The development of multi-trait selection indices for longwool sheep to breed halfbred ewes of superior economic performance

Executive summary

In 1997, a Defra/MLC-funded project was established, involving the Institute of Rural Sciences (IRS), the Scottish Agricultural College (SAC) and ADAS. The objectives were to provide the necessary information for the development of a multi-trait selection index for improving carcass quality of crossing sire sheep and their crossbred progeny without compromising reproductive performance or maternal ability in these breeds, using the Bluefaced Leicester (BFL) and its Mule progeny as the model. This represented the first study to measure the genetic parameters underpinning carcass traits in the crossing sire ('longwool') breeds and their progeny, and the first study to investigate the genetic relationships between carcass and reproductive/maternal traits.

During Phase 1 - the 'Production Phase' – a Sire Referencing Scheme was created involving 13 BFL flocks. Over a three-year period (1997, 1998 and 1999) the Scheme supplied 15 crossing rams per year of known genetic merit for carcass quality for mating by AI to the 1500 hill ewes (750 Scottish Blackface and 750 Hardy Specked Face ewes) in the project. The three crops of crossbred (Mule) lambs produced from these matings were assessed for growth and carcass traits. During Phase 2 - the 'Evaluation Phase' - reproductive and other maternal traits have been assessed in the Mule ewes produced. Finally, using all of the information gathered, genetic and phenotypic correlations have been estimated using appropriate statistical techniques, and a multi-trait economic selection index constructed for a defined set of traits appropriate to longwool crossing sire sheep breeds.

Over the three years of Phase 1, a total of 2083 Scottish Mule and 2763 Welsh Mule lambs were reared and evaluated for growth and ultrasound measures of carcass composition, while detailed carcass measurements were made on wether lambs on reaching finished condition (fat class 2/3L). Mule ewe lambs produced during Phase 1 were assessed in October each year for a number of traits related to growth, conformation, breed type and structural soundness before being distributed to the three 'evaluation' sites in England, Scotland and Wales for Phase 2 (Mule ewe maternal trait evaluation) and Phase 3 (Mule ewe longevity). At these evaluation sites, the Mule ewes have been assessed for their reproductive performance, maternal characteristics and longevity.

Detailed analysis of the genetic relationships between objectively measured growth/carcass traits and a range of subjectively assessed type traits indicated that crossbred heritabilities for type traits were low to high (0.11 to 0.59). However, the genetic correlations between type traits and growth/carcass traits were very low and variable, with the few correlations that were statistically significant being in the desirable direction. The consequence of this is that

selection for improved growth/carcass quality in BFL sheep will not compromise type traits in their Mule progeny.
To measure maternal characteristics, the Mule ewes have been evaluated over a number of lamb crops following mating to rams of the three major terminal sire breeds (Charollais, Suffolk and Texel). For most years, ewes were mated in single sire mating groups. Full records of reproductive performance and ewe longevity were collected over 5 lamb crops (i.e. to 6.5 years of age). Differences in reproductive performance between the two ewe breeds (Scottish and Welsh Mules) have been small. Pooled across the three evaluation sites and considered over all age groups and breeds, between 84.1 and 93.2% of ewes put to the ram have lambed each year. Mean litter size per ewe lambing increased from 1.75 for 2-year old ewes up to 1.95-1.98 for ewes 4 years of age and older. Between 80.3% and 83.5% of the total lambs born (born live and dead), and between 83.0% and 87.4% of lambs born alive, were reared.

Pooled over sites and ewe breeds, the incidence of ewe losses due to culling increased progressively with ewe age, from 6.9% in 2-year-old ewes to 34.4% in 6-year-old ewes. Losses due to ewe deaths were far smaller, ranging from 1.3% to 4.6%, with no effect of ewe age. The single most important reason for culling, particularly for younger ewes, at all three ewe evaluation sites has been udder condition (accounting for around 3.5% to 6.3% per year). The incidence of culling due to teeth/mouth problems increased from around 0.3% in 2- and 3-year old ewes up to 10.0% in 5-year old ewes and 22.1% in 6-year old ewes. However, differences between ewe breeds have been generally small.

Genetic parameter estimates for ewe longevity (survival within the breeding flock) were calculated for the full dataset. The heritability of ewe longevity was 0.27, suggesting that it would respond well to selection within a breeding program. Unfortunately, none of the genetic correlations between ewe longevity and a range of growth/carcass and type traits measured in the young animal were significantly different from zero, and cannot therefore be used as proxy measures for ewe longevity. The absence of appropriate correlations indicates that improvement of ewe longevity in Mule/Halfbred ewes will require the direct measurement of ewe longevity within the purebred longwool crossing sire flocks.

The results of analyses to estimate genetic parameters for reproductive traits, including both litter size and lamb survival (as a trait of the lamb and as a trait of the ewe), indicated that the crossbred heritability of litter size in Mule ewes was 0.12. The heritability of lamb survival as a trait of the lamb itself (i.e. due to its own genetic makeup) was 0.07, while the heritability of lamb survival as a trait of the ewe (i.e. the genetic influences of the ewe determining her ability to rear the lambs) was 0.14. Genetic correlations between litter size and lamb survival were low to moderate and in an unfavourable direction, and this will need to be accounted for in the design of the selection index.

Using all of the available information, a multi-trait economic selection index has been computed. The weighting factors for the individual traits included in the selection index were based on computer modelling using data generated within the project together with information on lamb carcass value, replacement ewe costs and cull ewe values. Modelling studies have also been undertaken to investigate likely responses to selection using the index, as well as the sensitivity of the individual components within the index to genetic progress.

Ewe longevity was found to be of high economic importance, reflecting the moderately high heritability and substantial genetic variation for the trait as measured in the Mule ewes in the project. Indeed, ewe longevity was found to be very dominant in selection indices where selection candidates have modest numbers of daughters with longevity records (‘proven sires’), and still of moderate to high importance when selection candidates were ‘unproven’ young rams with no progeny information available although with longevity information available on their older female relatives (e.g. dams and sibs of their sire and dam). The modelling studies undertaken using the selection index suggest that there are few benefits from recording either leg conformation score or ewe mature weight. In addition, when ewe mature weight was not recorded, the expected response in mature weight through selection on the index becomes less negative, which might be more sustainable in the long term.

At a 100% adoption rate within purebred crossing sire flocks and based on a total of 5.3m Mule/Halfbred ewes within the UK, the cumulative present value of benefits to the UK sheep industry from 10 years selection on the index would range between £21.4 million (‘unproven’ sires) and £30.4 million (mixture of ‘proven’ and ‘unproven’ sires). Approximately 13-20% of the benefits accruing from use of the index will be captured by hill sheep flock owners through the production of Mule/Halfbred wether lambs with better carcass quality, with the remaining majority being captured by Mule/Halfbred ewe flock owners through better ewe longevity, better carcass quality of their terminal sire cross lambs and enhanced lamb survival. Full details of the economic selection index have been provided to Signet for use within their Sheepbreeder service for the genetic improvement of the longwool crossing breeds. In addition, the benefits of using the index have already been provided to the BFL Sheepbreeders Association, who have identified the unique selling point of improved ewe longevity as a means of protecting their market share.

Introduction

Major differences in climate and topography across the UK dictate different systems of sheep production, with specific breed types used in these different environments. However, these systems of production are integrated through a stratified structure unique to the UK. The purpose of this cross breeding system is to generate a (longwool x hill) dam line for the lowlands which, when crossed with a terminal sire breed of ram, produces prime market lambs. At the same time, it provides a real purpose to sheep production in the less favoured areas.

This was, and still is, important for the economic sustainability of rural populations and the maintenance of the rural environments in such regions. Recent years have seen a major shift in emphasis away from quantity towards quality within the meat sector, and this is requiring sheep producers to respond by seeking to improve carcass quality through adoption of genetic improvement programmes. The development of national schemes to increase carcass quality was initially targeted at the terminal sire breeds because (i) the cost:benefit ratio of the research to develop such schemes was likely to be greatest since these breeds make the greatest genetic contribution to the slaughter generation, and (ii) the selection objectives were easiest to define for this particular breed type. Their primary role is to sire the slaughter generation out of crossbred ewes. Characteristics such as mothering ability and reproductive rate have little or no relevance to this role, with the consequence that the selection objectives can be limited to improving growth rate and carcass characteristics.

Now that improvement programmes are well established within this sector of the industry, the attention has turned to the genetic improvement of carcass quality in the hill and crossing sire ('longwool') breeds. These breeds also make a substantial contribution to the slaughter generation since they are the parental breeds of the Mule/Halfbred ewe that dominates lowland sheep flocks. However, given their different place in the stratified sheep production system, maternal and longevity traits are also relevant to these hill and longwool crossing breeds.

Defining appropriate selection objectives for them is therefore more complicated than for the terminal sire breeds. In the quest to improve carcass quality of these breeds, it is essential that any selection pressure applied for carcass traits does not compromise hardiness, longevity, prolificacy or mothering ability, which would be detrimental to overall economic performance of hill and Halfbred/Mule ewe flocks.

