

**The genetic improvement of carcass and maternal traits in
Scottish Blackface sheep**

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Declaration

I declare that this thesis is my own composition except where otherwise stated, and does not include work submitted for any other degree or qualification. The thesis reports on analyses done by me, and the data were collected by myself, or by other staff members of SAC. Chapters 2 and 3 have been published and are appended to this thesis.

Joanne Conington
July 1999

Dedication

This thesis is dedicated to the memory of Rebecca Stott (1973 - 1996).

Abstract

This thesis addresses the issues of genetic improvement of carcass and maternal traits in hill sheep. It i) compares the performance of two genetic lines of Scottish Blackface lambs divergent for subcutaneous fat, ii) quantifies the genetic components of carcass traits in extensive hill environments, iii) explores the implications of selecting for reduced fatness in hill lambs, iv) develops and describes methods to include carcass traits in the breeding goals for hill sheep, and v) gives predicted results from index selection for maternal and carcass traits, using indexes of overall economic merit.

For points i) to iii), approximately 2000 Scottish Blackface lambs were measured, sired by 32 rams divergent for subcutaneous fat depth, and born to 1660 unselected ewes in 1991 and 1992. They were reared under extensive conditions on two contrasting hill farms. Results showed that genetic differences in subcutaneous fatness arising from selection in an intensive environment are still expressed despite harsh rearing environments. Heritabilities (and standard errors) for birth weight, marking weight (at approximately 6 weeks of age) and weaning weight (at 17 weeks) were 0.07 ± 0.04 , 0.02 ± 0.03 , and 0.14 ± 0.05 , respectively. Heritabilities for ultrasonic muscle and fat depth were 0.27 ± 0.09 and 0.16 ± 0.06 , respectively. Heritability estimates for carcass traits were: pre-slaughter liveweight 0.36 ± 0.13 , cold carcass weight 0.39 ± 0.14 , fat class 0.13 ± 0.08 , conformation score 0.09 ± 0.07 , dissected lean weight 0.27 ± 0.27 , dissected bone weight 0.36 ± 0.13 (constant subcutaneous fatness), dissected intermuscular fat weight 0.10 ± 0.07 , subcutaneous fat weight 0.20 ± 0.09 (constant cold carcass weight). There was a strong maternal effect on live weight which declined with age from birth onwards. The rearing environment of the lambs was an important environmental effect on the heritability estimate for backfat thickness, being twice as large for animals reared on the improved pasture compared to those reared on hill pasture. Results indicate that selection for improved carcass traits is feasible,

but responses to selection are likely to be lower in more extreme (harsh) environments.

Incorporating the experimental results into breeding goals and estimating appropriate relative economic values was achieved by means of bioeconomic whole-farm modelling. To account for the diverse farm systems in the hill sector, three different hill farm types were modelled: an intensive hill farming system, a semi-intensive system and an extensive system. Pasture availability and offtake for hill and reseeded pastures throughout the year were integrated with dynamic programming techniques. This generated data for the derivation of economic values for 10 breeding goals, including maternal traits, carcass traits, and 'sustainability' traits (improving longevity and reducing lamb losses). Results showed that the extensive farm had greater limitations to the improvement of performance compared to the intensive hill farm system, and that economic values depend on the level of production for a given trait. Improving the number of lambs reared beyond the capacity of the farm to accommodate genetic change is likely to result in zero or negative economic values for the extensive farm system. Sensitivity analyses of the economic values to changes in the prices of major inputs to the sheep system show that in general the economic values are robust. The three sets of economic values were used to derive three selection indexes for the hill sheep sector. The evaluation of these indexes showed that improvements in maternal traits are possible, along with more modest improvements in carcass traits. Responses to selection are expected to be lower for the extensive farm in general, compared to the intensive farm. Evaluations of alternative indexes show that a sub-optimal index using measurements of fat and muscle on ewes rather than on lambs may be more cost-effective to implement in practice, compared to the optimal index.

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Chapter 1

Introduction

Breeding goals

Sheep breeding is part of long-term farm production planning to change the genetic merit of animals so that they become more efficient. The efficiency of a sheep production system can be defined relative to an overall breeding objective, which in turn can be broken down into individual breeding goals. Breeding goals in sheep production systems can be characterised as production traits (e.g. the number of lambs reared per ewe, lamb carcass weight, fleece weight,) and traits which increase efficiency by reducing input costs rather than increasing output, (often referred to as 'functional traits' in cattle breeding (Groen *et al.*, 1997). Traits belonging to this category include lambing difficulty, milking ability, maternal behaviour, health, longevity, lamb survival, disease resistance and efficiency of feed utilisation.

