collected on lambs slaughtered at different weights were considered as separate traits recorded on separate but related animals (as described by Thompson *et al.*, 1995). Genetic correlations between records collected within each group were estimated from a series of bivariate analyses using VCE. The animal model described previously for the within-slaughter-group analysis, was used.

From the preliminary within-slaughter-group analyses, phenotypic variances appeared to be heterogeneous, both before and after accounting for fixed effects. Within-group phenotypic variances were found to differ significantly from across-group estimates for some traits, indicating that the across-group variance was a poor approximation of variances within groups for these traits. Visscher *et al.* (1991) suggested that parameter estimates might be biased, if heterogeneity is evident between groups and these differences are not accounted for. Provided heritabilities are homogeneous across groups, Visscher *et al.* (1991) proposed that differences in phenotypic variance can be accounted for by scaling data by the ratio of within to across group phenotypic variances prior to analysis. Thus, the effect of such a scaling on parameter estimates was investigated.

Data were adjusted using $y_{ij}^s = y_{ij}\,(sd_p/sd_{pi})$ where sd_{pi} and sd_p were the phenotypic standard deviations within slaughter group i and overall (across groups), respectively, and y_{ij}^s was the scaled record. The within-group standard deviation was calculated ignoring other fixed and random effects. The across-group standard deviation was calculated from the maximum likelihood estimate of phenotypic variance when fitting slaughter group as the only fixed effect. Variances were then estimated for scaled records across slaughter groups using VCE. This method of scaling was preferred to a simple log transformation since the within-slaughter-group coefficients of variation were not constant across groups for all traits, which decreased with increasing target slaughter weight for most traits.

Estimation of (co)variance components. Selection of rams on index score began in the Suffolk flock in 1986. Although the progeny test was conducted shortly thereafter, if this sire selection was not accounted for parameter estimates could be biased. As proposed by Thompson *et al.* (1995) sire index and progeny carcass records were fitted as genetically correlated traits in bivariate REML analyses using VCE. Pedigree information and index scores for the 331 Suffolk rams that were performance tested up to and including 1988 were included in the analysis. The individual animal model described previously was fitted excluding the common environment term; when the common environmental effect was fitted, analyses failed to converge. Parameter estimates obtained from these bivariate analyses were not different from those obtained when sire index was not included. Similar findings were reported by Lewis *et al.* (1996). Index information for the purebred Suffolks was henceforth ignored.

The investigations of heterogeneity suggested that data from across slaughter groups could be combined and analysed jointly. Univariate estimates of variance components for genetic and common environmental effects were obtained for all traits using VCE for the pooled data, fitting the model previously described for across-group analyses.

For data combined across slaughter groups, estimates of genetic correlations between pairs of all traits were obtained from bivariate analyses using VCE, fitting the model described for across-group analyses. The correlations obtained were combined into a symmetric matrix (15×15), where the diagonal elements were the average of estimates

Table 2 *Across-group phenotypic variances and the ratio of within- to across-group variances for each slaughter group*†

Traits‡	Vp	Vp_1/Vp	Vp_2/Vp	Vp_3/Vp
MLCC	0·54	1·02	0·95	0·96
LGCONF	3·41	1·23	0·89	0·87
LNCONF	3·42	1·27	0·92	0·81
SHCONF	3·46	1·21	0·90	0·86
OVCONF	3·46	1·23	0·90	0·85
MLCF	4·30	1·00	0·93	1·04
ESTF	3·82	0·98	0·95	1·04
KKCF	0·41	0·91	0·98	0·98
LEAN	829	1·02	0·95	0·95
SFAT	565	0·89	1·00	1·10
IFAT	422	0·97	1·01	0·96
FAT	1181	1·00	1·00	0·95
BONE	164	1·15	0·96	0·86
LFR	0·10	1·43	0·90	0·63
LBR	0·06	0·99	0·86	1·05

† Vp is the across-group variance adjusted for fixed effects. Vp_1, Vp_2, Vp_3, are within-group variances adjusted for fixed effects for slaughter groups 35·5 kg, 41·5 kg and 47·0 kg respectively.
‡ Trait abbreviations are defined in Table 1.

from the bivariate runs. The genetic correlation matrix was not positive definite. The most negative eigen value was equal to –6·8, however all other negative roots were small, being less than –0·1.