The occurrence of any unwanted side effects of selection for improved carcass quality depends on the presence of undesirable genetic correlations between carcass traits on the one hand and maternal traits on the other. Little is yet known about these correlations or of any other genetic parameters for carcass and maternal traits in crossing sire breeds. This study is the first to measure the genetic parameters underpinning carcass traits in the longwool crossing breeds and their progeny, and the first to investigate the genetic relationships between carcass and reproductive/maternal traits in UK breeds.

Aims and objectives of the research project

The overall aim of this research project was to develop an appropriate multi-trait selection index for longwool crossing breeds to improve the carcass quality of their crossbred ewes (and their terminal sire-cross progeny) while maintaining maternal performance, using the Bluefaced Leicester (BFL) and its Mule progeny as the model. For this aim to be achieved, the genetic parameters (heritabilities, genetic and phenotypic correlations) underpinning performance traits of the longwool breeds and their halfbred (Mule) progeny needed to be evaluated, and the economic value of the traits to be changed in the index determined. This aim has been realised though a number of key objectives:

- undertaking detailed performance recording and genetic parameter evaluation of BFL sheep;
- conducting a robust progeny test of BFL rams, selected to represent various combinations of carcass composition (estimated ultrasonically) and subjective assessment of live conformation;
- investigating the genetic and phenotypic relationships between carcass and maternal traits (including longevity) in the female crossbred (Mule) progeny of these BFL rams;
- determining the relative economic value of the different growth, carcass and maternal traits, and
- based on this information, develop an appropriate selection index for use by the industry.

Experimental approaches

The project was designed in a stepwise manner, with each objective building upon another. Phase 1 was the Mule ‘Production Phase’ and consisted of: (i) establishing a sire referencing scheme within the BFL breed, together with all of the detailed pedigree and performance recording required, to supply information on the genetic parameters underpinning important production traits; (ii) creating Mule (halfbred) sheep over a three-year period, using 15 performance-recorded BFL rams each year to mate to 1500 hill ewes (750 Scottish Blackface, 750 Hardy Speckled Face); (iii) assessing growth and carcass traits (measured ultrasonically in both sexes) of Mule sheep, together with detailed estimates of carcass composition (wether lambs only) at slaughter; and, (iv) assessing structural and type traits in Mule ewe lambs.

Phase 2 was the Mule Ewe ‘Evaluation Phase’ and consisted of monitoring maternal performance of Mule ewes by: (i) assessing their reproductive performance over a minimum of three successive lamb crops; and, (ii) monitoring the growth and carcass characteristics of their terminal sire-cross progeny.
Phase 3 extended the Mule ewe evaluations to include details of the reasons for culling ewes to provide data on ewe longevity.
Based on the information collected over the entire project, the relative economic importance of the different parameters (growth, carcass, maternal traits) was modelled and this information was used to construct an appropriate economic selection index for the longwool crossing breeds that appropriately balances the need to improve carcass quality while maintaining maternal characteristics.

Phase 1: Mule ‘Production Phase’

Selection of performance recorded BFL rams to breed Mule sheep.

A pre-requisite for generating the genetic parameters needed for designing a multi-trait selection index was a robust progeny test of longwool crossing rams selected to represent the range of performance traits typical of the breed. The BFL breed was chosen as the model for this project due to its role as the dominant crossing sire breed within the UK stratified industry structure. At the outset of the project, few BFL flocks were involved in performance recording. A sire referencing scheme involving 13 breeder flocks was established in 1996 with support from the Bluefaced Leicester Sheep Breeders' Association. Performance records were collected on all sheep in breeder's flocks. These included lamb identity and pedigree (i.e. sire and dam), sex of lamb, birth weight, birth and rearing type, 8-week weight, and at about 21 weeks of age, live weight, and ultrasonic muscle and fat depths. At scanning, conformation (gigot), head colour and facial hair, jaw position and tooth angle, wool, structural soundness and breed type were scored subjectively using BFL Society-appointed assessors. All data were forwarded to SAC for genetic evaluation using Best Linear Unbiased Prediction (BLUP) estimation of breeding values, and calculation of a 'scheme index score'. This allowed identification of potential reference sires as well as potential crossing sires for mating to hill ewes in the project.

The project managed the Sire Referencing Scheme on behalf of its 13 member flocks for the first 3 years (up to and including the 1998 matings and the evaluation of the 1999-born progeny). Since the prime objective of this research project was to develop an appropriate multi-trait selection index for (longwool) crossing sire breeds, it was important for this scheme to continue so that there was a target group of breeders ready to take on the new index as soon as it became available. During the early part of 1999, the scheme members decided to set up their own limited company and open it up to wider membership. Responsibility for the data recording and analysis within the scheme has therefore now been passed to Signet as part of their Sheepbreeder service.

To facilitate selection of BFL sires for detailed progeny testing during Phase 1, it was necessary to devise a preliminary selection index. The goal of this index was to improve the carcass composition (the relative leanness) and conformation of crossing sire breed sheep and their crossbred progeny without jeopardising their reproductive merit. The goal traits used and their selection criteria are presented in Table 1. Live weight and litter size were included as 'restricted traits' in the goal. The index was derived based on the estimates of genetic and phenotypic parameters available from the scientific literature for other breed types (Wolf et al., 1981; Simm and Dingwall, 1989; Fogarty, 1995; Schrooten and Visscher, 1987) and unpublished data (Wolf, personal communications).

Table 1. Traits in the selection goal and used as selection criteria in the preliminary scheme index for the Penglas Bluefaced Leicester Sire Referencing Scheme.†

Selection goal	Selection criteria
Lean weight	Ultrasonic muscle depth
Fat weight	Ultrasonic fat depth
Conformation	Conformation score§
Live weight‡	Live weight
Litter size‡	Litter size

† As measured in lambs at about 21-weeks of age.
‡ Included as restricted traits in the index.
§ Subjective assessment of the gigot on a scale of 1 to 6, where 1 indicates poor conformation and 6 indicates excellent conformation.

Approximately 25 ram lambs were identified from within the Sire Referencing Scheme in each of three years (1997, 1998 and 1999), from which 15 were used as crossing sires to produce Mule lambs for further study. These rams were chosen to be as extreme as possible in their performance, based on in vivo predictions of carcass merit from measures collected at scanning age (21 weeks of age). In experiments designed to provide data to estimate genetic parameters, it is sensible that the design is such that these parameters are estimated as accurately as possible. When two traits are important - the bivariate case - a method to achieve this is by using a phenotypic selection ellipse as described by Cameron and Thompson (1986). An ellipse is defined as:

$$w^2 = \frac{x_1^2 + x_2^2 + 2r_p x_1 x_2}{1 - r_p^2}$$

and w is chosen so that a predetermined proportion of animals lie outside the ellipse and are then chosen as parents. In this experiment, the two traits defining the ellipse (x1, x2) were conformation score and an index score designed to increase the proportion of lean in a carcass of fixed weight, and rp is the phenotypic correlation between them. This index was used only for application in the ellipse, and was different from that used in the Penglas Sire Referencing Scheme in that it excluded conformation score and litter size.

Results from Penglas Bluefaced Leicester Group Breeding Scheme

Parameter estimates for the various traits recorded for sheep within the BFL Sire Referencing Scheme are presented in Table 2. The heritability of growth and carcass traits were all moderate, while the heritability of litter size was low. The genetic correlations among growth carcass traits were all high, while the genetic correlations between litter size and growth carcass traits were all low and often not significantly different from zero.

Table 2. Phenotypic correlations (above diagonal), heritabilities (on diagonal; bold) and genetic correlations (below diagonal) for traits recorded in BFL sheep. (SLW = scan live weight; UMD and UFD = ultrasonic measures of muscle and fat depth; CONF = live conformation of the gigot; LS = litter size)

Parameter	SLW	UMD	UFD	CONF	LS
SLW	0.37	0.69	0.63	0.57	0.15
UMD	0.73	0.33	0.48	0.51	0.00
UFD	0.74	0.64	0.35	0.44	0.00
CONF	0.70	0.53	0.59	0.28	0.00
LS	-0.12	0.02	0.05	-0.19	0.05

Progeny test of BFL rams

In each of the 3 years of Mule Production (Phase 1), 1500 hill ewes (750 Scottish Blackface and 750 Hardy Speckled Face) were mated by AI to the 15 performance-recorded BFL ram lambs. The ewes lambed in March and April and their lambs were weighed at birth, 5, 10 and 16 weeks, and when attaining ‘finished’ condition for all wether lambs sent for slaughter. At the Ewe Lamb Selection Days (in October each year), all female lambs were ultrasonically scanned, weighed, condition and conformation scored, and visually assessed for breed type, colour, wool and structural soundness. Each year, 615 of these ewe lambs were retained to go on to the next phase of the project involving Mule ewe evaluations (Phases 2 and 3).