The choice of breeding goals for sheep depends largely on their breed, location and preferences of the breeder. For example, the main breeding objective for terminal sire breeds (e.g. Suffolks, Texel and Charollais) is to produce heavier, leaner lambs. Breeding goals for 'maternal' breeds often depend on the environment in which they are reared. For example, increasing prolificacy would not be a major component of the breeding goal for Scottish Blackface sheep in the wet Western Highland region of Scotland, whereas it may be appropriate for the same breed reared in the Southern Uplands of Scotland. Other breeding goals for maternal breeds include litter size and milking ability, but improving lamb carcass characteristics as well as maternal traits has become important for some breeds, resulting in their breeding goals being more complex than that for terminal-sire breeds. With the growing consumer concern about how animals are reared and the perceived suffering from diseases and disorders which they succumb to, incorporating a balanced improvement of production and functional traits in the breeding objective would support consumer acceptance of lamb products and ensure that selection for production is not coupled with a deterioration in health or fertility.

Parameters

Some breeding goal traits are more easily improved than others. In general, the main factors affecting the rate of genetic gain are i) the heritability of the trait, ii) the selection differential, (i.e. the difference in mean performance of selected animals above the mean performance of the animals from which they were selected), and iii) the generation interval (i.e. the average age of parents when their offspring are born) (Simm, 1998). In a review of genetic and phenotypic parameters for the major breeding goal traits of sheep, Fogarty, (1995) reports the weighted mean heritabilities in live lambs from 30 published results for ultrasonic fat depth as 0.28, 0.31 for eye muscle depth from 24 published results, and 0.1 for litter size from 54 published estimates. In general, wool traits are easier to improve than fertility traits. For example, the average estimate of the heritability of mean fibre diameter is reported as 0.51 from 27 estimates, and 0.36 for clean fleece weight from 28 published estimates.

The choice of breeding goals for sheep should therefore take the heritability of the trait into consideration as, in general, traits with higher heritability estimates can be improved more readily than traits with lower heritabilities. When more than one trait is selected for simultaneously, the genetic and phenotypic correlations among them also affect the rate of response in each trait. With dual or multi-purpose sheep, it follows that with a high number of traits to be improved, there is a greater chance that one or more traits may be unfavourably correlated with another resulting in lower responses than if the traits are selected for individually.

Using selection index theory (Hazel, 1943), the weighted sum of genotypic values for several traits is used to represent the total genetic merit of an animal (or 'aggregate genotype'). These genotypic values are weighted by their relative contribution to the improvement of the breeding goal by the time and frequency

of future expression of genetic superiority for the trait (or ‘cumulative discounted expression’) and economic benefit at the moment of expression of genetic superiority for the trait (or ‘economic value’).

Economic values

Economic values often defined as the marginal profit resulting from a genetic change of one unit in a trait, for example, the increase or decrease in profit as a result of a 1 kg change in lamb live weight. Economic values are influenced by costs of production and prices received for products, and should be influenced by knowledge of likely future market and commodity price changes. Most calculations of economic values for individual traits are calculated at the animal, herd or farm level (Groen and Ruyter, 1990), and are rarely calculated at a national or sector level because of difficulties of methodology (Groen *et al*, 1997; Weller, 1994). It is also agreed that economic values calculated at a national level are too remote, as indexes need to be most relevant to the people using them (Amer, pers.comm.). The criteria for economic evaluation have been described as i) profit maximisation, ii) economic efficiency, iii) biological efficiency (defined as unit output per unit feed energy input), and iv) return on investment. The first two are arguably the same, the third option ignores the differing value of products e.g. meat from old versus young animals, and that it is possible to breed for increased economic efficiency without affecting biological efficiency. The fourth is difficult to justify for economic evaluation of individual trait changes (Weller, 1994).

In principle, the methods used to derive economic values are the same, but they differ in practice. Profit equations have been used to derive economic values for the main farm animal species (review by Harris and Newman, 1994). In their simplest form, economic values are defined as the change in marginal revenues minus marginal costs from a unit increase in a goal trait. If the relationship is linear, then the difference in monetary returns is equal to the partial derivative of

the relationship between increased performance and increased economic return. Profit equations are derived by describing a production system and solving the equations mathematically. Although essentially the same approach in principle, bio-economic (or 'multi-equation') models have been developed to simulate production systems which typify those for which the economic values are intended. Again, partial derivatives of the changes in revenue due to changes in simulated production are calculated as the economic values. The benefit of such models lies with the multitude of possibilities to apply different prices, production levels and size of production system. With complex production systems (such as multi-purpose sheep breeding systems) which vary according to production levels and physical constraints such as pasture quality, a model framework is arguably the most appropriate approach to deriving economic values.