Results

Heterogeneity of variances

Ratios of within to across slaughter group phenotypic variances for each trait are shown in Table 2. These variances were corrected for fixed effects. Although the ratios indicate that heterogeneity of phenotypic variance was present for most traits, differences between within- and across-group estimates were generally small. Within-group variances appeared to be most heterogeneous for shoulder lean : fat ratio (LFR).

Tests of heterogeneity of variances are shown in Table 3 for six traits that are representative of the carcass visual scores and shoulder tissues measured. As noted earlier (Table 2), heterogeneity of phenotypic variance was found to be present for each of the 15-point conformation scores (some not shown). Variances within the lightest slaughter group (35·5 kg) were significantly higher than across groups variances [$P < 0·05$; hypothesis (i)].

Heterogeneity was also present for shoulder bone content (BONE) and LFR. For both these traits the heterogeneity was largely due to scaling effects. Within-group coefficients of variation were constant across slaughter groups — means and variances

Table 3 *Estimates of within slaughter group* h^2 *and* c^2 *(s.e.), and likelihood ratio tests of heterogeneity of within-group phenotypic variance (hypothesis (i)) and* h^2 *and* c^2 *ratios as a proportion of within-group phenotypic variance (hypothesis (ii)), relative to across-group values*

Traits†/groups	h^2 (s.e.)	c^2 (s.e.)	Δ_1	Δ_2
MLCC				
35·5	0·31 (0·07)	0·00 (0·00)‡	1·19	0·94
41·5	0·19 (0·08)	0·08 (0·05)	1·16	0·62
47·0	0·27 (0·07)	0·00 (0·00)	0·53	0·25
OVCONF				
35·5	0·29 (0·09)	0·00 (0·00)	9·87	1·20
41·5	0·10 (0·09)	0·21 (0·07)	3·17	1·00
47·0	0·29 (0·12)	0·06 (0·07)	5·17	0·19
MLCF				
35·5	0·16 (0·08)	0·05 (0·05)	0·18	0·15
41·5	0·16 (0·10)	0·01 (0·05)	2·03	0·87
47·0	0·26 (0·09)	0·05 (0·05)	0·69	0·42
LEAN				
35·5	0·35 (0·10)	0·07 (0·05)	0·94	0·81
41·5	0·28 (0·10)	0·05 (0·05)	1·66	0·53
47·0	0·37 (0·08)	0·00 (0·00)	1·15	0·34
BONE				
35·5	0·25 (0·09)	0·06 (0·06)	6·64	0·17
41·5	0·32 (0·10)	0·05 (0·05)	0·99	0·40
47·0	0·13 (0·08)	0·18 (0·05)	7·83	1·64
LFR				
35·5	0·27 (0·10)	0·14 (0·05)	42·52	2·43
41·5	0·22 (0·08)	0·09 (0·04)	5·28	0·61
47·0	0·33 (0·11)	0·02 (0·05)	50·21	0·28

† Trait abbreviations are defined in Table 1.
‡ Standard errors of less than 0·005 are shown as 0·00.
Δ_1, Twice the difference in log likelihoods when within-group phenotypic variances were fixed at across group estimates.
Δ_2, Twice the difference in log likelihoods when within group variances were fixed relative to the across group estimates of h^2 and c^2 and the within group phenotypic variance.
All Δ_1 and Δ_2 values greater than 7·82 indicate heterogeneity was present ($P < 0·05$).

decreased with increasing slaughter weight. This was not the case for the 15-point conformation scores, where mean score increased with increasing slaughter weight, whilst the within-group variances decreased.

Within-slaughter-group estimates of h^2 and c^2 (hypothesis (ii)) did not differ from the across group estimates ($P > 0·05$) for any traits (some not presented). This in part reflects the imprecision of the within-group estimates of parameters (large standard errors). For the 15-point conformation scores, the estimates of h^2 were smaller whilst those for c^2 were larger in the 41·5 kg than in the 35·5 and 47·0 kg slaughter group. The 15-point scores were collected in only 2 years and partitioning variation

Table 4 *Estimates of between slaughter group genetic correlations (s.e.)*

Traits† / groups	35·5, 41·5	35·5, 47·0	41·5, 47·0
MLCC	1·00 (0·00)‡	0·93 (0·15)	0·96 (0·17)
OVCONF	1·00 (0·00)	1·00 (0·06)	1·00 (0·00)
MLCF	1·00 (0·00)	1·00 (0·00)	0·97 (0·24)
LEAN	0·79 (0·16)	0·97 (0·07)	0·77 (0·15)
BONE	1·00 (0·00)	1·00 (0·00)	1·00 (0·00)
LFR	0·83 (0·24)	1·00 (0·00)	0·74 (0·21)

† Trait abbreviations are defined in Table 1.
‡ Standard errors of less than 0·005 are shown as 0·00.

into genetic and common environmental components was therefore less accurate than for other traits.