The relationship between the sire’s index score and the performance of its Mule progeny was determined using a statistical model that accounted for year of birth (1998, 1999 or 2000), production site (ADAS Pwllpeiran, IRS Morfa Mawr, and IRS Tan-y-graig), dam breed (Scottish Blackface or Hardy Speckled Face), birth-rearing type (six classes: born and reared as single; born as twin, reared as single; born as triplet reared as single; born as single reared as twin; born as twin reared as twin; born as triplet reared as twin), fostered or reared normally (artificially reared lambs were discarded), and age of the (rearing) dam (1 to 2, 3, 4 to 6, or more than 6 years old). The interaction between year and site was shown to be of importance and was therefore also taken into account. When appropriate, the measurements were adjusted to a common age (Ewe Lamb Selection Days data), or to a common condition score (‘finish’ data). The importance of the sire’s index score was investigated using linear regression.

‘Predicted means’ presented are estimated using Residual Maximum Likelihood (REML) methodology. Note that these means are based on average factor classes not weighted according to actual numbers of animals in each class. For example, the estimated effect of a given year was calculated taking into account the imbalance in other factors. This means that although ADAS Pwllpeiran carried more hill ewes and thus produced more data records than other sites in each year, the predicted mean for a given year was calculated as if all sites had the same number of data records.

Lambs were considered 'finished' when reaching a fat score at the boundary of fat class 2/3L. Until the ewe lamb selection days, both ewe and wether lambs were assessed fortnightly for level of finish. After the ewe lamb selection days, ewe lambs were distributed to the three Mule ewe evaluation sites (ADAS Rosemaund, IRS Aberystwyth, SAC Edinburgh) regardless of whether 'finished' condition had been reached, whereas the wether lambs continued to be assessed fortnightly. Hence, the 'finish' data on ewe lambs is necessarily incomplete and is therefore not considered here.

Table 3 shows the mean performance for the in vivo measures of carcass merit recorded on wether lambs by breed. The offspring of Scottish Blackface ewes finished slower but at a higher weight, with a lower fat depth and higher muscle depth, than offspring of Hardy Speckled Face ewes.

Table 3. Predicted mean performance of Mule wethers for measures recorded at finished condition by dam breed

	No. of Lambs	Age of finish	Live wt (kg)	Fat depth (mm)	Muscle depth (mm)	Conformation Shoulder	Loin	Gigot
Scottish Blackface	962	205	36.4	3.5	22.5	3.23	3.45	3.22
Hardy Speckled Face	1280	187	33.5	3.7	21.8	3.14	3.42	3.20
P-value †		***	***	***	***	***	**	

† Level of significance of the effect: ***P < 0.001; **P < 0.01

Slaughter data on Mule wether lambs

A total of 2208 lambs went for slaughter over the three years of the Mule Production Phase: 573 from IRS Morfa Mawr, 931 from ADAS Pwllpeiran and 704 from IRS Tan-y-graig. In total 1262 lambs had a Hardy Speckled Face dam and 946 lambs had a Scottish Blackface dam. Across the three years, between 82 and 88% of lambs were selected for slaughter at the target fat class of 2/3L. The predicted means for the two dam breeds for detailed carcass traits are presented in Table 4. Scottish Blackface offspring took on average 18 days longer to achieve the target fatness for slaughter, but their empty body weight was 35.5 kg as compared to 31.8 kg for Hardy Speckled Face offspring, resulting in a cold carcass weight of 16.3 kg and 15.5 kg, respectively. The Scottish Mules had higher conformation scores on the 15-point scale and a larger eye muscle area and circumference of the buttock, but their dressing percentage was significantly lower.

Table 4. Predicted means for carcass measurements in abattoir and from dissection by breed adjusted to a constant level of finish (SBF=Scottish Blackface; HSF=Hardy Speckled Face)

	Slaughter age (days)	15-point conformation score				Cold carcass wt (kg)	Dressing percent	Eye muscle area (mm)		Circumference of buttock (mm)
		Overall	Gigot	Loin	Shoulder			3rd lumbar	12th rib	
SBF	201	6.6	6.4	6.7	6.8	16.3	47.3	12.2	11.0	600
HSF	183	6.4	6.0	6.6	6.7	15.5	48.6	11.5	10.6	589
P-value †	***	***	***		*	***	***	***	***	***

† The factor explained a significant amount of variation (***P < 0.001; **P < 0.01; *P < 0.05)

A total of 789 carcasses went for dissection: 158 for full side dissection and 631 for shoulder dissection. Hill ewe breed differences were observed in the dissection results (Table 5). When comparing the percentage lean and fat in the different joints of the carcass, the Scottish Mules had in most cases more lean and less fat. However, these differences were often not significant for the joints other than shoulder due to the much smaller number of carcasses that underwent a full side dissection as opposed to a shoulder dissection only. A substantial difference was found in lean and fat percentage in the joints of Mule lambs sired by high as opposed to low index BFL rams. These tissue percentages were regressed on the index score of the rams used in the project, and the results are shown in Table 6. The index score of the sire had a large effect on the carcass composition of its offspring; high index sires produced progeny with less fat and more lean in every joint of the carcass. Only for ‘middle neck’ and ‘scrag’ was the effect of the sire’s index score not significant.

The regressions of age at slaughter, empty body weight, cold carcass weight, dressing percentage and the three 15-point conformation scores on the sire’s Scheme Index were all non-significant. This implies that a higher index score does not result in larger, faster growing animals, which is in line with expectation since live weight was restricted (allowing only a limited increase) in the design of the Scheme Index.

Although in a cross-breeding situation, such as that used in the current study, it is not possible to completely disentangle the additive and non-additive (dominance, epistasis) components of genetic variation, it is notable that the relationships between carcass traits in the BFL sires and their Mule progeny is consistent with the heritability of carcass traits estimated within the BFL sire referencing scheme.

Table 5. Predicted mean percentage of lean and fat in the 8 different joints, and in 7 joints combined (all except shoulder), of carcasses from wether Mule lambs of Scottish Blackface (SBF) or Hardy Speckled Face (HSF) dams

Joint	Percentage lean SBF	Percentage lean HSF	P-value †	Percentage fat SBF	Percentage fat HSF	P-value †
Shoulder (n=788)	60.08	59.13	***	22.11	23.09	***
Leg	66.74	66.59		14.18	14.05	
Chump	61.11	59.33	**	22.47	23.58	*
Loin	62.85	61.43		20.66	21.62	
Breast	50.86	49.53		31.48	32.62	
Best end neck	53.03	52.16		26.87	27.54	
Middle neck	62.77	62.34		13.99	14.70	
Scrag	53.08	53.73		14.94	13.90	
Total of 7 joints (n=158)	60.91	60.26		19.58	20.03	

† Dam breed explained a significant amount of variation for the joint (***P < 0.001; **P < 0.01; *P < 0.05)

Table 6. Parameters of regression lines (constant and regression coefficient) for percentage of lean and fat in the 8 separate joints, and in 7 joints combined (all except shoulder), regressed on sire's Scheme Index

Joint	Percentage lean Constant	Percentage lean Regr. coef.	P-value †	Percentage fat Constant	Percentage fat Regr. coef.	P-value †
Shoulder (n=788)	60.8	0.014	***	21.7	-0.015	***
Leg	66.8	0.010	**	14.7	-0.012	**
Chump	62.6	0.017	**	20.9	-0.023	**
Loin	63.6	0.032	***	20.6	-0.033	***
Breast	53.0	0.030	***	30.9	-0.033	**
Best end neck	54.0	0.028	***	27.1	-0.037	***
Middle neck	64.8	0.006		13.4	-0.011	
Scrag	54.4	0.014	*	13.7	-0.019	
Total of 7 joints (n=158)	61.9	0.018	***	19.4	-0.022	***

† The factor explained a significant amount of variation (***P < 0.001; **P < 0.01; *P < 0.05)

Assessment of the Mule ewe lambs at Selection Days

A total of 2446 Mule ewe lambs were assessed at the Selection Days in October 1998, 1999 and 2000. Of these, 1845 were transferred to the Mule Ewe Evaluation sites for Phases 2 and 3 of the project. The Mule ewe lambs were assessed for a number of objective and visual traits. The differences in the objectively measured traits and the conformation scores are shown in Table 7 by dam breed. Similar to the wethers, the ewe lambs from Scottish Blackface dams were larger and had less fat than lambs from Hardy Speckled Face dams. Their muscle depths, however, were similar.

Table 7. Predicted means for the objective traits and conformation scores of Mule ewe lambs on ewe lamb selection days in October (1998 to 2000) by dam breed (SBF = Scottish Blackface; HSF = Hardy Speckled Face)

	Live wt (kg)	Muscle depth (mm)	Fat depth (mm)	Conformation score		
				Gigot	Loin	Shoulder
SBF	33.1	20.0	2.67	3.10	3.08	2.77
HSF	31.9	19.9	3.11	3.06	3.09	2.61
P-value †	***		***	*		***

† The effect explained a significant amount of variation (***P < 0.001; **P < 0.01; *P < 0.05)

The predicted means for visual traits are shown in Table 8, grouped by dam breed, year and production site. The most obvious differences found were between breeds, with the Scottish Blackface dams producing offspring with darker heads and a more distinct colouring of the head. Their offspring also scored higher for style and structural soundness, which might be due to their larger size. Interestingly, the regression of the traits on the sire's Scheme Index score was significant for muscle depth (positive) and fat depth (negative), as well as for face colour (positive). This suggests that a high index sire will not only give a better carcass composition in its progeny but can also give a 'prettier' face.

