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Genetic relationships among objectively and subjectively assessed traits measured on crossbred (Mule) lambs

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Abstract

Sheep farming in the UK is characterized by a crossbreeding system where 'Longwool' sire breeds are mated with hill dam breeds, with the crossbred (F_1) ewe lambs retained for mating to terminal sires. The F_1 wether and terminal-sire cross lambs are marketed for meat. At selection, F_1 females are typically assessed visually for type traits relevant to dam lines, and these traits could be considered as goal traits. Their offspring and their male sibs derive their value from carcass traits. This study investigated the genetic relationships between type (subjective) and carcass (objective) traits in F_1 lambs, and their potential impact on genetic improvement within this production system. Bluefaced Leicester rams were crossed with Scottish Blackface and Hardy Speckled Face ewes to produce F_1 ('Mule') lambs. The wether lambs (no. = 2197) were selected for slaughter at a target condition (a carcass fat score of 2/3L) and a number of live and carcass traits were measured. Carcass dissection data were collected on approximately one-third of these wether lambs. The ewe lambs (no. = 2423) were measured for similar live traits but at a fixed age (195 ± 5·5 days). In addition, they were subjectively assessed for a number of functional and type traits. Genetic parameters among these traits were then estimated. Heritabilities for the ewe traits were generally moderate (0·18 to 0·31) and genetic correlations between the traits were variable, with some moderate to high correlations (favourable in direction) of growth/carcass traits with overall type traits. Live weight at slaughter in wethers was highly correlated to live weight at constant age in ewes (r = 0·72). In the wethers, live, cold carcass and lean weight had moderately high heritabilities (between 0·26 and 0·46), and were positively correlated with slaughter age (≥ 0·79). However, age at slaughter in wethers was highly negatively correlated with growth/carcass and overall type traits in ewes (between − 0·45 and − 0·97), perhaps reflecting differences in maturity in lambs measured at a target fatness versus age. The correlations of most other type traits in ewes with wether traits were non-significant. These results show that the subjectively assessed type traits (at least as measured in this study) will not deteriorate, and some will in fact be improved, in a selection programme aiming to improve carcass merit.

Keywords: *carcass composition, crossbreeding, lambs, type score.*

Introduction

Crossbreeding systems generally aim to utilize heterosis, and are often designed to make best use of the different attributes of sire and dam lines. If these differences are complementary, overall efficiency can be improved (Smith, 1964). For a dam line, maternal traits such as number of offspring born, maternal care and offspring survivability are of particular importance, whereas for a sire line the emphasis lies on growth and carcass quality. Although selection in dam lines is primarily focussed on maternal traits, dams also contribute to the genetic merit for meat production in their progeny. Hence, there may be advantage in improving (or at least avoiding deterioration in) growth and carcass traits alongside maternal traits in dam lines. The opportunity to do so within a selection program depends on the genetic associations of maternal traits with growth and carcass traits.

In the UK sheep industry, lamb production is predominantly based on a three-way cross, where the dam line used in the lowland sector for the terminal cross is the result of a cross between males of 'Longwool' or crossing sire breeds and females of hill breeds. The hill breeds contribute hardiness to the cross and are available in large numbers, with the specific breed used largely determined by region (e.g. Scottish Blackface in Scotland, Swaledale in Northern

England and Hardy Speckled Face in Wales). The crossing sire breeds contribute milkiness, size and good maternal ability to the cross; most popular are the Bluefaced and Border Leicester. The F_1 females of sufficient size, type and soundness are used as breeding stock. The F_1 males are effectively a by-product of the crossbreeding system but, because they are sent for slaughter, any improvement in their carcass quality will have a direct impact on the profitability of the system. For the F_1 females, breed type and soundness are of overriding importance at point of sale. However, since these females are mated to terminal sires to produce market lambs, any improvement in carcass characteristics would (through their offspring) also improve overall profitability.

Historically, selection within sheep breeds was primarily based on visual assessments, including traits such as breed type, soundness, wool quality and size. With the advance of technology, a number of objective measurements have been added to the list, varying from weight, ultrasonic fat and muscle depth for meat animals, to fibre diameter for wool sheep. Although objective measurements have large advantages over subjective assessments (e.g. more robust statistical properties like continuity of scale, and less dependency on the acumen of assessors), there are drawbacks as well. Breeders may feel that their breeding goal is not fully described by the available objective measurements. Lack of subjectively assessed traits can also have direct financial impact. For example, the value of lamb carcasses can partly depend on a subjective conformation score, and the value of fleeces can partly depend on the subjective assessment of a wool grader. Sometimes the financial implications are less tangible; the colour of a sheep's face is not known to affect its carcass quality but, in the case of Mule (Bluefaced Leicester × Hill) sheep, it does affect its market value when sold as replacement breeding female.

Research on subjectively assessed traits in sheep has been fairly limited to date. Australian work suggests that subjectively assessed (wool) traits have moderate to high heritabilities but, given their generally small genetic correlations with objectively measured wool traits, should not be used exclusively (Lewer *et al.*, 1995; Brown *et al.*, 2002). Snyman and Olivier (2002) concluded that most subjectively assessed (conformation) traits would not be negatively influenced when selection is based on the economically important (objectively measured) production traits. The purpose of this study was to evaluate genetic correlations between objectively measured growth and carcass composition traits, and subjectively assessed carcass quality and mouth and breed type scores. The aim was to examine whether selection to improve objectively measured growth and carcass traits would adversely affect subjectively assessed type traits deemed important in prospective (crossbred) breeding animals, and vice versa.