Genetic correlations between measures of a trait collected at different target slaughter weights are shown in Table 4. For all traits (some not shown), the genetic correlation did not significantly differ from one (hypothesis (iii)). In conclusion, these results, in combination with those from the tests of heterogeneity of within-group parameter estimates, indicate that separate within-slaughter group analysis was not required for the range of target slaughter weights considered in this study.

Within-group phenotypic variances did appear heterogeneous even after correction for fixed effects (Table 2) and were found to be significantly different from across-group variance for some traits (Table 3).

Table 5 *Univariate estimates of* h^2 *and* c^2 *(s.e.) for data unscaled and scaled for differences in within group phenotypic variance*

Traits†	h^2	c^2	h^2_s	c^2_s
MLCC	0·24 (0·04)	0·04 (0·02)	0·23 (0·04)	0·03 (0·02)
LGCONF	0·27 (0·07)	0·08 (0·03)	0·27 (0·07)	0·08 (0·03)
LNCONF	0·19 (0·05)	0·11 (0·03)	0·18 (0·05)	0·12 (0·02)
SHCONF	0·15 (0·05)	0·11 (0·03)	0·15 (0·04)	0·12 (0·02)
OVCONF	0·20 (0·05)	0·05 (0·02)	0·20 (0·05)	0·05 (0·02)
MLCF	0·20 (0·06)	0·09 (0·03)	0·20 (0·05)	0·10 (0·03)
ESTF	0·16 (0·06)	0·11 (0·03)	0·16 (0·05)	0·11 (0·03)
KKCF	0·13 (0·04)	0·03 (0·02)	0·13 (0·04)	0·03 (0·02)
LEAN	0·33 (0·06)	0·01 (0·02)	0·33 (0·05)	0·02 (0·02)
SFAT	0·29 (0·05)	0·03 (0·02)	0·29 (0·04)	0·03 (0·02)
IFAT	0·12 (0·04)	0·04 (0·02)	0·12 (0·04)	0·04 (0·02)
FAT	0·29 (0·06)	0·04 (0·02)	0·29 (0·06)	0·04 (0·02)
BONE	0·24 (0·05)	0·09 (0·02)	0·24 (0·05)	0·09 (0·02)
LFR	0·26 (0·06)	0·04 (0·02)	0·27 (0·06)	0·04 (0·02)
LBR	0·30 (0·05)	0·05 (0·02)	0·30 (0·06)	0·05 (0·03)

† Trait abbreviations are defined in Table 1; h^2_s, c^2_s, parameter estimates for data scaled by the ratio of within to across group phenotypic variance.

However the phenotypic scaling used in this study had little effect on estimates of h^2 and c^2 from analysis of the combined data (Table 5).

Estimation of (co)variance components

Univariate estimation. Univariate estimates of h^2 and c^2 for combined unscaled data, are given for each trait in Table 5. In general h^2 estimates were higher for shoulder tissue measures (around 0·3) than for carcass visual scores (around 0·2).

Common environmental effects accounted for a moderate proportion of phenotypic variance (around 0·1) in most carcass visual scores. They defined more variation for those scores with more (15-point conformation scores and estimated subcutaneous fat (ESTF)) rather than fewer (MLC carcass conformation (MLCC), MLC subcutaneous fat (MLCF) and KKCF) categories. Common environmental effects were generally not significant for shoulder tissue proportions ($P > 0·05$), except for those associated with bone.

Bivariate estimation. The bivariate estimates of genetic and phenotypic correlations between all traits are shown in Table 6. Although not shown, estimates of genetic correlations between traits for the scaled data were of the same size (coefficients differed by less than 0·01). The heritabilities reported are based on the simple mean of the additive and phenotypic variance from the 14 bivariate analyses for each trait. Genetic correlations between visual conformation scores and between the fat scores were close to 1 ($P < 0·05$). As expected, lean and fat proportion were strongly negatively correlated (genetic correlation coefficients greater than –0·75). The correlation between bone and both lean and fat were smaller.