Table 8. Predicted means for the visual traits scored on Mule ewe lambs (1998-2000) by dam breed (SBF = Scottish Blackface; HSF = Hardy Speckled Face), year and production site

	Style	Wool	Structural soundness	Face colour	Distinction of face colour	Face hair	Jaw position	Tooth angle	Tooth length
Dam breed									
SBF	5.7	6.5	4.8	2.7	3.7	3.73	-1.3	0.6	0.5
HSF	4.6	6.2	4.3	1.6	2.9	3.66	-1.3	0.8	0.7
P-	***	***	***	***	***	***		***	***
Year									
1998	5.4	6.5	4.6	1.9	3.3	3.4	-1.0	0.6	0.7
1999	5.1	5.9	4.4	2.0	3.2	3.7	-1.4	0.8	0.7
2000	5.0	6.6	4.6	2.5	3.4	4.0	-1.4	0.8	0.5
P-value †	***	***	***	***	*	***	***	***	***
Production									
Morfa Mawr	5.4	6.7	4.5	2.1	3.6	3.6	-1.4	0.7	0.6
Pwllpeiran	4.5	6.0	4.3	2.1	3.1	3.9	-1.2	0.8	0.8
Tan-y-graig	5.7	6.4	4.8	2.1	3.2	3.6	-1.2	0.7	0.5
P-value †	***	***	***		***	***	***	***	***
Ideal score	10	10	10	5	5	3	0	0	0

† The factor explained a significant amount of variation (***P < 0.001; **P < 0.01; *P < 0.05)

Faecal egg counts in Mule lambs

Because of increasing concern about the rising incidence of parasite resistance to anthelmintic drugs in the UK, there is a need to investigate alternative control strategies. The breeding structure of the project offered an ideal opportunity to estimate genetic parameters for parasite resistance in both growing Mule lambs and peri-parturient Mule ewes, and to further evaluate the correlation between these traits and measures of production, with faecal egg counts (FEC) being used as an indicator of resistance to intestinal parasite infection. Faecal samples were collected from growing Mule lambs at all sites, and also from Mule ewes over the peri-parturient period in 2000 – 2004 at IRS and ADAS sites only.

Mean FEC in Mule lambs were generally low, but increased progressively and significantly ($P < 0.01$) from a mean of 46 eggs/g at 10 weeks of age up to 192 eggs/g at 26 weeks of age. They also varied across sites and years, and, while the site-year effect was statistically significant ($P < 0.001$) at all lamb ages, there was no consistent pattern that emerged between sites. Faecal egg counts were consistently and significantly ($P < 0.05$) lower in Mule lambs from Hardy Speckled Face mothers, in single compared with multiple lambs ($P < 0.05$) and in female lambs ($P < 0.05$) at most lamb ages.

Estimates of the heritability of FEC in Mule lambs were initially low and not significantly different from zero, but increased with age up to a figure of 0.14 ± 0.05 at both 22 and 26 weeks of age (Table 9). Phenotypic correlations between FEC at different ages were consistently low, but the genetic correlations were generally high.

Table 9. Estimates of the heritability of log10 (FEC+20), with genetic correlations (below) and phenotypic correlations (above the diagonal), at various ages in Mule lambs

Age (weeks)	Age (weeks): 10	14	18	22	26
10	0.09 ± 0.04	0.12	0.07	0.09	0.09
14	inestimabl	0.04 ±	0.16	0.14	0.14
18	0.04 ± 0.34	0.45 ±	0.09 ± 0.03	0.24	0.19
22	0.48 ±	0.92 ±	inestimable	0.14 ± 0.05	0.36
26	0.67 ± 0.24	0.94 ±	0.70 ± 0.20	0.74 ± 0.17	0.14 ± 0.05

Phases 2 and 3: 'Mule ewe evaluation'

Reproductive performance

The reproductive performance of the Mule ewes lambing between 2000 and 2006 is summarised in Table 10. The average number of lambs born per ewe increased from 1.75 in ewes of 2 years of age to 1.98 in ewe of 4 years of age, and remained at almost this level thereafter. The peri-natal mortality (lambs dead/dying at birth as percentage of the total number of lambs born) was low, ranging from 3.2 to 5.6%. Postnatal mortality (lambs dying after birth as percentage of the number of lambs born alive) ranged from 12.6 to 17.0% across parities. The average number of lambs reared per ewe lambing increased steadily with increasing ewe age up to the fifth year of age. This was due to the combined effects of ewe age on both litter size born and postnatal mortality. The percentages of ewes lambing of those mated showed little variation over all age classes for the first four parities, ranging from 90.7 to 93.2%, but then declined to 87.3% for 6 year old ewes.

Table 9. Mule ewe reproductive performance over 7 years (2000 – 2006) by age of ewe

Parameter	Age of ewe				
	2	3	4	5	6
Number ewes to ram	1806	1611	1392	1167	827
Number ewes lambing	1671	1485	1298	1059	722
% ewes lambing of number mated	92.5	92.2	93.2	90.7	87.3
Number lambs born	2927	2791	2565	2077	1410
Average litter size (born)/ewe lambing	1.75	1.88	1.98	1.96	1.95
Number lambs born alive	2790	2688	2483	1982	1353
Average litter size (born alive)/ewe lambing	1.67	1.81	1.91	1.87	1.87
Number lambs reared	2438	2330	2060	1702	1155
Average number lambs reared/ewe lambing	1.46	1.57	1.59	1.61	1.60
Average number lambs reared/ewe to ram	1.35	1.45	1.48	1.46	1.40
% lambs reared of lambs born	83.3	83.5	80.3	81.9	81.9
% lambs reared of lambs born alive	87.4	86.7	83.0	85.9	85.4

Ewe survival

The Mule ewes were assessed for all traits relevant to their economic performance, and an important aspect of this was their longevity. Ewes can be culled for a number of health-related problems, or may die (or be euthanized) for acute reasons. The percentage of ewes culled and died over the duration of the project is shown in Table 11 by both age and reason of culling/death. It should be noted that all remaining non-culled ewes were at least 6½ years of age at the final culling assessment in September 2006.

The most prevalent reason for culling younger ewes has been udder condition. As expected, the number of ewes culled for teeth condition was low for two and three-year old ewes, but increased markedly for the two eldest ages. The most frequent reason of death was 'internal' sickness/disease, which includes severe mastitis, pneumonia and listeriosis. The second most frequent reason for death was the pregnancy/lambing-associated category, which includes septicaemia and prolapse. Losses due to death were largely independent of ewe age up to 5 years of age and then decreased.

Table 11. Percentages of Mule ewes culled/died by reason and by age up until 1 September 2006 (percentage of total number in age group at beginning of year)

		Age of ewe at culling death (years)				
	Reason for culling/death	2	3	4	5	6
	Total number of ewes	1803	1611	1392	1167	886
Culling	Teeth/mouth condition	0.2	0.4	3.4	10.0	22.1
	Udder condition	4.0	4.6	5.8	6.3	5.2
	Foot/leg problems	1.3	1.4	1.0	1.0	1.1
	Other*	1.3	2.6	1.7	2.8	6.0
	Subtotal	6.9	9.0	11.9	20.1	34.4
Death	Pregnancy/lambing associated	1.1	1.7	1.2	0.9	0.5
	'Internal' sickness/disease	1.9	1.9	1.2	0.9	0.3
	Other§**	0.8	1.0	2.0	1.2	0.5
	Subtotal	3.8	4.6	4.4	3.0	1.3
	Total	10.7	13.6	16.3	23.1	35.7

* Includes: prolapse, other injury/abnormality, poor body condition and barren twice in successive years

§ Includes: injury and unknown reasons

Genetic associations between longevity and objectively or subjectively assessed traits of Mule ewes using linear censored models

Longevity or length of productive life of ewes is a trait of high economic importance that is associated with a decrease in culling rate and consequently with a reduction in the cost of female replacements. Type traits could potentially be used as early predictors for longevity if they are correlated, and could increase the reliability of estimated breeding values for longevity of young sires. Furthermore, longevity may be correlated with production traits such as growth and carcass quality. Assessment of genetic parameters for longevity, along with subjective type traits and production traits, is also necessary in order to construct a multi-trait selection index.

Different approaches have been used for the genetic evaluation of longevity such as linear models and survival (failure-time) analysis. The advantages of survival analysis over linear models are that the former analysis accounts for both censored and uncensored records as well as for the skewed distribution of longevity data. Censored records arise from ewes still in the flock and, therefore, their future culling age is not known. In contrast, uncensored records are from ewes for which the culling age is known. Additionally, time-dependent environmental effects can be included in the survival analysis model. However, the interpretation of the parameters from survival analysis is less straightforward because of the non-linear relationship between hazard and longevity, and its high computational requirements for large data sets when using an animal model. Moreover, survival analysis does not at the present time allow for multiple-trait analysis of survival with other traits. By comparison, linear models have less computational requirements than survival analysis and can also be easily extended to multiple-trait analysis. In addition, the parameters from linear models do not need to be transformed in the final selection index. A modification of the GIBBSF90 programme using the MCMC approach accomplished the implementation of a linear model considering both censored and non-censored data and was therefore used within the final data analysis of this project.