Another approach to the derivation of economic values is to use linear programming. Essentially, linear programming determines maximum profit by optimising a production system. After a unit change in a goal trait, the system is re-optimised and the difference in profit after the change is defined as the economic value. However, linear programming breaks the ground-rules for the derivation of economic values as it does not hold other traits constant. Linear programming has been used to derive economic values for dairy cattle traits according to environmental policies (Steverink *et al.*, 1994) and for milk yield and herd life (Harris and Freeman, 1993).

Groen *et al.*, (1997) believed that it is not possible to come up with a 'best' method to derive economic values, because it depends on the trait in question and production circumstances. Most economic values reported for sheep breeding programmes have been derived by the profit equation approach (Jones, 1982; Simm *et al.*, 1987; Simm and Dingwall, 1989; Fogarty, 1987; Ponzoni, 1986; Ponzoni, 1987; Banks, 1990). Bio-economic models have been reported for

deriving economic values for ewe prolificacy and lamb survival in New Zealand sheep (Amer *et al.*, 1999), and for lamb and wool production (Wang and Dickerson, 1991).

Breeding programmes

Sheep breeding programmes using multi-trait economic selection indexes have been used for meat and dual-purpose breeds since the mid 1980s (Collins, 1999). In the UK, breeders using the Sheepbreeder recording scheme under the auspices of Signet, (the national organisation which undertakes genetic evaluations of sheep and cattle) have had a choice of four breeding goals: lamb growth, litter size, ewe mature size and maternal ability (lamb growth expressed as a trait of the ewe). These breeding goals are either used individually or weighted by different economic values to give different selection indexes. More recently, ultrasonic measurements of fat and muscle depth have been included in the breeding goal for terminal sire sheep, based on research at SAC, to derive and test a selection index to increase carcass lean and carcass weight at a constant age, without a corresponding increase in fatness.

Since the introduction of this index, and with the advent of BLUP (Best Linear Unbiased Prediction), group breeding schemes known as Sire Reference Schemes (Simm and Wray, 1991) have been initiated in about 15 major breeds to compare animals across different flocks. The success of the sire reference schemes has resulted in over half of the flocks in Sheepbreeder becoming members (Simm, 1998). Since the Suffolk sire reference scheme started, lamb live weight at 20 weeks has increased by 3.5 kg and muscle depth has increased by 1.5 mm whilst maintaining fat depth more or less constant, between 1990 and 1998 (MLC, 1999). Sire Reference Schemes have also been initiated in maternal breeds such as the Scottish Blackface and Lleyn. Since 1990, average lamb weight at eight weeks for the Scottish Blackface breed has increased by 0.8 kg, and maternal ability by 0.12 kg. (MLC, 1999). In recent years, some breeders of (traditionally)

maternal breeds such as the Welsh Mountain, Beulah and Scottish Blackface have used ultrasonic measurements of fat and muscle alongside their maternal index, as an aid to improving carcass merit, but the information has not been included in an index of overall economic merit.

Using different selection indexes to suit individual producers (or groups of producers with the same breeding objective) is known as customising selection indexes. In the UK, eleven different indexes are used according to the breed of sheep, although two slightly different ones are used for Dorset Horn sheep according to whether lamb production is an early or conventional lambing system (Collins, 1999). In Australia, personalised breeding objectives are used for individual Merino breeders using OBJECT, a computer programme which predicts likely rates of genetic progress for alternative selection criteria and economic values, to help breeders with selection decisions (Atkins *et al.*, 1994). A similar programme, BREEDOBJECT is used in conjunction with BREEDPLAN, the national beef genetic evaluation scheme for Australian beef producers (Barwick *et al.*, 1994). For the Australian dairy industry, a computer programme called Selectabull is used. Customised indexes are likely to be most beneficial when the the breeding objective is not dominated by a group of highly correlated traits, so the advantages from customising indexes might be larger for beef cattle situations than dairy situations (Visscher and Amer, 1996). The Australian computer programmes will ensure the greatest adoption and commitment to the use of breeding objectives (Harris and Newman, 1994), and if acceptance to the use of indexes in the industry is enhanced through their use, it may lead indirectly to larger profits (Visscher and Amer, 1996).

Hill Sheep

Despite the unfavourable conditions in which they live, hill sheep are by far the most important sector for producing ewes for breeding, representing 40% of the total number of breeding ewes and contributing 56% of the genes of breeding ewes in the UK. The predominant hill breeds are the Scottish Blackface, Welsh Mountain and Swaledale which comprise an estimated 3.6, 1.7 and 1.5 million ewes, respectively (MLC, 1998). As well as being important producers of pure and crossbred breeding stock, hill sheep are the second most important contributors to lamb carcass production (after terminal sire breeds), with 30% of the genes of all slaughtered lambs in Britain originating from hill breeds (MLC, 1998). It is widely recognised that lamb carcass quality from some hill breeds does not meet target, home market specifications.