The five visual scores of conformation all had a positive genetic correlation with visual fat score (MLCF) although for two (leg and shoulder conformation) the coefficient did not differ significantly from zero. With the exception of the positive genetic correlation between overall conformation and intermuscular fat, the estimates of genetic correlations between visual conformation scores with shoulder tissue proportions did not significantly differ from zero. Conversely, the genetic correlations between fat scores and tissue composition traits were in general high and in the expected direction — positive with fat and negative with lean.

For most traits phenotypic correlations were smaller than genetic correlations, although consistent in direction. Phenotypic correlations between visual fat scores and all conformation scores were positive (greater than 0·32). The phenotypic correlations of all

conformation scores with lean composition were negative (less than –0·12), whilst those with fat were positive (less than 0·21), although small. Phenotypic correlations between fat scores and both lean and fat were consistent in direction with those between conformation and both lean and fat but the coefficients were twice as large.

Discussion

Heterogeneity of variance

In this study, visual and objective measurements of carcass quality were recorded on Suffolk-cross lambs at slaughter at 35·5, 41·5 and 47·0 kg live weight. These weights were chosen so that the data reflected the range of carcass weights typical in commercial lamb production in the United Kingdom. A central aspect of the present investigation was to determine whether records collected at each of these endpoints could justifiably be combined and analysed together for each trait measured. If so, it implies that heritable variation in performance was consistent over the range of carcass weights found in industry. This would simplify the use of crossbred information in selection programmes designed to improve carcass quality.

Tests of heterogeneity indicated that there was no significant variation between estimates of h^2 and c^2 within slaughter groups. Records collected at the different slaughter weights also acted as repeated measures of a single trait. That is, genetic correlations between measures recorded at each slaughter point did not significantly differ from one. Excluding the 15-point conformation scores, lean to fat ratio, and bone proportion, there was no heterogeneity in phenotypic variance detected between slaughter groups for the traits measured. Scaling for any phenotypic heterogeneity that was present did not affect parameter estimates. Together, these tests indicate that heterogeneity in variance, even if present, was sufficiently small not to bias parameter estimates.

Parameter estimates

The amount of improvement in carcass composition achieved by selection on visual scores depends on the magnitude of genetic correlations that exist between them and the tissue composition measures. Of the visual scores considered, only the subcutaneous fat scores (MLCF, ESTF) provided a consistent indication of carcass composition. The genetic correlations between these scores and shoulder tissue composition were high (0·57 and larger) and in the expected direction — negative with lean content and positive with fat content. The more detailed ESTF estimate of subcutaneous fatness offered little additional information about carcass

Table 6 *Estimates of genetic and phenotypic correlations (× 100) between traits*†‡

	MLCC	LGCONF	LNCONF	SHCONF	OVCONF	MLCF	ESTF	KKCF	LEAN	SFAT	IFAT	FAT	BONE	LFR	LBR
MLCC	**23**	89	87	88	89	32	35	25	–6	11	7	15	–17	–12	11
LGCONF	100(1)	**27**	94	94	96	43	43	30	–9	16	13	18	–27	**–17**	18
LNCONF	100§	97§	**19**	96	97	49	49	32	–12	19	14	21	–29	–21	18
SHCONF	100§	99§	99§	**15**	98	47	46	30	**–10**	17	14	19	–28	–16	19
OVCONF	100§	99§	99§	100§	**20**	46	46	30	–10	17	14	19	–29	–20	19
MLCF	37 (13)	25 (16)	42 (15)	29 (18)	34 (15)	**20**	91	54	–36	47	21	45	–41	–42	13
ESTF	19 (18)	8 (22)	26 (20)	**10** (24)	16 (21)	100§	**16**	59	–33	47	20	43	–41	–40	15
KKCF	45 (15)	33 (18)	43 (19)	38 (12)	38 (11)	73 (11)	85 (9)	**13**	–24	34	17	32	–32	–29	15
LEAN	1 (13)	2 (14)	1 (17)	2 (18)	0 (17)	–57 (7)	–60 (12)	–44 (18)	**33**	–76	–67	–93	26	11	45
SFAT	**–4** (15)	**–11** (15)	–3 (17)	–7 (18)	–6 (16)	76 (6)	78 (10)	66 (15)	–86 (4)	**29**	19	81	45	–77	–11
IFAT	15 (18)	19 (19)	18 (22)	25 (22)	27 (8)	33 (17)	15 (25)	–28 (27)	–75 (7)	49 (13)	**13**	73	–46	–71	–4
FAT	2 (15)	–1 (17)	6 (18)	5 (18)	6 (17)	75 (7)	70§	45 (16)	–94 (2)	93 (2)	78 (7)	**29**	–59	–96	–10
BONE	–13 (14)	–9 (17)	–27 (17)	**–27** (18)	–25 (17)	–67 (10)	–52 (7)	–25 (20)	13 (13)	–49 (11)	–28 (17)	–46 (11)	**24**	49	–74
LFR	1 (15)	4 (18)	–3 (18)	1 (29)	–2 (18)	–76 (7)	–73 (10)	–43 (15)	98 (1)	–93 (3)	–75 (8)	–99§	31 (13)	**26**	19
LBR	17 (15)	11 (17)	24 (18)	25 (19)	22 (17)	24 (14)	–9 (20)	–19 (21)	59 (10)	–19 (14)	–32 (16)	–28 (12)	–73 (7)	42 (12)	**30**