Material and methods

Sheep resource

Crossbred 'Mule' (Bluefaced Leicester × hill breed) lambs were produced over a 3-year period (1998–2000) at three experimental farms near Aberystwyth in Wales. A total of 1500 hill ewes (approx. equal proportions of Scottish Blackface and Hardy Speckled Face) were inseminated each year with fresh semen from 15 Bluefaced Leicester ram lambs per year (45 in total). Ewes were allocated to single-sire mating groups balanced by numbers of ewes at each farm and their breed, age and condition score. The ewes were mated by artificial insemination over a 10-day period. The Hardy Speckled Face (HSF) ewes were all sourced locally, whereas the Scottish Blackface (SBF) ewes were sourced from the north of England and south central Scotland. No pedigree information was available on the hill ewes.

The Bluefaced Leicester (BFL) rams were selected from approximately 800 ram lambs born each year between 1997 and 1999 in the 13 pedigree and performance recording flocks of the Penglas Bluefaced Leicester Group Breeding Scheme (Van Heelsum *et al.*, 2001). These flocks were genetically linked by common use of reference sires. The crossing rams were selected by applying an elliptical design (Cameron and Thompson, 1986) with regard to their (unscaled) 'lean' index score and their residual (live) conformation score (after correction for fixed effects). The lean index included live weight and ultrasound fat and muscle depth, and was designed to increase lean body mass while restricting increases in fat. The elliptical design was implemented in order to ensure that the range of performance levels for the traits were represented in the BFL rams sampled i.e. that the extremes of the bi-variate distributions of the two criteria considered were fully sampled. This sampling approach helped ensure that differences among individual BFL animals could be detected within the group chosen i.e. increased the power of the design. The selection of crossing rams is described in more detail elsewhere (Van Heelsum *et al.*, 2003).

A total of 5537 Mule lambs were born, of which close to 90% were reared up to at least 10 weeks of age. From 10 weeks of age, body condition was subjectively assessed at 2-weekly intervals until 'finished' condition was reached. The male lambs, which were castrated at birth, were then slaughtered. The age at which lambs achieved finished condition varied between 74 and 300 (average 188) days. Finished condition was defined as being borderline between carcass fat classes 2 and 3L, based on the Meat and Livestock Commission (MLC) scale for visual assessment of fat cover from 1 (low fat), through 2, 3L, 3H, 4L, 4H to 5 (very fat).

Measurements on wether lambs

Table 1 summarizes the traits measured on the 2197 crossbred wether lambs. Once reaching finished condition, the wether lambs were weighed (Finwt) and their conformation was subjectively assessed at the shoulder, loin and gigot and scored on a scale from 1 (poor) to 6 (excellent). The average of the three scores was used for statistical analysis (Finconf). The wethers were also ultrasound scanned to determine fat and muscle depth. Ultrasonic muscle depth (Finumd) was measured at the deepest point of the eye-muscle (*m. longissimus lumborum*), at the third

Table 1 *Description of traits measured on Mule wethers at reaching 'finished' condition (live and on carcass), including number of valid records (N) and indication of subjectivity of assessment*

Abbreviation	N	Subj[†]	Description
Finwt	2197		Live weight at reaching 'finished' condition (kg)
Finumd	2197		Ultrasonic muscle depth at third lumbar position (mm)
Finufd	2197		Ultrasonic fat depth at third lumbar position (average of three measurements) (mm)
Finconf	2197	*	Average of shoulder, loin and gigot conformation scores in live animals (scale 1 to 6)
Slage	2193		Age at slaughter (days)
Emptylwt	2100		'Empty' live weight before slaughter (kg)
C15all	2193	*	Overall carcass conformation on 15-point scale
Subfat	2193	*	Estimated subcutaneous fat percentage (visually assessed)
Coldcw	2134		Cold carcass weight (kg)
Killout	2040		Killing-out percentage (Coldcw as part of Emptylwt)
Leancw	788[‡]		Weight (g) of lean in the carcass

[†] Subjectively assessed traits are indicated with asterisk; all other traits were measured objectively.
[‡] On 158 of these carcasses, the weight (g) of lean was measured on the full side, whereas on the remainder only lean in the shoulder joint was measured, which was then used to predict weight of lean in the full carcass.

lumbar vertebra. Ultrasonic fat depth was measured at the same position and 1 and 2 cm lateral to the first position. For statistical analysis, the average of the three fat measurements was used (Finufd).

Food was withheld overnight from lambs that went for slaughter to determine 'empty', live weight (Emptylwt). Age at slaughter (Slage) was recorded and included in the analysis as a dependent variable because of the economic importance of this trait. In the abattoir, carcasses were weighed and given an MLC fat score (described above) and a conformation score. Conformation was visually assessed on a 15-point scale (where 15 was best). Shoulder, loin, gigot and overall conformation were assessed separately, but only the overall score (C15_all) was used for statistical analysis. In addition to the MLC fat score, fatness was also assessed on a more continuous visual scale as percentage of subcutaneous fat (Subfat), which was used for statistical analysis. The same person carried out all abattoir assessments. After chilling overnight, cold carcass weights were recorded (Coldcw).