In response to consumer preferences for leaner meat, considerable research effort has been expended in recent years on approaches to identify genetically leaner animals (Bennett, 1990; Simm, Dingwall, Murphy and FitzSimons, 1990; Simm, 1992; Cameron and Bracken, 1992; Fennessy, Bain, Greer and Johnstone, 1992; Waldron, Clarke, Rae, Kirton and Bennett, 1992; Bishop, 1993, Olesen and Husabo 1994). However, the majority of selection experiments and genetic parameter estimates for growth, fat and muscle come from either terminal sire breeds or other sheep managed with less limiting nutritional inputs than those in hill flocks. With the exception of one well-documented flock (Atkins, 1984, 1986 and Atkins and Thompson, 1986), and results for Welsh Mountain lamb growth, (Pollot et al., 1994; Aslaminejad *et al.*, 1999), a dearth of genetic information exists, of animals extensively managed on poor quality grass in hill environments. For example, the ability to manipulate body composition through genetic selection in such environments has not been addressed to date. It is possible that selecting for leaner meat in hill breeds increases mortality and decreases lamb liveweight gain, as a result of ewes having lower fat reserves on which to draw when nutrition is poor or limited. It is also possible that a

selection index suited to sheep reared in certain hill environments may not be appropriate for others reared in different (e.g. harsher) hill environments.

Background, objectives and description of research

In an attempt to address the problem of lack of knowledge in the genetics of hill sheep, a joint Scottish Agricultural College (SAC) and Roslin Institute (RI) experimental programme was instigated in 1990/91 to: i) investigate the consequences of selection for reduced carcass fatness on the performance and survival of hill sheep; ii) to estimate the phenotypic and genetic parameters for growth, carcass attributes, maternal ability, wool characteristics and maternal behaviour; and iii) to determine whether selection for divergent carcass fatness of rams under *ad libitum* feeding conditions has been effective in altering carcass composition of their progeny reared under extensive (hill) situations.

Using data from Scottish Blackface sheep recorded in this research project, the aim of this thesis is to go some way towards bridging the gap between existing knowledge and that necessary to derive appropriate, multi-trait selection indexes for sustainable improvement of hill breeds in the UK. The experiment is described in some detail in Chapter 2. The environmental effects, and estimates of genetic parameters for lamb growth and ultrasonic measurements of body composition for lambs reared in contrasting hill environments, are also reported. The implications for selection in such environments are highlighted. Measurements at slaughter and carcass dissection results from the same lambs are reported in Chapter 3, together with parameter estimates for these traits and lamb growth, adjusted to three different 'end points': at a constant dissected subcutaneous fat weight, at a constant age at slaughter and at a constant cold carcass weight. The feasibility of establishing breeding programmes to select for improved carcass traits in hill sheep is discussed in these two Chapters.

A bio-economic model is described in Chapter 4, to derive relative economic values (REVs) for a combination of maternal traits, carcass traits and 'sustainability' traits (longevity and lamb losses), tailored to suit three different hill farming production systems, typical of those found in the UK. Despite the fact that hill farm systems vary considerably, the objectives of farms within this sector are arguably the same: to produce breeding females capable of surviving and rearing progeny with high carcass value, in adverse climatic conditions. However, it is possible that the economic value of each component of the breeding goal might differ considerably for the three farm systems, as a result of differences in the physical constraints of farm size, pasture availability and quality, and the biological limits of the sheep themselves. In addition, the financial benefits of increasing a trait differ in magnitude from the financial penalties of decreasing that trait by the same amount. This is the case for carcass fat class where the benefits from increasing leanness are smaller than the penalties from increasing fatness. Using a whole farm model tailored to suit the different farm systems allows these issues to be addressed in the derivation of relative economic values for hill sheep. Using a flexible, multi-disciplinary model facilitates detailed sensitivity analyses of changes in the base prices for the major costs and returns of the sheep farm system to be examined.

The implications of using selection indexes combining maternal, carcass and sustainability traits are discussed in Chapter 5. Three selection indexes for UK hill sheep tailored (or 'customised') to suit the different hill farm systems are evaluated, together with the predicted responses for each goal trait and predicted discounted annual economic returns. The question of who benefits most from genetic improvement in hill flocks is discussed, and alternative strategies for selection with different breeding goals and different breeding strategies to meet the same goals, are examined. The sensitivities of the indexes to changes in the heritabilities for subcutaneous fat and weaning weight and to changes in the economic values above and below those used in the original index calculations

are examined.