Ewe lambs were assessed for a number of growth and type traits (four different trait groups: growth/carcass, mouth scores, face colour/hair scores and overall type traits). The data set consisted of 1,797 records of Mule ewes for each growth and type trait, and the longevity of these ewes was recorded. Longevity was defined as the time in years from 2 years of age (equivalent to the age at first lambing for most ewes) to the age at culling or death. The censored data comprised 24% of the total longevity records. Bi-variate analyses were used to analyse ewe longevity with each growth and type trait by fitting linear Bayesian models considering censoring. The genetic-statistical model of longevity included as fixed effects year-farm of culling (21 levels - 7 years x 3 farms), and dam breed (SBF or HSF). The estimates of heritabilities, as well as the genetic correlations between longevity and objectively and subjectively assessed traits in Mule ewes, are presented in Table 12.

The heritability of longevity was 0.27 and its 95% highest posterior density interval (HPD) ranged from 0.22 to 0.33. The heritabilities of the growth traits were low to high and ranged from 0.11 for the average of shoulder, loin and gigot conformation to 0.39 for live weight at first mating. Type traits showed heritabilities in the range from 0.13 for jaw position to 0.52 for face colour. However, the genetic correlations between ewe longevity and both growth/carcass and type traits were low and ranged from 0.17 to -0.23. The HPD intervals of these correlations included zero so that all of these correlations were not significantly different from zero.

Table 12. Posterior means of the heritabilities of ewe longevity and of growth/carcass traits, mouth scores, face colour/hair scores and overall type traits as measured in Mule ewe lambs at selection in October (approx. 6 months age) or at first mating (approx. 18 months age).

Trait	Heritability (HPD95%†)	Genetic correlation (HPD95%†) to ewe longevity
Ewe longevity	0.27 (0.22 to 0.33)	
Growth/carcass traits of ewe lambs		
Live weight at assessment in October (kg)	0.14 (0.03 to 0.25)	-0.01 (-0.40 to 0.41)
Ultrasonic muscle depth at third lumber position (mm)	0.16 (0.06 to 0.28)	-0.08 (-0.45 to 0.28)
Ultrasonic fat depth at third lumbar position (average of three measurements)	0.24 (0.11 to 0.39)	-0.09 (-0.43 to 0.23)
Average of shoulder, loin and gigot conformation scores in live animals - scale 1 (poor) to 6 (excellent)	0.11 (0.03 to 0.19)	-0.15 (-0.65 to 0.36)
Growth/carcass traits prior to first tupping (at approximately 18 months)		
Live weight at first mating (kg)	0.39 (0.18 to 0.60)	0.05 (-0.24 to 0.35)
Body condition score at first mating – scale 1 (too lean) to 5 (overly fat)	0.23 (0.12 to 0.35)	-0.10 (-0.47 to 0.24)
Ultrasonic muscle depth at first mating (mm)	0.22 (0.09 to 0.35)	-0.20 (-0.60 to 0.19)
Ultrasonic fat depth at first mating (mm)	0.31 (0.16 to 0.47)	-0.01 (-0.35 to 0.31)
Mouth scores of ewe lambs		
Jaw position – scale –5 (lower jaw 5 mm back from upper jaw) to +5 (5 mm in front of upper jaw)	0.13 (0.03 to 0.23)	0.05 (-0.45 to 0.53)
Tooth angle – scale –3 (45o forward) to +3 (45o back)	0.21 (0.10 to 0.32)	0.17 (-0.16 to 0.52)
Tooth length – scale –2 (very short) to +2 (very long)	0.32 (0.17 to 0.49)	0.07 (-0.21 to 0.38)
Face colour/hair scores of ewe lambs		
Face colour – scale 0 (no pigmentation) to 6 (black head colour)	0.52 (0.34 to 0.72)	-0.06 (-0.28 to 0.15)
Face colour distinction – scale 1 (very blotchy) to 5 (very distinct)	0.34 (0.21 to 0.49)	0.05 (-0.21 to 0.33)
Degree of covering of short hair in face – scale 0 (bare skin) to 5 (80-100% hair)	0.21 (0.09 to 0.34)	-0.23 (-0.62 to 0.13)
Overall type traits of ewe lambs		
Style or breed type – scale 1 (poor) to 10 (ideal)	0.23 (0.11 to 0.38)	-0.06 (-0.42 to 0.31)
Fleece quality and uniformity throughout the body – scale 1 (poor) to 10 (ideal)	0.37 (0.15 to 0.61)	0.07 (-0.23 to 0.36)
Structural soundness – scale 1 (poor) to 10 (ideal)	0.23 (0.09 to 0.38)	-0.08 (-0.45 to 0.33)

†95% highest posterior density (HPD95%) intervals are in parenthesis

The linear model used, which considers censoring, allows for a straightforward implementation of multiple-trait analysis of longevity together with other traits (production, reproduction and type traits). The parameters based on a linear model do not need to be transformed in the final selection index. The relatively high heritability estimated for longevity of Mule ewes may be due to the use of the same scheme of culling at all three sites, the exact recording of all culling decisions, and the consistent husbandry practices at the experimental farms. Due to its moderately high heritability, selection for longevity would allow for its rapid genetic improvement. Since the genetic correlations of longevity with growth/carcass and type traits were all low and non-significant, genetic gains in longevity may be achieved without adverse consequences on these other traits. However, this also means that measures routinely collected, such a live weights and ultrasonic measures, or that could be measured in young sheep, such as type traits, cannot be used as proxies for longevity. Incorporating longevity into selection programs will require measuring longevity directly in purebred longwool flocks.

Genetic parameters for pre-tupping weight, litter size and lamb survival at birth in Mule ewes calculated using Bayesian multiple-trait linear-threshold model

Threshold models have been shown to be more appropriate for the analysis of categorical or binary traits. The inclusion of a correlated continuously measurable trait in a multiple-trait linear-threshold model improves the stability of the estimates of categorical threshold traits. Additionally, the efficiency of the threshold model is increased by the inclusion of a continuously distributed trait in the model. Lamb survival (one for alive and zero for dead) can be treated as a trait of the lamb or a trait of the ewe, but most appropriately as a trait of both the lamb (direct genetic effect) and ewe (maternal genetic effect) simultaneously in one genetic threshold model. Careful investigation of the genetic covariance between direct and maternal effects of lamb survival is needed before a negative or positive genetic correlation between these effects is used in the genetic evaluation. Negative or positive genetic correlations may be an artefact due to the data structure (large in-depth pedigree information with records on the trait of interest is necessary to disentangle direct and maternal effects) or sire by year interactions as reported by many authors.

About 5,400 observations of litter size at birth (number of lambs born per ewe lambing) and pre-tupping weight were available from 1,756 Mule ewes repeatedly measured from 2000 to 2004. Data of lamb survival at birth were recorded on 10,128 offspring from these Mule ewes. Litter size and lamb survival at birth were fitted in the model because of their categorical expression as threshold traits, whereas pre-tupping weight with its continuously measured observations was fitted as a linear trait. Fixed effects included in the model were farm-year of lambing (15 levels) and parity-age of ewe at lambing (9 levels). Mule genotype (Scottish Mule or Welsh Mule) was additionally included for analyses of litter size and pre-tupping weight. For analyses of lamb survival, sex of lamb (2 levels) and lamb genotype (6 levels based on 2 different Mule genotypes and 3 different sire breeds) were fitted instead.

Preliminary analysis on simulated data sets, using the same pedigree and data structure of the studied data and assuming different genetic correlations (negative, positive, low, high) between the direct and maternal genetic effects, resulted in all cases (even for high positive genetic correlation) in negative estimates of genetic correlations between direct and maternal effects. This indicates that, based on the structure of the data with limited pedigree and performance information over generations, in particular on the maternal side, it is not possible to reliably estimate the correlation between direct and maternal genetic effects for lamb survival. Therefore, the direct and maternal genetic effects of lamb survival at birth were assumed to be uncorrelated and set to zero in the present analysis. In contrast, the data structure did not affect estimates of genetic correlations between genetic effects of lamb survival and those of litter size or pre-tupping weight, so that these correlations have been estimated from the actual data.

The residual covariances between survival at birth and litter size or pre-tupping weight were assumed to be zero because the former trait was measured on lambs and the latter two traits were measured on the Mule ewes. Estimates of the heritabilities and genetic and residual correlations of these traits are presented in Table 13. Of these traits, pre-tupping weight showed the highest heritability at 0.46. The heritability of litter size was low at 0.12 but clearly within the range found in the literature. For lamb survival, the maternal heritability (0.14) was twice as high as the direct heritability (0.07). Both heritabilities were significantly different from zero so that it was necessary to fit a direct and maternal genetic effect for lamb survival. Both effects can then be simultaneously improved by selection.