A sample of 794 carcasses underwent dissection. Of these, 158 (20%) had a full side dissected and the remaining 635 carcasses had only a shoulder joint dissected (part-dissection). Fully dissected carcass sides were separated into eight joints (leg, chump, loin, breast, best end neck, middle neck, shoulder and scrag), as described by Cuthbertson *et al.* (1972). All joints were dissected into lean, fat, bone and waste. For fully dissected carcasses, the total amount of lean was then calculated as the sum of lean in each joint. For part-dissected carcasses, the total amount of lean in the carcass was predicted using a regression equation with three variables (weight of lean in the shoulder, total weight of the joint, and total weight of the side), as recommended by Fisher (1990). The regression coefficients were obtained using the data on fully dissected carcasses. Predicted values for part-dissected carcasses were then scaled to the same mean and standard deviation as the observed values on fully dissected carcasses.

Measurements on ewe lambs

Each year around mid October, all ewe lambs (regardless of having reached finished condition) were assessed for a number of growth and type traits. Performance data were available on 2423 crossbred ewe lambs, ranging in age between 180 and 208 days (average 195 days). Four groups of traits were measured on the ewe lambs, as summarized in Table 2: (i) growth/carcass traits; (ii) mouth scores; (iii) face colour/hair; and (iv) overall type traits. The first category included live weight (Octwt), ultrasonic muscle and fat depth (Octumd and Octufd, where the latter is the mean of the three ultrasonic fat depth measurements), and subjective conformation score (Octconf, average of the shoulder, loin and gigot score). A single (very experienced) assessor scored all traits in the second and third category. The second category included: jaw position [Jawpos; position of the lower jaw in relation to the upper jaw and skull, scored from -5 (undershot) to $+5$ (overshot)], tooth angle [Toothang; angle of incisor teeth in relation to the lower jaw scored from -3 (45° backward) to $+3$ (45° forward)], and tooth length [Toothlen; scored from -2 (very short) to 2 (very long)]. Category (iii) comprised four traits: face colour [Facecol; reflecting the amount of pigmentation on a scale of 0 (no pigmentation $\equiv$ white) to 6 (black face colour)], face colour distinction between black and white colour areas [Coldist; scored from 1 (very blotchy) to 5 (very distinct)], and face hair [Facehair; the amount of covering with short hairs scored from 0 (bald) to 5 (face fully covered)]. Three highly experienced industry representatives assessed the three traits in category (iv), which were considered as of particular importance to female Mule breeding stock. These were style or breed type (Style), fleece quality and uniformity throughout the body (Wool) and structural soundness, in which included correctness of fore and hind limbs, angle of pasterns, and straightness of legs (Struct). These three traits were scored on a scale from 1 (poor) to 10 (ideal).

Statistical models

A number of fixed effects were considered for inclusion in the model by analysing each trait with a full fixed effects model plus a random animal effect (linked to pedigree) using ASREML (Gilmour *et al.*, 1998). Fixed effects for which the F ratio (adjusted for all other terms in the model) was deemed non-significant ($P > 0{\cdot}05$) were subsequently dropped from the model, although for consistency some non-significant terms were kept if important to other related traits.

The full model tested for both ewes and wethers included the fixed effects of farm-year (9 levels; 3 farms and 3 years (1998, 1999 or 2000)), dam breed (SBF or HSF), birth-rearing type (4 classes), fostered or reared normally (artificially reared lambs were discarded), and age of the (rearing) dam (4 classes: 1 or 2, 3, 4 to 6 or more than 6 years old). The four birth-rearing type classes were: (1) born and reared as single; (2) born as multiple, reared as single; (3) born as

Table 2 *Description of traits measured on Mule ewe lambs at assessment days in October, including number of valid records (N) and indication of subjectivity of assessment*

Abbreviation	N	Subj[§]	Description
Growth/carcass traits			
Octwt	2423		Live weight at assessment in October (kg)
Octumd	2422		Ultrasonic muscle depth at third lumbar position (mm)
Octufd	2422		Ultrasonic fat depth at third lumbar position (average of three measurements) (mm)
Octconf[†]	2422	*	Average of shoulder, loin and gigot conformation scores in live animals (scale 1 to 6)
Mouth scores			
Jawpos[†]	2422	*	Jaw position – scale −5 (lower jaw 5 mm back from upper jaw) to 5 (lower jaw 5 mm in front of upper jaw)
Toothang[†]	2422	*	Tooth angle – scale −3 (45° forward) to 3 (45° back); ideal position is at right angle with lower jaw
Toothlen[†]	2422	*	Tooth length – scale −2 (very short) to 2 (very long)
Face colour/hair scores			
Facecol[†]	2422	*	Face colour – scale 0 (no pigmentation) to 6 (black head colour)
Coldist[†]	2422	*	Face colour distinction – scale 1 (very blotchy) to 5 (very distinct)
Facehair[†]	2422	*	Degree of covering of short hair in face – scale 0 (bare skin) to 5 (80–100% hair); 3 is considered ideal
Overall type traits			
Style[‡]	2415	*	Style or breed type – scale 1 (poor) to 10 (ideal); includes alertness, prowess, shape and position of head and ears, and length of neck and body.
Wool[‡]	2416	*	Fleece quality and uniformity throughout the body – scale 1 (poor) to 10 (ideal)
Struct[‡]	2414	*	Structural soundness – scale 1 (poor) to 10 (ideal); indicates correctness of limbs (angle of pasterns, straightness of legs)