Chapter 2

Early lamb growth and ultrasonic measurements

Introduction

It is widely recognised that lamb carcass quality from some hill breeds does not meet target, home market specifications. The main problem is that many lambs from the hill breeds tend to reach the desired fatness (MLC fat class 2-3L) at light weights, which leads to a financial penalty unless specialist markets for light lambs can be identified. A certain amount of reticence exists amongst the farming community towards improving carcass characteristics in hill breeds, in particular selection for reduced fatness. This may be due not only to the difficulties of recording in such conditions, but also to the uncertainty of the effects which selection might have on the overall performance and survival of ewes. As part of the SAC/ Roslin Institute experimental programme described in Chapter 1, animal performance, phenotypic and genetic parameters for early lamb growth and ultrasonic carcass measurements at weaning are described in this Chapter for two lines of Scottish Blackface lambs (LEAN and FAT), in four contrasting hill environments. The purpose of this work is to determine whether selection for divergent carcass fatness of rams under *ad libitum* feeding conditions has been effective in altering carcass composition in their progeny reared under extensive (hill) situations. Results from these analyses will help to determine whether selection for improved carcass traits in hill sheep is feasible, and whether the environment in which they are reared influences the rate at which genetic progress may be achieved.

Materials and methods

Management of animals

The lambs described in this study were born on two SAC hill farms over a period of two years. They were sired by thirty-two rams from the two divergent selection lines (FAT and LEAN) of Scottish Blackface sheep described by Bishop (1993). These rams had been selected under intensive rearing conditions since 1988 based on an index described by Cameron and Bracken (1992), i.e.

$$0.204 \times W20_s - 0.996 \times FAT_s$$

where W20 is 20 week body weight, and FAT is the average of ultrasonic backfat thickness measurements taken over the 13th rib and the 3rd lumbar vertebra at 20 and 21 weeks of age, and the subscript s indicates that both traits were corrected for known fixed effects and standardised to have a residual standard deviation of 1.0. As intended, the above index did not change live weight of the two lines so that differences between lines were a function of carcass composition rather than a function of body weight or maturity. It is from these two lines that rams for this experiment were used. Nine rams from each selection line were used in the first year, and ten LEAN, and nine FAT line sires were used in the second year. Five of these sires were used in both years to provide genetic links between years. A total of 2303 matings were made by laparoscopic artificial insemination (AI) to unselected Scottish Blackface ewes on these two SAC hill farms during 1990 and 1991. AI was used to enable all sires to be represented on both farms, and to concentrate the lambing period. A total of 1660 ewes lambed to AI over the two years.

The two SAC farms represent two contrasting hill environments typical of those found in Scotland. Farm 1 is located in the Pentlands National Park, Midlothian, and rises from 305 to 488 metres above sea level, with an average rainfall of 800 mm. Farm 2 is located near Crianlarich, West Perthshire, and is a much harsher, wetter farm rising from 180 to 1034 metres with 2900 mm average rainfall. Ewes in this trial were managed according to normal farm policy alongside the remaining ewes in each flock. Management policy was similar on the two farms except in two matters. Firstly, preferential feeding and housing were given to multiple bearing ewes from approximately week ten of pregnancy until lambing at farm 2, but not on farm 1. Secondly, all ewes from farm 1, but only single bearing ewes from farm 2, lambed outside in hill paddocks. Multiple bearing ewes on farm 2 were housed and lambed indoors, being transferred to pasture between 12 and 36 hours post lambing. Recording took place within 24 hours of

ewes giving birth. Ewes either reared one or two lambs; single lambs were reared on the hill, and twin lambs were reared on enclosed and improved pasture (inbye). This grazing distinction between rearing types is common practice on hill farms, and hence was followed here, although it does lead to confounding of some effects in subsequent analyses. Within hill grazings, distinct groups of ewes graze on specific areas of the open hill, with no fencing between them. This is known as 'hefting', and generally a ewe born into a heft will 'home' to that area during its life within the flock. It was therefore important to distinguish between ewes from different hefts, as hefting can have an extremely important environmental influence on their performance.

Three weights were recorded; birth weight (BWT), marking weight (MWT) at an average age of 6-7 weeks (when lambs are ear marked to show ownership and male lambs are castrated), and weaning weight (WWT) at an average age of 17 weeks. At weaning, all lambs were ultrasonically scanned at the level of the 3rd lumbar vertebra using a Vetscan ultrasonic machine with a 5 MHz 56 mm probe. Photographed scan images were subsequently interpreted using computer-based semi-automatic image analysis software. Four individual fat depth measurements (FD1 - FD4) were taken from the boundary of the vertical process of the vertebra and the *longissimus dorsi* muscle at 10mm intervals. Average fat depth (AVFD) was calculated between the 1st and 4th depth site (not as the average of the four individual measurements). One muscle depth measurement was also taken at the deepest point on the muscle.