† Trait abbreviations are defined in Table 1.

‡ Heritabilities (mean heritability estimate from all bivariate analyses) in bold and underlined along the diagonal, phenotypic correlations above the diagonal, and genetic correlations below the diagonal. Standard errors for genetic correlations are shown in brackets. Standard errors for phenotypic correlations are less than 0·03.

§ Problems encountered with convergence.

fatness than the standard MLC fat score, since the estimated genetic correlation between MLCF and ESTF was 1·0.

Estimates of phenotypic correlations between visual conformation scores and lean content were negative while those for fat content were positive. This is consistent with reports from other studies (Wolf *et al.*, 1981; Simm and Murphy, 1996). As a result most people have concluded that conformation score is of relatively little value other than identifying generally fatter carcasses. Kempster *et al.* (1981) found that when conformation scores were corrected for dissected subcutaneous fat proportion, an increase in conformation corresponded with an increase in the proportion of carcass lean. However when the correction was based on a five-point MLC fat score, adding conformation score did not improve the prediction of carcass lean content. Since only the MLC fat score and not carcass fat content is evaluated at abattoirs, there is no obvious method to commercially assess conformation independently of fatness.

The genetic correlations between visual conformation scores and tissue composition were not significantly different from zero. These estimates are in contrast with those of Wolf *et al.* (1981) who reported high negative correlations between conformation and both lean and bone proportion and high positive correlations with fat proportion. The reasons why correlation estimates differ between both studies is unclear, however Wolf *et al.* (1981) estimated a genetic correlation of unity between conformation and fat scores which indicates complete confounding between both visual scores.

Despite the considerable volume of research which has indicated that there is little to no value of conformation as a predictor of carcass lean proportion (Kirton and Pickering, 1967; Jackson and Mansour, 1974; Kempster *et al.*, 1981; Simm and Murphy, 1996), current commercial classification schemes place a premium on carcasses of higher conformation as well as reduced fat content. Kempster *et al.* (1981) suggested that, regardless of its value in predicting lean content, if conformation is a factor in commercial classification schemes it should also be included to some extent as a selection objective in breeding schemes. The low genetic correlations between conformation scores and tissue proportions reported here suggest that a selection programme could be designed to improve composition in crossbred lambs while simultaneously increasing conformation score.

The potential benefits of incorporating crossbred information in purebred evaluations depends on how easily information can be collected from the crossbreds and on the genetic correlations between traits measured on purebred and crossbred individuals. Visual scores enhance the ease with which crossbred information can be collected. To be of value, genetic correlations between the purebred and crossbred performance must be sufficiently low to justify any added cost of recording. Van der Werf, *et al.* (1994) suggest that the use of crossbred information would improve responses if genetic correlations between purebred and crossbred performance are less than 0·75. The estimation of genetic correlations between purebred and crossbred measured carcass traits in sheep will be the focus of a subsequent study.

Implications

Visual scores offer a routine and rapid evaluation of carcass composition in crossbred lambs. From the findings of this study MLC visual fat score provides useful information about carcass composition, but conformation score is less useful. Selection to reduce progeny MLC fat score, by its incorporation as a criterion in a selection index for purebreds, would cause a reduction in conformation score. However given the relatively low genetic correlation between these traits, if deemed important a restriction on any change in conformation would be possible while reducing carcass fatness.