[†] Traits assessed by one experienced assessor.
[‡] Traits assessed by a team of three highly experienced industry representatives.
[§] Subjectively assessed traits are indicated with an asterisk; all other traits are measured objectively.

single or twin, reared as twin; (4) born as triplet or more, reared as twin. All triplet litters were split up at birth through cross fostering, such that no ewe reared more than two lambs.

The wethers were slaughtered over a wide age range but at approximately the same degree of fatness ('finish'); the average subcutaneous fat percentage was 11·1 ± 1·7%. To account for slight differences in fat cover, the full model included subcutaneous fat percentage as a covariate for all wether traits, nested within farm-year level. By fitting subcutaneous fat percentage, most (genetic) variation in Finufd was removed, and therefore Finufd was excluded from further analysis.

In contrast to wethers, ewe lambs were all measured at near-equal age, because with use of AI, lambs were born over a relatively short time period (average age at assessment was 195·7 ± 5·5 days). Therefore a covariate to correct for any age difference (also nested within farm-year) was included in the full model for ewe lamb traits. Several operators took part in the ultrasound scanning of ewe lambs across the three farms; hence an operator effect was included for Octumd and Octufd. In the case of Finumd and Finufd (measured on wether lambs) the operator effect was completely confounded with farm and was therefore not fitted explicitly.

Because they were not significant ($P > 0·05$), foster and dam age effects were dropped for all wether and ewe traits, except for Octwt, Octumd, Octufd and Octconf. Foster effect was also included for Slage and Finufd. The age effect was dropped for six of the ewe traits: Jawpos, Toothang, Toothlen, Facecol, Coldist and Facehair.

The importance of three random effects (besides the residual) was considered in forming the final mixed-model fitted. The simplest model included (besides a residual term) an 'animal' (additive genetic) effect, which was linked to the pedigree. In the second model, a maternal environmental effect of rearing dam was added. The third model included an animal and residual effect plus a maternal environmental effect of litter (equivalent to rearing dam within year). Finally a 'full' model including animal, rearing dam, litter and residual effect was tested. A Log-likelihood ratio test was used to determine the 'best' fit ($P < 0·05$) random effect model for each response variable considered. For Octwt, Octumd, Octufd, Octconf, Style, Wool and Struct, a litter effect was included in addition to the animal effect, and for Finwt, Finufd, Slage, Emptylwt and Coldcw, the rearing dam effect was included. For all other traits, the model included the animal effect and residual as random effects only.

Given the structure of these data (no records on pure lines or reciprocal crosses), any heterotic effects could not be estimated. Unfortunately no pedigree data were available on the hill ewe dams. Lack of pedigree makes it impossible to partition genetic variance into an additive and non-additive component. Therefore the heritability, which was computed as the animal variance component divided by the total variance, was based mainly on between-sire differences. Because all animals with performance records were crossbred, the heritability is referred to as 'crossbred' heritability.

Multivariate analyses
The program ASREML (Gilmour *et al.*, 1998) was used to analyse all possible pairs of ewe traits with a bivariate

model (78 combinations). Random and fixed effects fitted were as described above. The same was done for all combinations of wether traits (45 combinations). Subsequently, all combinations of a wether and a ewe trait were analysed bivariately (130 combinations). For all combinations, ASREML was used to estimate genetic and phenotypic correlations with corresponding standard errors. Correlations were considered significant if $P < 0{\cdot}05$ using a simple *t* test. Values for which P was between 0·05 and 0·10 are also reported but indicated as such. Correlations for which $P > 0{\cdot}10$ are not reported.

Results

In all tables showing genetic parameters, estimates for which P was between 0·05 and 0·10 are shown in italic font, whereas estimates for which $P > 0{\cdot}10$ are not shown at all. Where phenotypic correlations were deemed non-significant ($P > 0{\cdot}10$), the estimates were (very) close to zero. For the genotypic correlations this was not always the case; a small number of estimates was between 0·20 and 0·29.

Ewe traits

Table 3 shows the estimates of crossbred heritabilities of ewe traits and significant ($P < 0{\cdot}1$) genetic and phenotypic correlations.

Estimated crossbred heritabilities were generally moderate, with exceptions of a few high (0·59 for Facecol and 0·42 for Coldist) and low (0·08 for Octconf and 0·11 for Jawpos) estimates. Despite the low heritability of Octconf, estimates of genetic correlations of this trait with the other growth/carcass traits were high.