Statistical Analysis

The data were analysed initially using the GENSTAT package (Lawes Agricultural Trust, 1983) to identify significant sources of variation, using regression. GENSTAT residual maximum likelihood (REML) was then used to calculate fixed effect means. The main effects fitted were sire selection line (lean or fat), dam age (2, 3+4 or 5+ years), sex and grazing code fitted within farm,

where grazing code accounted for heft, birth type, rearing type and year. The covariable day of birth was fitted for post-birth traits, and a covariable for day of marking was fitted for marking weight. Weaning took place over 2 days in each year and at each farm, whereas marking was spread over a 2-week period for farm 2 in the second year as weather conditions prevented the sheep from being gathered. The interactions of dam age by farm, dam age by year and birth type by farm were used in the model for all traits. The first two interactions take into account different performance levels between ewes of the same age on the two farms, and in the two years, respectively. The interaction between birth type and farm accounted for preferential feeding of twin rearing ewes on farm 2. Finally, sire was fitted as a random effect, nested within line.

Within-line univariate genetic parameters were calculated for all traits using a derivative free REML algorithm (DFREML) (Meyer, 1989), fitting an animal model and the fixed effects described above. The fitted pedigree included all genetic relationships between the sires, but all ewes were assumed to be unrelated as their pedigrees were not known. The observed variation for each trait was partitioned into additive genetic and maternal common environmental (c^2) components, which were assumed to be uncorrelated. The c^2 effect potentially includes maternal genetic as well as maternal environmental effects. However, given the structure of the dataset it was not possible at this stage to disentangle these two components. A total of 736 ewes had 2 or more lambs and hence contributed to the c^2 estimated. The DFREML algorithm was assumed to have converged when the difference in the variances of the log likelihoods of successive iterations was less than 10^{-6} .

Within-line genetic and phenotypic correlations between traits were calculated using multivariate REML techniques (REMLPK; Meyer, 1985) fitting a sire model for all traits, and fitting the fixed effects described above. This was the best software available at the time these analyses were undertaken. The sire

model (see Results section) gave almost identical heritability estimates to the animal model including maternal effects, as well as allowing standard errors for all variance components and correlations to be estimated readily. The analysis continued therefore with the sire model for computational ease. The REML algorithm was assumed to have converged when the maximum proportional difference in genetic variance components on the canonical scale was less than 10^{-5} between iterations.

Due to the strong environmental influences on the performance of the lambs, genetic parameters were also estimated separately for hill-reared and inbye-reared (on improved, fenced pasture) lambs, again using REMLPK and fitting a sire model.

Results

Phenotypic Performance

The number of ewes artificially inseminated, the number lambing and the resulting number of lambs born alive are shown in Table 2.1, for each farm and for each year:

The mean number of lambs per sire group used for this analysis was 56.3, which ranged from 41 to 91 for rams used in one year only. For the five rams with 2 years data, the mean was 125.8, ranging from 95 to 148 lambs per sire. There were similar numbers of lambs born in each sire line each year.

Table 2.1 *Two year lambing performance summary*

	1991		1992	
	Farm 1	Farm 2	Farm 1	Farm 2
No. ewes Inseminated	586	588	558	571
No. ewes lambing To AI (%)	376 (64.2)	428 (72.8)	438 (78.5)	418 (73.2)
No. lambs born alive Per ewe lambing (%)	560 (148.9)	628 (146.7)	675 (155.0)	523 (125.1)

The number of lambs used in this analysis, their mean body weights from birth to weaning and ultrasonic measurements are shown in Table 2.2, together with the phenotypic standard deviation of each trait. Despite the small absolute depths of fat (less than 2.5 mm at all measurement sites), fat depth measurements were much more variable than muscle depths, and particularly so towards the lateral edge of the muscle. The average liveweight, fat and muscle depths were similar for both years.

Table 2.2 *Least squares mean (LSM) values, phenotypic standard deviations (sd) and coefficients of variation (CV, as a percentage) for lamb liveweights and ultrasonic measurements*

	No.	LSM	sd	CV%
Liveweight (kg):				
at birth	2085	4.01	0.63	15.8
at marking	2067	13.81	1.98	14.3
at weaning	1922	28.52	3.36	11.8
Scan measurements(cm:)				
Fat depth 1	1896	0.19	0.065	34.2
Fat depth 2	1896	0.19	0.071	37.4
Fat depth 3	1896	0.22	0.087	39.5
Fat depth 4	1896	0.24	0.094	39.2
Average fat depth	1896	0.21	0.074	35.2
Muscle depth	1896	1.77	0.192	10.8