The true value of incorporating MLC fat scores into purebred selection indices depends on the genetic correlations that exist between traits measured on the purebred and on their crossbred progeny. To be useful, correlated responses in composition to selection on MLC fat score must be higher than can be achieved through selection on traits measured on the purebred parent. Further study is required before the value of combined purebred and crossbred selection in sheep can be confirmed.

Acknowledgements

The financial support of Ministry of Agriculture, Fisheries and Food, the Meat and Livestock Commission and the Suffolk Sheep Society for this research is gratefully acknowledged. We thank Biggar Quality Meats, Biggar, for their assistance. We are also grateful to SAC colleagues Sue Murphy, Jack FitzSimons, Jim Fraser and Hazel Brown for their input to this trial and to Sue Brotherstone and Bill Hill (University of Edinburgh) for their comments on the text. SAC receives financial support from the Scottish Office Agriculture, Environment and Fisheries Department.

References

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.

Boldman, K. G., Kriese, L. A., Van Fleck, L. D., Van Tassell, C. P. and Kachman, S. D. 1995. *A manual for use of MTDFREML.* US Department of Agriculture, Agricultural Research Center, Clay Center, Nebraska.

Cameron, N. D. 1992. Correlated responses in slaughter and carcass traits of crossbred progeny to selection for carcass lean content in sheep. *Animal Production* **54:** 379-388.

Cook, G. L., Jones, D. E. and Kempster, A. J. 1983. A note on a simple criterion for choosing among sample joints for use in double sampling. *Animal Production* **36:** 493-495.

Groeneveld, E. 1996. *REML VCE a multivariate model restricted maximum likelihood (co)variance component estimation package version 3.2 user's guide.* Federal Research Centre of Agriculture, Mariensee, Germany.

Guy, D. R. and Croston, D. 1994. UK experience and progress with sheep sire referencing schemes. *Proceedings of the fifth world congress on genetics applied to livestock production, Guelph, vol. 18,* pp. 55-58.

Harrington, G. and Kempster, A. J. 1989. Improving lamb carcass composition to meet modern consumer demand. In *Reproduction, growth and nutrition in sheep* (ed. O. R. Dyrmundsson and S. Thorgeirrsson), pp. 79-90. Agricultural Research Institute and Agricultural Society, Iceland.

Jackson, T. H. and Mansour, Y. A. 1974. Differences between groups of lamb carcasses chosen for good and poor conformation. *Animal Production* **19:** 93-105.

Kempster, A. J., Cook, G. L. and Grantley-Smith, M. 1986. National estimates of the body composition of British cattle, sheep and pigs with special reference to trends in fatness. A review. *Meat Science* **17:** 107-138.

Kempster, A. J., Croston, D. and Jones, D. W. 1981. Value of conformation as an indicator of sheep carcass composition within and between breeds. *Animal Production* **33:** 39-49.

Kirton, A. H. and Pickering, F. S. 1967. Factors associated with differences in carcass conformation in lamb. *New Zealand Journal of Agricultural Research* **10:** 183-200.

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.

Mood, A. M., Graybill, F. A. and Boes, D. C. 1973. *Introduction to the theory of statistics.* McGraw-Hill, New York.

Patterson, H. D. and Thompson, R. 1971. Recovery of inter-block information when block sizes are unequal. *Biometrica* **58:** 545-554.

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 *Recent advances in sheep and goat research* (ed. A. W. Speedy), pp. 193-215. CAB International.

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

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.

Thompson, R., Crump, R. E., Juga, J. and Visscher, P. M. 1995. Estimating variances and covariances for bivariate animal models using scaling and transformation. *Genetics, Selection, Evolution* **27:** 33-42.

Visscher, P. M., Thompson, R. and Hill, W. G. 1991. Estimation of genetic and environmental variances for fat yield in individual herds and an investigation into heterogeneity of variance between herds. *Livestock Production Science* **28:** 273-290.

Wei, M. and Werf, J. H. J. van der. 1994. Maximizing genetic response in crossbreds using both purebred and crossbred information. *Animal Production* **59:** 401-413.

Werf, J. H. J. van der, Wei, M. and Brascamp, E. W. 1994. Combined crossbred and purebred selection to maximize genetic response in crossbreds. *Proceedings of the fifth world congress on genetics applied to livestock production, Guelph, vol. 18,* pp. 266-269.

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.

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.

(*Received* 6 *April* 1999—*Accepted* 8 *July* 1999)