Toothang and Toothlen were highly genetically correlated ($r = 0{\cdot}59$), as were Facecol and Facehair ($r = 0{\cdot}70$), which is not unexpected given the morphology of these traits. Coldist did not appear to be genetically linked to either Facecol or Facehair. Style and Wool, and Style and Struct had high genetic (and phenotypic) correlations, and the genetic correlation between Wool and Struct was moderate. Phenotypic correlations among mouth scores and also among face colour/hair scores were generally fairly low, with the main exception being the correlation between Jawpos and Toothang (− 0·41), suggesting that the more undershot the animal was, the more the teeth leaned forward.

Phenotypic correlations of growth/carcass traits with overall type traits were moderate to high for correlations with Style and Struct, and somewhat lower for Wool. Phenotypic correlations of growth/carcass traits with mouth scores and face colour/hair traits, of mouth scores with face colour/hair traits and overall type traits, and of face colour/hair traits with overall type traits were generally close to zero, if at all significant. The few exceptions were for phenotypic correlations between Facecol, Coldist, Style and Struct.

Estimates of genetic correlations between the ewe traits were generally more variable than these of phenotypic correlations. Octwt had a moderate genetic correlation with Coldist (0·37), and a very high genetic correlation with Style (0·81) and Struct (0·86). The latter suggests that larger animals were genetically of better quality (presumably healthy, well-grown animals show more prowess and are less likely to have any deformations in the legs). This could also explain the substantial genetic correlations between Octumd and Struct (0·41) and between Octconf and Style (0·49). Genetic correlations of Octufd with Facecol (− 0·42) and Facehair (− 0·36) and of Octumd with Jawpos (0·41) were also moderately high in the desirable direction, but Facecol had no significant genetic relationship with Octwt or Octumd.

Unexpectedly, the genetic correlation between face colour/-hair scores and mouth scores was significantly different from zero in a number of cases, i.e. of Facecol with Jawpos (0·39) and of Coldist with Jawpos (0·46), Toothang (− 0·45) and Toothlen (− 0·29). This suggests that animals with (genetically) darker, more distinctly coloured faces were less undershot, and (therefore) their teeth were leaning forwards less and were shorter. There does not seem to be an obvious functional reason for these traits to be genetically

Table 3 *Phenotypic correlations (above diagonal), crossbred heritabilities (on diagonal; bold) and genetic correlations (below diagonal)*† *for Mule ewe traits*

	Growth/carcass				Mouth scores			Face colour/hair			Overall type		
	Octwt	Octumd	Octufd	Octconf	Jawpos	Toothang	Toothlen	Facecol	Coldist	Facehair	Style	Wool	Struct
Octwt	**0·23**	0·62	0·50	0·54		− 0·12	− 0·13	*0·05*	0·06		0·67	0·25	0·61
Octumd	0·43	**0·21**	0·48	0·53		− 0·10	− 0·13		*0·04*		0·43	0·15	0·41
Octufd		0·56	**0·24**	0·47		− 0·04	− 0·07		0·05	− 0·07	0·36	0·19	0·29
Octconf	0·58	0·71	0·75	**0·08**		− 0·11	− 0·12		0·06	− 0·01	0·42	0·18	0·37
Jawpos		0·41			**0·11**	− 0·41	0·12						
Toothang						**0·18**	0·24		*− 0·04*	− 0·05	− 0·11		− 0·11
Toothlen	*− 0·30*				*0·33*	0·59	**0·31**	0·06	− 0·05	0·05	− 0·06		− 0·09
Facecol			− 0·42		0·39			**0·59**	0·13	0·28	0·20		0·17
Coldist	0·37	*0·29*			0·46	− 0·45	− 0·29		**0·42**		0·14	0·06	0·15
Facehair			− 0·36					0·70		**0·24**			0·05
Style	0·81	*0·32*		0·49	0·43	− 0·35			0·34		**0·36**	0·41	0·66
Wool											0·58	**0·41**	0·32
Struct	0·86	0·41		*0·42*			*− 0·31*	*0·26*	0·53		0·86	0·36	**0·23**

† Roman font: $P < 0{\cdot}05$; italic font: $0{\cdot}05 < P < 0{\cdot}10$; a space indicates $P > 0{\cdot}10$.

correlated. Other (moderately) large genetic correlations among type traits were of Style with Jawpos (0·43), Toothang (−0·35) and Coldist (0·34), and of Struct with Coldist (0·53). Wool did not appear to be related to any of the other type traits, except to Style and Struct.

Wether traits

As opposed to the ewe lambs, which were measured at the same age, wether lambs were measured at the same level of finish but at variable age. Age at slaughter (Slage) was highly and positively correlated with live (Finwt), cold carcass (Coldcw) and lean weight (Leancw) (≥0·79) (Table 4). This implies that animals that required more days to reach finished condition were generally heavier, without being fatter (given that subcutaneous fat percentage was fitted in the model).