Table 2.3 shows the least squares means of each line and the standard error of differences between them, for all traits. As expected, no differences were seen in liveweights between the two lines (the aim of the selection index used to create the two Roslin Institute selection lines was to produce divergent lines for carcass fat content without a correlated response in liveweight). Lambs born from FAT line sires had significantly greater fat depths at all measurement sites than lambs from LEAN line sires. The average difference in backfat depth between the two lines was proportionately 0.15 overall, although this difference was not uniform between the two years (differences were proportionately 0.11 and 0.18 in 1991 and 1992 respectively). No difference between the two lines in the depth of muscle was apparent. Again, this is in line with results obtained in the Roslin Institute (RI) flock (Bishop, 1993).

Table 2.3 *Least squares means of growth and ultrasonic measurements according to sire line*

Sire line:	<u>Lean</u>		<u>Fat</u>		s.e.d.
	No. obs.	Mean	No. obs.	Mean	
Liveweight (kg):					
at birth	1037	3.99	1048	3.95	0.039
at marking	1033	13.85	1034	13.65	0.112
at weaning	961	28.70	961	28.38	0.266
Scan measurements (cm):					
Fat depth 1	945	0.18	967	0.21	0.005**
Fat depth 2	945	0.18	967	0.21	0.005**
Fat depth 3	945	0.20	967	0.24	0.006**
Fat depth 4	945	0.22	967	0.26	0.007**
Average fat depth	945	0.19	967	0.22	0.006**
Muscle depth	945	1.76	967	1.78	0.019

** (p<0.01)

The dam age was an important component in the analysis; the effects of which can be seen in Table 2.4. Lambs from gimmers (2 year old ewes) and older ewes (5+ years) were lighter, had less fat and had less muscle than lambs from ewes of intermediate age. All values were significantly different from each other with the exception of fat depths 2, 4 and AVFD between 3+4 and 5 year old ewes.

Table 2.4 *Least squares means of live weight and ultrasonic measurements according to dam age*

	<u>Dam age</u>			Average s.e.d.
	2	3 + 4	5+	
Liveweights (kg):				
at birth	3.71 (558) †	4.04 (1085)	4.16 (442)	0.037
at marking	13.1 (552)	14.2 (1075)	13.9 (440)	0.121
at weaning	27.5 (494)	29.3 (1010)	28.9 (418)	0.210
Scan measurements (cm):				
Fat depth 1	0.18 (493)	0.20 (1005)	0.19 (414)	0.004
Fat depth 2	0.18 (493)	0.21 (1005)	0.20 (414)	0.004
Fat depth 3	0.20 (493)	0.23 (1005)	0.22 (414)	0.005
Fat depth 4	0.22 (493)	0.25 (1005)	0.25 (414)	0.005
Average fat depth	0.19 (493)	0.22 (1005)	0.21 (414)	0.004
Muscle depth	1.75 (493)	1.79 (1005)	1.76 (414)	0.011

† Figures in brackets represent number of lambs observed

Differences between farms for most traits reflect the difference in mature liveweight of about 10 kg for the ewes, and the severity of the environment in which lambs were reared. Table 2.5 shows how preferential treatment (rearing inbye) of multiple-born lambs on farm 2, benefited their performance. This is because there is a greater contrast between the quality of inbye and hill grazings on farm 2 compared with farm 1. This resulted in their post-birth liveweights being heavier than those of single born lambs reared on the hill. Performance of the multiple-born lambs reared inbye on farm 1 was poorer than their single born counterparts, being 1.6 kg and 3.1 kg lighter at marking and weaning respectively.

Male lambs were heavier than females at each weighing session, they had less fat at all scan measurement sites, and they had similar muscle depths to female lambs.

Table 2.5 *Least squares means of live weights and ultrasonic measurements according to farm and rearing type/location†*

	Farm 1		Farm 2		Average s.e.d
	Inbye	Hill	Inbye	Hill	
Liveweights (kg):					
at birth	3.76	4.63	3.32	4.17	0.147
at marking	12.82	14.41	14.98	12.97	0.491
at weaning	28.04	31.14	27.67	25.57	0.861
Scan measurements (cm):					
Fat depth 1	0.18	0.22	0.19	0.16	0.017
Fat depth 2	0.19	0.24	0.19	0.16	0.018
Fat depth 3	0.21	0.26	0.21	0.19	0.022
Fat depth 4	0.23	0.28	0.24	0.21	0.024
Average fat depth	0.19	0.15	0.21	0.17	0.019
Muscle depth	1.73	1.83	1.82	1.67	0.049

† Rearing location is confounded with rearing type

Genetic Analyses

Table 2.6 summarises univariate heritability estimates and maternal common environmental effects for all traits. Heritability estimates for both pre-weaning weights were below 0.1, although that for liveweight at weaning was slightly higher (0.12). Heritability estimates for ultrasonic fat measurements ranged between 0.13 and 0.17 with an average of 0.14. The selection of rams on an index based on fat depth is expected to have reduced the within-line heritability for fat depth, and this effect is quantified and discussed by Bishop *et al.*, (1996).