The total heritability can be calculated as:

$$h_T^2 = (\sigma_a^2 + 1.5\sigma_{am} + 0.5\sigma_{\mathbf{m}}^2)/\sigma_T^2$$

where h2T is the total heritability, σ2a and σ2m are the additive genetic variance of direct and maternal effects, respectively, σam is the covariance between the direct and maternal genetic effects and σ2T is the total phenotypic variance. As the covariance between direct and maternal effects of lamb survival has been assumed to be zero, the total heritability is the sum of the direct heritability and one half of the maternal heritability. In the present study this is 0.14.

Table 12 Residual correlations (above diagonal), heritabilities (on diagonal; bold) and genetic correlations (below diagonal) for litter size at birth, pre-tupping weight, and direct and maternal effects of lamb survival at birth†

Trait	Litter size	Pre-tupping weight	Survival (direct)	Survival (maternal)
Litter size	0.12 (0.07 to 0.18)	0.05 (0.03 to 0.08)	0	0
Pre-tupping weight	0.10 (-0.09 to 0.30)	0.46 (0.35 to 0.57)	0	0
Survival (direct)	-0.23 (-0.71 to 0.27)	0.19 (-0.32 to 0.67)	0.07 (0.03 to 0.11)	0
Survival (maternal)	-0.38 (-0.67 to –0.06)	-0.48 (-0.72 to –0.24)	0	0.14 (0.09 to 0.20)

†95% highest posterior density (HPD95%) intervals are in parenthesis

The genetic correlation of litter size and pre-tupping weight was positive as shown in Table 13. Moderate unfavourable genetic correlations were estimated between maternal genetic effects of lamb survival and litter size and pre-tupping weight, which were both significantly different from zero. Also a small negative genetic correlation was estimated between direct genetic effects of lamb survival and litter size, but this was not significantly different from zero. Although the genetic correlation of direct genetic effect of the lamb survival and pre-tupping weight was positive, it too was low and not significantly different from zero. The residual (phenotypic) correlation between litter size and pre-tupping weight was also low and positive but again was not significantly different from zero.

The ratio of permanent environmental variance to phenotypic variance due to repeated observations of litter size was low at 0.10, and slightly lower than its heritability of 0.12. The ratio of permanent environment to phenotypic variance for pre-tupping weight was substantially lower than its heritability (0.22 vs. 0.46). Litter environmental effects showed a strong influence on lamb survival at birth and accounted for 42% of the total phenotypic variation.

Genetic parameters of faecal egg counts in peri-parturient Mule ewes
A single faecal sample was collected from all ewes at housing (approximately 6 weeks prior to lambing) over five years from 2000 to 2004 for the Mule ewes at IRS and ADAS, providing a minimum of 3 and a maximum of 5 samples per ewe for those ewes remaining in the breeding flock. These data were analysed using a repeatability model, including all significant fixed effects (ewe age, ewe breed, ewe condition score, birth type, site, year and the site-by-year interaction).

Mean FEC at housing was low at 50 eggs/g, and the results of the analysis presented in Table 14 (attached) show that two-year old (first parity) ewes had significantly ($P < 0.001$) higher FECs, with no significant difference between animals aged between three and six-years of age. Breed of dam also had a significant effect on FECs, with Mule ewes out of Hardy Speckled Face dams having lower FECs than Mule ewes out of Scottish Blackface dams, though the magnitude of the difference was not large. Ewes in poorer condition at housing had significantly ($P < 0.001$) higher mean FEC, and ewes carrying multiples had significantly ($P < 0.001$) higher mean FEC than those carrying singles. Large differences ($P < 0.001$) were found between years, with higher FECs in 2001 and 2003 compared to the other three years. In each year the FECs were significantly ($P < 0.001$) higher at ADAS compared with IRS, and site differences were particularly large in 2001 and 2003, giving rise to a significant year-by-site interaction.

The heritability estimate when all FECs collected at housing over the 5 years were included in the model was 0.21 (s.e. 0.06) and the repeatability of the trait was 0.38 (s.e. 0.04). A blood sample for analysis of plasma IgA and IgE concentrations (immunoglobulins thought to be involved in parasite resistance of sheep) was taken at the same time as faecal samples from all ewes. However, the genetic correlations between plasma immunoglobulins and FECs were low and generally not significantly different from zero, indicating that these parameters cannot realistically be used as a proxy measure for parasite resistance.

Relationships between FECs and production traits of Mule ewes
Table 15 presents the results of analyses to investigate relationships between housing FECs and production traits in Mule ewes. The phenotypic correlations between housing FEC and production traits were low but favourable and some were significantly different from zero. Similarly, the direction of the genetic correlations between FEC and production traits were also favourable (negative), but none were significantly different from zero due to their large standard errors.

Table 15. Phenotypic and genetic correlations between ewe live-weight at housing, total litter birth weight, ewe live-weight at 5 weeks post-lambing, ultrasonic fat depth and ultrasonic muscle depth at five weeks post-lambing and FECs in Mule ewes calculated using a repeatability model. Standard errors are shown in parentheses.

	Phenotypic correlation	Genetic correlation
Ewe live weight at housing	-0.04 (0.03)	-0.33 (0.27)
Litter weight at birth	-0.02 (0.03)	-0.30 (0.34)
Ewe live weight 5 weeks post-lambing	-0.06 (0.03)*	-0.32 (0.28)
Ewe ultrasonic fat depth 5 weeks post-lambing	-0.15 (0.03)***	-0.03 (0.28)
Ewe ultrasonic muscle depth 5 weeks post-lambing	-0.09 (0.03)***	-0.25 (0.29)

*P<0.05, **P<0.01, ***P<0.001.

Relationship between FECs in lambs and in the same animals as late pregnant ewes

The phenotypic and genetic correlation between FECs in lambs at 14 and 18 weeks of age (when treated as a single repeated trait) and FEC in the same animals as mixed aged ewes (between three and six years of age) are presented in Table 16. None of the estimates were significant at 14 weeks of age, but at 18 weeks of age the genetic correlation with FEC in the same animals as adult ewes was high and statistically significant.

Collectively, these results indicate that FEC at approximately 6 weeks before lambing is a heritable trait, and, since the genetic correlation between lamb and adult FECs is favourably high (genetic correlation = 0.59), these results suggest that progress in reducing faecal egg counts of ewes during the pre-parturient period should be possible by selecting for reduced FEC in purebred longwool crossing sire sheep. Lower levels of pasture contamination from more resistant ewes should reduce the levels of infection to which their terminal sire-x lambs are exposed, with benefits of improved performance and reduced anthelmintic requirement.

Table 16. Parameter estimates for Log10 (FEC+20) collected at 14 and 18 weeks of age from Mule ewe lambs with Log10 (FEC+20) collected from the same animals during the peri-parturient period (housing and lambing) at two years of age. Standard errors are shown in parentheses.

	Phenotypic correlation	Genetic correlation
14 weeks of age	0.01 (0.05)	-0.17 (0.33)
18 weeks of age	0.14 (0.04)***	0.59 (0.28)*

*P < 0.05, ***P < 0.001.

Development of the Longwool selection index

Breeding goal and selection criteria

The main objective of the Longwool project is the development of a multiple-trait selection index for improving carcass quality of crossing sire sheep and their crossbred progeny without compromising reproductive performance and maternal ability in these breeds. A selection index combines all traits depending on their economic importance in order to provide an overall assessment of an animal's genetic merit. In order to design any selection index it is necessary to define: (i) which traits should be genetically improved (the breeding goal); (ii) what traits are or will be measured (the selection criteria); (iii) how the criteria being measured are genetically and phenotypically related to the breeding goal (i.e., heritabilities, correlations); and, (iv) the economic importance of each trait in the breeding goal. Breeding goal traits in Mule ewes, and the selection criteria of BFL, are shown in Table 17.

Table 17. Breeding goal in Mule ewes and selection criteria of Bluefaced Leicester

Category	Variable	Definition	Units
Criteria (in BFL)	bSLW	Live weight at scanning (at constant scanning age)	kg
	bUMD	Ultrasound muscle depth (at constant scanning age)	mm
	bUFD	Ultrasound fat depth (at constant scanning age)	mm
	bCONF	Leg conformation (at constant scanning age)	points
	bPTLW	Ewe replacement live weight at 18 month pre-tupping	kg
	bSURVd	Lamb survival direct additive effect (trait of lamb adjusted for litter size)	0,1
	bSURVm	Lamb survival maternal additive effect (trait of lamb adjusted for litter size)	0,1
	bLS	Litter size (number born)	count
	bLONG	Ewe longevity	year
Goal (in Mule)	mSLAGE	Slaughter age (at constant estimate SQ fat%)	day
	mCONF15	15-point conformation score (at constant estimate SQ fat%)	points
	mLNWT	Lean weight (at constant estimate SQ fat%)	kg
	mPTLW	Ewe mature pre-tupping live weight (after first lambing)	kg
	mSURVd	Lamb survival direct additive effect (trait of lamb adjusted for litter size)	0,1
	mSURVm	Lamb survival maternal additive effect (trait of lamb adjusted for litter size)	0,1
	mLS	Litter size (number born)	count
	MLONG	Ewe longevity	year

Genetic and environmental parameters

Because of the high number of traits, the complexity of the genetic models fitted, and the structure of the purebred (BFL) and crossbred (Mule) data, it was necessary to conduct the analysis in several steps. The genetic analyses of BFL lambs (SLW, UMD, UFD and CONF) and of Mule wether lambs (SLAGE, CONF15 and LNWT) were obtained using a multiple-trait analysis. All other genetic parameters were obtained by bi-variate analyses between traits. Since the genetic variance-covariance matrix was not positive definite, the bending technique was used to obtain a positive definite matrix. This matrix is necessary to develop a selection index and to estimate breeding values. The genetic parameters after bending are presented in Table 18 (attached). Selection traits were recorded on BFL sheep and breeding goal traits were recorded on Mule sheep. The performance traits of BFL lambs showed heritabilities in the range of 0.28 for conformation to 0.37 for slaughter weight. All of these traits had high genetic correlations with slaughter weight and moderate correlations among each other. Heritabilities for performance traits measured on Mule wether lambs were generally lower and in the range from 0.12 for conformation to 0.36 for lean weight. In addition, the genetic correlations among these traits were low, in the range from 0.05 to 0.32.