As anticipated, the genetic correlation between live weight at finish (Finwt) and pre-slaughter (Emptylwt) was near unity and the phenotypic correlation was 0·94. These two weights were measured only a day or so apart and thus the main difference should merely be gut fill. Therefore, results on Emptylwt are not shown. Weight measurements on the live animal and on the carcass were highly correlated to the weight of lean in the carcass. This is partly due to fitting Coldcw in the regression function to estimate the Leancw for the 80% of carcasses that were only part dissected. The prediction equation had a high R-square of 0·97. This is however lower than 1.0, so residual variation in the predicted observations would under-reflect the actual variation in measured Leancw. Therefore, predicted Leancw was standardized to have the same mean and variance as the measured Leancw, which would help address this issue.

Estimates of crossbred heritabilities for Finwt and Finumd (measured at the same estimated percentage of subcutaneous fat) were 0·26 and 0·28, respectively, which was slightly higher than for Octwt and Octumd (0·23 and 0·21, respectively, but measured at the same age). The genetic correlation between Finumd and conformation on the live animal (Finconf) was estimated as 0·33 but was non-significant, whereas the correlation between Finumd and conformation of the carcass (C15_all) was high (0·68) and significant. Finumd was also highly genetically (and to a lesser extent phenotypically) correlated with Coldcw ($r = 0·57$) and Leancw ($r = 0·58$). This suggests that at the same subcutaneous fat percentage, more muscular animals (as measured by ultrasound) did not necessarily look better conformed alive, but did look better conformed on the hook and also gave more lean weight. However, the genetic correlation between live conformation score (Finconf) and Leancw was much higher (0·49) than between carcass conformation score (C15_all) and Leancw (0·06; but $P > 0·10$). This would suggest that at least when corrected for subcutaneous fat percentage, Finconf would give a useful prediction of genetic potential for lean weight in the carcass, were it not that the heritability of Finconf is very low. Fitting the same model without the covariate for subcutaneous fat percentage (results not shown) gave a lower correlation between Finconf and Leancw of 0·35, which was however not significant ($P > 0·10$).

Correlations between ewe and wether traits

Live weight (Octwt and Finwt) and ultrasound muscle depth (Octumd and Finumd) were genetically highly correlated between ewes and wethers (0·72 and 0·67, respectively), despite being measured at different stages in life (Table 5).

Slage had strong negative correlations with the four growth/carcass traits measured on the ewes (between −0·60 and −0·97), and with Style and Wool (−0·49 and −0·45, respectively). This implies that genetically, sisters of late-finishing wethers were smaller, had less muscle and fat cover, had poorer conformation, were less stylish, and had poorer wool when assessed in October (at approximately the same age), than sisters of early-finishing males. The high positive correlations between Octwt in the ewes and Finwt in the wethers (0·72), and between Finwt and Slage in the wethers (0·79), did not result in a high positive correlation between Octwt (in ewes) and Slage (in wethers); instead the genetic correlation was large and negative (−0·64). A higher Finwt in wethers can be achieved in two ways: by growing faster in a given amount of time and/or by growing over a longer period of time before reaching finished condition (i.e. an increase of Slage). It is the first aspect that likely caused the high positive correlation between Finwt and Octwt. The second aspect likely caused the negative correlation between *Octwt and Slage*. Wethers that finish late are also later maturing (assuming fatness, or 'finish', is an indicator of maturity) and therefore their sisters are less mature at a given point in time; as a consequence, when measured in October they are smaller, have less muscle and fat, are poorer conformed, and score less for the overall type traits.

Generally the mouth and face colour/hair scores measured on the ewes were not highly correlated with slaughter traits

Table 4 *Phenotypic correlations (above diagonal), crossbred heritabilities (on diagonal; bold) and genetic correlations (below diagonal)† for Mule wether traits*

	Finwt	Finumd	Finconf	Slage	Coldcw	Killout	C15_ all	Leancw
Finwt	**0·26**	0·28	0·24	0·46	0·84	−0·25	0·13	0·80
Finumd	0·44	**0·28**	0·18	0·17	0·40	0·20	0·33	0·38
Finconf			**0·06**	−0·07	0·30	0·07	0·20	0·18
Slage	0·79			**0·18**	0·45	−0·13	0·05	0·42
Coldcw	0·94	0·57		0·81	**0·35**	0·17	0·28	0·95
Killout		0·48			*0·40*	**0·09**	0·27	0·19
C15_all		0·68				0·71	**0·16**	0·21
Leancw	0·93	0·58	0·49	0·89	0·98			**0·46**

† Roman font: $P < 0·05$; italic font: $0·05 < P < 0·10$; a space indicates $P > 0·10$.

Table 5 *Genetic correlations*† *between ewe traits (vertical) and wether traits (horizontal)*

	Finwt	Finumd	Finconf	Slage	Coldcw	Killout	C15all	Leancw
Octwt	0·72	*0·29*		−0·64	0·69	−0·56		
Octumd		0·67		−0·60				
Octufd	−0·54	*−0·31*		−0·86	−0·54		*−0·34*	−0·67
Octconf	−0·51			−0·97	−0·51			−0·88
Jawpos								
Toothang								
Toothlen					*−0·25*			
Facecol		0·33		0·37	*0·26*		*−0·29*	0·37
Coldist								*−0·28*
Facehair		0·35						
Style	0·46	*0·28*	0·55	−0·49	0·44			
Wool			0·77	−0·45	*0·26*			
Struct	0·62	0·34	0·54		0·62			

† Roman font: $P < 0·05$; italic font: $0·05 < P < 0·10$; a space indicates $P > 0·10$.

measured on wethers, except that face colour was positively correlated with Finumd (0·33), Slage (0·37) and Leancw (0·37). The type traits Style and Struct again behaved similarly, both showed a (moderately) high positive correlation with live and carcass weights (≥0·44) and live conformation (≥0·54) in wethers.

Discussion

Subjective scores v. *objective measurements*

Historically, selection in the BFL breed has mainly been based on visual assessments of face colour, style, structure and wool type. The industry view has been that doing so improves the quality of the crossbred ewe. The information presented in this paper provides some insight into the soundness of that view. If indeed some of these visual traits are sufficient indicators of improved productivity (as defined by growth and carcass measures in this paper, and perhaps by maternal and longevity traits to be described in subsequent papers) then their formal incorporation in selection programs may be justified. Doing so may also encourage the uptake of recording.

The majority of visually assessed traits collected on the ewes in this study showed, however, no substantial genetic association with slaughter traits of wethers. The few that did were correlated in the desirable direction. Style and structural soundness were genetically positively correlated with live weight at an age (in ewes) or level of condition (in wethers), which is a favourable association for slaughter lamb production. Face colour had a positive genetic correlation with ultrasound muscle depth (0·33) in wethers at finished condition and, accordingly, with lean carcass weight (0·37), but was unrelated to ultrasound muscle depth of ewes at time of assessment. While face colour is inconsequential to slaughter lambs, it is of major importance to breeders of crossbred ewes because it provides a ‘trade mark’ for this type of sheep. The current results show that it is very well possible to use BFL rams with high genetic potential for carcass related traits that also provide the desired colouring, style and structure in the crossbred ewe. The possibility that some of the same loci, or separate loci that are in close proximity on the genome, affect both type and performance traits cannot be excluded.

In the industry, jaw position, tooth angle and tooth length are believed to be factors that influence length of productive life of a ewe. It is therefore encouraging that neither of these traits showed a strong link with any of the slaughter traits measured on wethers. Toothang is a trait with a rather non-normal nature; 88% of observations were in class 1, with the remainder primarily in classes 0 and 2. Hence, the scale may not sufficiently discriminate differences among animals in tooth angle within the normal range observed. A wider range of scores were recorded for Jawpos (between −5 and 2) and Toothlen (between −2 and 2), although for both close to 50% of observations were in the most common class (−1 and 0, respectively). This study suggests that there is no genetic correlation between mouth quality and carcass traits, but given the relative novelty of the mouth quality traits, further research should be carried out to confirm these findings. A study has been planned regarding repeated measurements on mouth quality of these same female animals later in life in conjunction with productivity. This will give further insights into changes in mouth characteristics over the lifetime of a sheep and the relationship between mouth quality as a lamb and ewe longevity. These additional measurements will also contribute to a better understanding of the link between mouth quality of the dam and slaughter traits in her offspring.

Snyman and Olivier (2002) considered a number of subjectively assessed traits that were similar to those considered in this study. They found moderate heritabilities for head conformation and front quarters (0·32 and 0·22, respectively), but a low heritability (0·06) for top line. These three traits were likely factors in our assessment of style/breed type, which had a heritability of 0·36. Their wool traits varied in heritability from 0·26 to 0·51, which is comparable with an estimate of 0·41 for overall wool quality in the present study. Their assessments of hock, front and hind pasterns are likely factors included in our overall assessment of structural soundness (legs). They found heritabilities of 0·36, 0·21 and 0·08 for these three traits, respectively, whereas we found 0·23 for structural soundness, which was well within their range. They found a high heritability for face pigmentation (0·50), which is in agreement with our findings (a heritability of 0·59 for face colour). Their high genetic correlations between weight traits and head conformation (between 0·82 and 0·85) is in agreement with our estimate of 0·81 for the correlation between style/breed type and October live weight. We found a genetic correlation of 0·86 between structural soundness and October live weight, whereas the correlations between any of their leg assessments and live weights were much lower (0·19 at the most). This apparent disagreement is likely not caused by a difference in genetics of these populations, but rather by their three separate leg assessments (for hocks, front and hind pasterns) not adding up to our overall assessment of structural soundness and additional factors being of importance as well. This highlights the importance of accurate trait definitions, a requirement more acute in subjectively assessed traits than in objectively measured traits. Snyman and Olivier (2002) concluded that their general conformation traits would not deteriorate in a selection programme that has increased body weight as its aim. Based on our own findings, we would suggest that mouth scores, face colour/hair and overall type traits as measured in our study will not deteriorate in a selection programme for increased muscle mass and decreased fatness.

Bias in parameter estimates

The results in this paper are based on measurements on crossbred animals without considering performance information on their sires or dams. Because no pedigree information was available on the dams, and no information on grand-offspring was included, it was not possible to partition the contribution from the dam into genetic and non-genetic effects. If the random model includes only the animal's additive genetic term (as for the ewe mouth scores and face colour/hair traits), some of the non-genetic dam effects are likely captured in this term, and therefore the additive genetic variation may be inflated. Conversely, when fitting an additional (non-genetic) term for rearing dam or litter (as for the ewe growth/carcass and overall type traits), this term could well include some of the direct additive genetic variation between dams, and therefore the total additive genetic variance may be underestimated.