Pre-tupping weight of Mule ewes showed the highest heritability (0.45) of all analysed traits. For BFL, pre-tupping weight has not been recorded so genetic parameters from the literature had to be used. Low heritabilities were estimated for direct and maternal genetic effects of lamb survival and litter size of Mule ewes and were in the range from 0.02 to 0.05. Because preliminary analyses of the present data had shown that the genetic correlation between direct and maternal genetic effects of lamb survival cannot be estimated accurately (see earlier section), the correlation was set to zero in these genetic analyses. Longevity showed a moderate heritability (0.30) based on the Mule ewe data, and can therefore be efficiently improved by genetic selection. Because lamb survival and longevity are not currently recorded in the BFL, the same estimates as those obtained for Mule ewes were assumed for the development of the selection index. Also, the genetic correlations between lamb survival and longevity in the BFL with the corresponding traits in Mule ewes were taken from the literature.

Phenotypic variances of the index traits are shown in Table 19 (attached). Only some traits were influenced by the litter effect. The phenotypic fraction of the litter variance was low for performance traits measured on BFL lambs (0.07 to 0.09) but substantially higher for Mule wether lambs, ranging from 0.14 to 0.33. For lamb survival, the ratio of environmental litter to phenotypic variance was 0.21, much higher than the total heritability of this trait (0.05). For litter size a repeatability model was fitted for the repeated litter records of each ewe, so that permanent environmental variance had to be estimated. The contribution of the permanent environmental effect of litter size as a proportion of phenotypic variance was 0.01 for BFL and 0.09 for Mule ewes.

Derivation of economic values

Economic values for goal traits in the crossbred descendants of crossing sire sheep (both Mule/Halfbred and terminal sire cross) were calculated, based on modelling the performance of Mule sheep recorded within the project. These economic values were expressed in pounds (£) per unit change in the goal trait. These economic values reflect the ‘true’ economic returns generated by genetic change in the individual traits in the breeding goal. Economic values were derived for three carcass traits (days to finish, weight of lean in the carcass, and carcass conformation score) assuming lambs were slaughtered at a target percentage of subcutaneous fat in the carcass. Economic values were calculated separately for three factors affected by ewe mature weight, including annual ewe maintenance feed requirements, cull ewe value, and feed costs to rear replacements. Economic values were also calculated for number of lambs born per ewe lambing, for lamb survival, and for ewe longevity. Ewe longevity is defined as the average age in years at which a female sheep leaves the flock. It is modelled to reflect a distribution of animals that are culled or die over a range of ages. By increasing survival rates from one age to the next, an improvement in longevity occurs.

Litter size

The economic value of litter size was shown to be highly dependent on the current average value for lambing percentage in commercial flocks. This relationship is identified in Figure 1 where the solid line plots the increase in economic returns ('net profit') for an additional lamb born when triplet survival is 0.69 (as recorded in the current project). The broken line shows what the relationship would be if triplet lamb survival declined from 0.69 to 0.55 in a given flock. For such a flock, having a current average litter size of 193% (as for mature ewes in the current project), the economic value of additional lambs born per ewe lambing would be zero, and so the current lambing percentage would be optimum. This example illustrates that with only a modest deterioration in triplet survival from that recorded in the current project, the economic value of increasing litter size becomes zero.

Discounted genetic expressions

Discounted genetic expressions coefficients are used to translate economic values for genetic traits which differ in their timing and frequency of expressions onto a common basis for comparison. The basis for comparison used here relates to the expression of genes of a commercial crossing sire purchased for mating within a hill flock to produce crossbred ewes. The equations of Amer (1999) were adapted for this purpose by separating the expression of genes affecting lamb traits into expression in Mules/Halfbreds and expression in their terminal sire cross lambs. The parameters used in the equations were adapted to be relevant to the UK sheep industry. Rams were assumed to be mated to 60 ewes for a maximum of three years, but with 18% of breeding rams lost successively in the second and third years after mating to give an average of 2.5 years per commercial ram purchased.

Formulation of economic weights for goal traits

The economic weights are the weights applied to estimated breeding values for goal traits in the index. They are formulated by multiplying trait economic values with appropriate discounted genetic expressions coefficients. Aggregate economic weights for the individual goal traits are obtained by combining the expression of genes in Mule/Halfbred and their terminal sire cross lambs. Traits typically differ in economic weight due to differences in units of measure (e.g., kg, lamb) and in the amount of genetic variation they possess. By multiplying the aggregate economic weight by genetic standard deviations such differences are effectively removed providing a better indication of a goal trait's relative importance in the index. Such standardized weights are shown in Table 20.

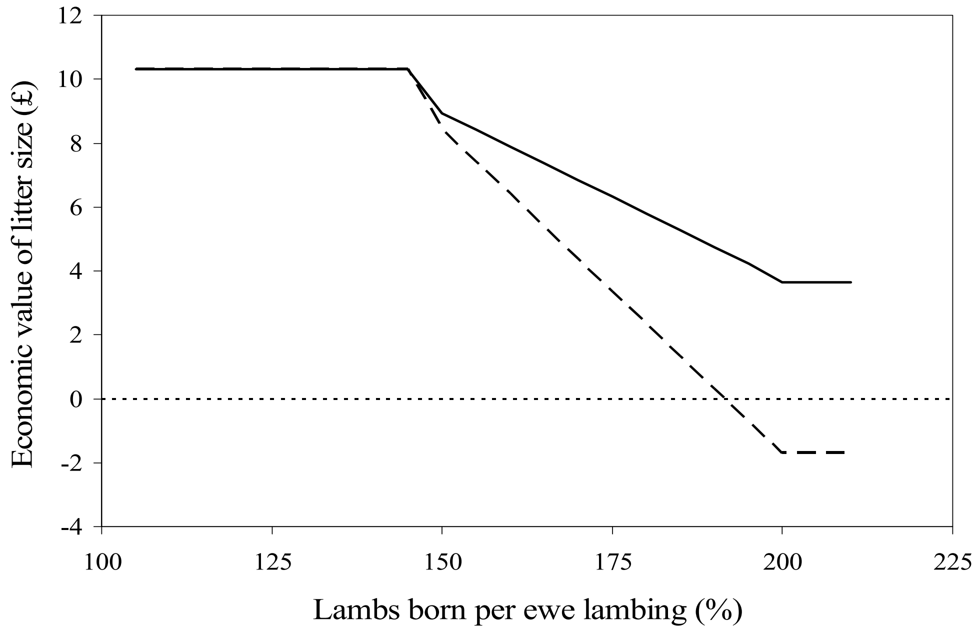

Figure 1. Relationship between mean lambing percentage and the economic value of litter size in Mule/Halfbred ewes

Table 20. Standardized economic weights for goal traits in Mule/Halfbred and their terminal sire cross sheep

Goal trait	Aggregate econ. wt. (£)	h2 †	Phen. var.	Gen. S.D.	Standard. weights (£)
Days to target finish	-0.068	0.23	2784	25.44	-1.7
Lean weight (kg)	5.87	0.36	1.1	0.62	3.6
Carcass conf. score (15-point scale)	0.55	0.12	1.1	0.37	0.2
Ewe mature weight (kg)	-0.50	0.45	48	4.6	-2.3
Lamb survival, direct (lamb)	38.82	0.04	0.09	0.056	2.2
Lamb survival, maternal (lamb)	15.56	0.02	0.09	0.044	0.7
Litter size (lamb)	4.70	0.05	0.30	0.13	0.6
Mule ewe longevity, 1-year increase (ewe lambing)	11.20	0.30	1.5	0.67	7.5

† Heritability.

Mule ewe longevity followed by lean weight were shown to be the most important goal traits in the index, with carcass conformation score least important. Litter size also has a relatively low value, implying that the crossbred ewes are already close to their economically optimal lambing percentage. Maternal lamb survival is also of relatively low importance, mainly because maternal traits are not expressed in the lambs of the crossing sires at their birth. The maternal traits are only expressed when female lambs join the crossbred ewe flock.

Expected responses in goal traits when selecting young (unproven) rams on the index

Selection index calculations based on conventional selection index theory were set up using parameters (genetic and phenotypic variance covariance matrices) provided by the project. The following assumptions were made to correspond to a crossing sire breeding programme that exclusively uses young crossing sire rams (i.e., no progeny information at time of selection) to mate crossing sire ewes in the breeding programme:

- selection candidates have their own record for scan live weight, ultrasonic muscle depth and ultrasonic fat depth;
- selection candidates have information for scan live weight, ultrasonic muscle depth and ultrasonic fat depth from 20 half sibs;
- selection candidates have information for direct lamb survival from 40 half sibs;
- selection candidates have information for ewe live weight, maternal lamb survival and litter size (all repeated twice) and ewe longevity from their mother (note that with censored survival genetic evaluation approaches, a ewe having survived to a second or third lambing has a significant amount of information on her survival);
- selection candidates have information for ewe live weight, maternal lamb survival and litter size (all repeated twice) and ewe longevity from 5 half sisters of their mother;
- males are selected from the top 5% of all ram lambs born and evaluated based on the above information sources.

As the base scenario, no leg conformation information is available. Table 21 (attached) shows the expected superiority of the top 5% of selected males over the average of all males born in the same year in trait units and economic increments. The majority of benefits of genetic progress come from improvements in the weight of lean in crossbred lambs (both Mule/Halfbred and terminal sire cross) and in Mule/Halfbred ewe longevity. A reduction in ewe mature size is expected with selection on the index. Table 22 also shows some perturbations on the traits actually recorded. Notably, dropping ewe live weight, or adding leg conformation score, as selection criteria (recorded traits) makes minimal difference to the overall economic response to selection. However, when scanning traits in addition to ewe live weight are dropped as selection criteria, the impact is more severe, as is the case with dropping ewe longevity.

Expected responses in goal traits when selecting extensively used (proven) stock sires

The following assumptions were made to correspond to a crossing sire type breeding programme which exclusively uses proven crossing sire rams (progeny information for both lamb and ewe traits at time of selection) to mate to crossing sire ewes in the breeding programme:

- selection candidates have their own record for scan live weight, ultrasonic muscle depth and ultrasonic fat depth;
- selection candidates have information for scan live weight, ultrasonic muscle depth and ultrasonic fat depth from 80 progeny;
- selection candidates have information for direct lamb survival from 80 progeny;
- selection candidates have information for ewe live weight, maternal lamb survival and litter size (all repeated twice) from 30 daughters and ewe longevity from 15 daughters; and
- males are selected from the top 5% of all ram lambs born and evaluated based on the above information sources.

As the base scenario, no leg conformation information is available. Table 22 (attached) shows the expected superiority of the top 5% of selected males over the average of all males born in the same year in trait units and economic increments. With daughter information available, Mule ewe longevity becomes the economically dominant trait in the index, with direct lamb survival, ewe mature weight and weight of lean of secondary importance. As for the unproven ram scenarios considered in the previous section, there are negligible economic benefits from recording leg conformation score or ewe mature weight. When ewe mature weight is not recorded, the expected reduction in ewe mature weight with selection on the index is decreased.

It is possible to derive the proportion of economic benefits from genetic change accrued in hill versus Mule/Halfbred flocks, assuming that there is no premium paid for replacement Mule ewes bred by proven sires. The proportion of benefits accruing to hill flock owners is 20% for the unproven sire breeding programme, and 13% for the combined proven and unproven sire breeding programme. The higher proportion of benefits to Mule/Halfbred flock owners with the combined proven and unproven sire breeding programme reflects the importance of genetic progress in Mule/Halfbred longevity achieved when selecting among proven sires.

Cumulative benefits of selection over 10 years results in 37 times the benefits from a single year's selection returned in one year when a discount rate of 7% is assumed. However, there is delay before benefits from genetic merit accrued in crossing sire flocks are realised in the commercial Mule/Halfbred and terminal sire cross sectors. This delay is assumed to be on average 6 years. That length of time is necessary for lambs born in crossing sire flocks to become old enough for sale as commercial breeding rams, for their progeny to be born and, subsequently, for their daughters to be kept as replacement Mule/Halfbred ewes. A delay of 6 years with a discount rate of 7% reduced benefits to 66% of what they would be if they were obtained immediately. Finally, it is necessary to account for the fact that only one half of the genes of sires in the crossing sire breeding programme are transferred to the commercial sector.

If it is assumed that 3.9 million hill ewes are mated by crossing sire rams each year, if each of these matings generates 0.45 Mule/Halfbred lambs suitable for breeding, and if each Mule/Halfbred ewe averaged three lambings per lifetime, we calculate an industry of approximately 5.3 million Mule/Halfbred ewes lambing per year. Thus 5.3 million multiplied by 37 for 10 years cumulative benefits, multiplied by 0.66 to account for delays, and by 0.5 to account for Mule/Halfbred ewes containing one-half of the genes of the crossing sire breed divided by 3 to account for the three lambings of the Mule/Halfbred ewes, generates approximately £21 m/year (in present value terms) with the unproven crossing sire breeding programme scenario. The equivalent value if breeders were to use a combination of proven and unproven sires in their purebred crossing sire flocks would be a present value of approximately £30.4 m

This calculation does not account for costs for recording and genetic evaluation. A performance recorded breeding population of 47,000 crossing sire type ewes should be sufficient to generate the crossing sire type rams needed to service an industry of this size. This is based on assumptions that:

- 0.4 crossing sires are generated per crossing sire ewe mated;
- breeding rams survive at a rate of 0.8 per year from one breeding season to the next with a maximum working life of 4 years; and,
- 40 commercial females are mated per male.

If Signet/MLC membership costs of £8.50 per ewe in a recorded flock are used to reflect the costs of performance recording and genetic evaluation, then costs to achieve the genetic improvement would be approximately £400,000. Over the ten years, and at a discount rate of 7%, the full cost of recording would be £3.0 m. These costs would be incurred by the crossing sire sheep breeders.

The above calculations assume 100% adoption of performance recording and use of the index in crossing sire flocks. The estimated costs and benefits are directly proportional to the adoption rate. The adoption rate for performance recording in the crossing sire breeding industry is currently estimated to be approximately 10%.

In summary, at a 100% adoption rate, the cumulative present value of benefits from 10 years selection on the index would range between £21 m (unproven sires) and £30 m (mixture of proven and unproven sires) with recording and genetic evaluation costs incurred by the breeders of £3 million. Approximately 13-20% of the benefits will be captured by hill sheep flock owners, with the remaining majority being captured by Mule/Halfbred ewe flock owners.

Conclusions

The primary aim of this research project was to provide the necessary information (heritabilities, genetic and phenotypic correlations of important traits) to underpin the development of a multi-trait selection index tailored to the longwool crossing breeds. The aim of that index was to improve the carcass quality of their crossbred progeny without compromising important maternal characteristics of their Mule/Halfbred daughters, which dominate the lowland sector of the UK sheep industry. The BFL and its Mule progeny were used as the model. Following the establishment of a Sire Referencing Scheme within the BFL breed involving 13 industry flocks detailed performance recording was undertaken to derive genetic parameters for important traits, and to supply performance recorded crossing rams, representing the spectrum of carcass traits, for detailed progeny testing involving both growth/carcass and maternal traits of their Mule progeny.

Based on all of the information collected, and modelling of the economic importance of the different traits in Mule progeny and their terminal sire-x lambs, an economic selection index has been derived specifically for use within the longwool crossing breeds. Ewe longevity was shown to be the dominant trait within the index, especially when a combination of 'proven' (own records plus progeny records available) and 'unproven' (own performance records only available) sires are used within the purebred longwool crossing sire flocks, and was also shown to be moderately heritable. Litter size was already close to the economic optimum in Mule sheep. Widespread adoption of this new index within the longwool crossing breeds has the potential to increase returns by £21 m to £30 m after 10 years of selection through a combination of improved carcass quality, increased ewe longevity and enhanced lamb survival. At present, ewe longevity and lamb survival are not routinely collected in the BFL Sire Referencing Scheme, and changes to recording will need to be implemented to maximise the usefulness of the index.

Parasite resistance has not been included in the index because of difficulties in estimating its economic worth relative to the other traits. However, since the results suggest that it is a heritable trait, selection for reduced FEC is possible. Instead of including it in the selection index, it is suggested that a separate estimated breeding value for FEC be calculated, and that selection decisions within the purebred longwool crossing breeds be based on the combination of high index scores and low FEC estimated breeding values.

The project has been overseen by a Project Steering Committee made up of sponsors, development agencies and producers throughout its duration, and more detailed data originating from the project are contained in the annual reports provided to Committee members. Not only did the Steering Committee ensure that the project remained focussed on the needs of the industry and that the objectives were being met, but it also has provided a forum for knowledge transfer to the industry. The new index parameters have been provided to Signet for use in their Sheepbreeder service, and discussions have already been held to promote the index to the BFL Sheepbreeders Association. The demonstrated importance of ewe longevity from the study, its moderate heritability and its inclusion in the economic selection index was acknowledged by them to provides both a unique selling point for Mule/Halfbred producers and a way to protect their market share into the future, meaning that the new index was received very positively by the breeders.

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