Another cause of bias in the estimates of the genetic (co-) variances is heterosis. Krause *et al.* (1965) reported that additive genetic variation observed in crossbred progeny can contain both additive genetic variation found in pure lines and some of the purebreds' non-additive variance, therefore leading to over-estimation of heritability. It was therefore surprising to find that the (crossbred) heritabilities for Octwt, Octumd, Octufd and Octconf were all about one and a half to two times lower than the (purebred) heritabilities found for BFL sheep, the sire breed used in this study (Van Heelsum *et al.*, 2001). This could be partly due to the different models fitted. For the four ewe traits, the model included both an animal genetic effect and a litter effect, which could have led to some of the genetic variance having been partitioned into the litter effect (possibly exacerbated by pedigree structure and lack of pedigree data on hill ewe dams). Conversely, Van Heelsum *et al.* (2001) did not fit a non-genetic litter or dam effect, which could have led to over-estimation of the genetic variance. It should also be noted that the sheep in this study were kept in a near-commercial farming system and, therefore, environmental (non-genetic) variation was greater than in a pedigree farming system. Estimates of genetic correlations between Octwt and Octumd (0·43) and between Octwt and Octufd (0·16; $P > 0{\cdot}10$) found in the present study were much lower than in BFLs, where values of 0·71 and 0·66 were found (Van Heelsum *et al.*, 2001) but correlations with Octconf were higher than in purebred BFLs. Phenotypic correlations within the growth and carcass traits in the purebred BFL were similar to those obtained here for their crossbred progeny.

In these data, it was not possible to separate non-additive genetic effects (heterosis) from additive genetic effects because reciprocal crosses were not available (i.e. hill ewe rams mated to BFL ewes). Only the additive component of the genetic variance is transferred to the offspring of the crossbred ewes, although they benefit from heterosis in maternal traits of their mothers (this might be captured in a maternal genetic effect if fitted). Because these offspring are themselves the result of a cross, and therefore likely to benefit from a new source of heterosis, it is hard to anticipate the effect on total genetic variance in this generation. This will make the prediction of the response to selection in the overall breeding scheme less accurate.

Measuring at equal age v. *at equal finish*

A number of measurements were taken on both wethers and ewes, for example live weight and ultrasound measurements. However, the timing of the measurements was very different. This made, for example, an ultrasonic muscle depth of a ewe (all measured within a narrow age range of between 180 and 208 days) a very different trait from an ultrasonic muscle depth of a wether (all measured at an equal amount of 'finish', covering a vast age range of between 65 and 304 days).

Other studies have mainly focussed on traits measured at a constant weight (in particular where slaughter measurements are involved; e.g. Jones *et al.* (1999)) or at a constant age (in particular for growth measurements; e.g. Van Heelsum *et al.* (2001)). Pollott *et al.* (1994), however, looked at lamb carcass measurements at three different end points, namely at the same level of fatness (visually assessed subcutaneous fat cover of the carcass), at the same (cold carcass) weight, and at the same age. In their experimental design, lambs were slaughtered at one of a range of predefined weights, corresponding with an expected amount of fat cover for the particular breed and farm type. This meant that the decision to send lambs for slaughter did not directly depend on fat cover (as was the case in our study), but instead on weight, which was used as an indicator for fat cover (among other factors). This might explain the much higher heritability for age at slaughter (0·34) reported by Pollott *et al.* (1994) as compared with our study (0·18). They found an even higher value (0·53) when they adjusted to an equal weight end point. For the same reason, it is not surprising that their heritability estimate for cold carcass weight is much lower than in our study (0·08 *v.* 0·35), because much of the variation in cold carcass weight would have been taken out by the experimental design. The authors acknowledge that their design has not fully succeeded in selecting lambs at a given body condition.

Although body size and fatness are genetically correlated, this correlation is not equal to unity, which is exploited by breeding schemes aiming to increase size without increasing fatness. We noted earlier that, although a higher slaughter weight can be achieved by growing faster in a given amount of time, it can also be achieved by growing over a longer period of time before reaching finished condition. Selecting for higher finishing weight at the same level of fatness would therefore result in a longer finishing period and also in lambs that are less mature at a given point in time. A longer finishing period raises issues of increased costs and price variation over the season. Maturity at a given point in time is a particular issue for the ewe lambs that are usually sold at predetermined sale dates in autumn. If slaughter weight at constant fatness were to be included in a selection index, it is therefore vital to consider age at slaughter as well.

Conclusion

This study shows that there is substantial scope to improve a breeding goal including both carcass and type traits in crossbred sheep. Estimates of genetic correlations between objectively measured growth and carcass traits, *versus* subjectively assessed type traits relevant to the value of ewe lambs as breeding animals, suggest that when selecting for improved carcass traits, type traits will not consequently deteriorate. In fact, selecting on some performance traits, especially live weight at a given age, will result in positive correlated responses in some type traits (e.g. style or breed type and structural soundness). This is important to any breeder producing crossbred ewes for the production of slaughter animals.

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