Bivariate analyses accounting for this prior selection, but ignoring maternal effects, resulted in a heritability estimate for fat depth of 0.25 (Bishop *et al.* 1996). The heritability for muscle depth was higher at 0.23. Maternal common environmental effects were greater for the liveweight measurements than for the ultrasonic measurements, with the effects being larger at younger lamb ages. At birth, for example, almost half of the observed phenotypic variation in liveweight is due to maternal effects.

Table 2.6 *Univariate heritability estimates (h^2) and maternal common environmental (c^2) effects*

	h^2	c^2
Liveweights:		
at birth	0.08	0.41
at marking	0.02	0.23
at weaning	0.12	0.18
Scan measurements:		
Fat depth 1	0.13	0.10
Fat depth 2	0.17	0.11
Fat depth 3	0.14	0.08
Fat depth 4	0.12	0.10
Average fat depth	0.14	0.12
Muscle depth	0.23	0.10

Table 2.7 shows correlations and heritability estimates for all traits measured on all lambs, calculated using a sire model. The heritabilities for liveweights were estimated using a univariate model, because of different numbers of records for each weight and slightly different fixed effects and covariates, whereas the heritabilities for, and correlations between, ultrasonic measurements were estimated simultaneously using a multivariate model.

Table 2.7 *Estimates of heritabilities†, genetic‡ and phenotypic§ correlations for liveweights and ultrasonic measurements for all lambs*⊞

	BWT	MWT	WWT	FD1	FD2	FD3	FD4	AVFD	MD
BWT	0.07(0.04)	0.50(0.01)	0.36(0.02)	0.03(0.02)	0.02(0.02)	0.02(0.02)	0.04(0.02)	0.03(0.02)	0.08(0.02)
MWT	0.42(0.36)	0.02(0.03)	0.63(0.01)	0.21(0.02)	0.20(0.02)	0.19(0.02)	0.19(0.02)	0.22(0.02)	0.34(0.02)
WWT	0.48(0.27)	0.85(0.17)	0.14(0.05)	0.40(0.02)	0.40(0.02)	0.36(0.02)	0.35(0.02)	0.40(0.02)	0.55(0.02)
FD1	-0.10(0.31)	-0.29(0.37)	-0.20(0.29)	0.15(0.06)	0.81(0.01)	0.73(0.01)	0.71(0.01)	0.83(0.01)	0.31(0.02)
FD2	-0.10(0.30)	0.08(0.35)	-0.11(0.28)	0.91(0.06)	0.18(0.07)	0.86(0.01)	0.81(0.01)	0.94(0.00)	0.31(0.02)
FD3	-0.09(0.31)	-0.19(0.36)	-0.23(0.28)	0.86(0.08)	0.92(0.04)	0.16(0.06)	0.90(0.00)	0.96(0.00)	0.33(0.02)
FD4	-0.01(0.31)	-0.18(0.37)	-0.25(0.29)	0.77(0.12)	0.84(0.08)	0.98(0.02)	0.15(0.06)	0.93(0.00)	0.35(0.02)
AVFD	-0.09(0.30)	-0.08(0.41)	-0.21(0.29)	0.92(0.05)	0.97(0.02)	0.99(0.01)	0.94(0.03)	0.16(0.06)	0.35(0.02)
MD	-0.41(0.26)	0.17(0.36)	0.30(0.24)	-0.39(0.25)	-0.20(0.26)	-0.17(0.26)	-0.14(0.27)	-0.21(0.26)	0.27(0.09)

† On the diagonal. ‡ Below the diagonal. § Above the diagonal. ⊞ Standard errors of estimates shown in brackets.

BWT = birth weight, MWT = marking weight, WWT = weaning weight, FD1 - 4 = ultrasonic fat measurements 1-4, MD = muscle depth, AVFD = average fat depth.

The heritability estimates were almost identical to those in Table 2.6, with pre-weaning weights both below 0.1, and liveweight at weaning slightly higher at 0.14. Heritability estimates for ultrasonic fat measurements ranged between 0.15 and 0.18 with an average of 0.16. The heritability of ultrasonic muscle depth was 0.27. By comparing the heritability estimates in Tables 2.6 and 2.7, it can be seen that the two computational procedures produced similar results.

The fat depth measurements were very strongly positively correlated with each other, both genetically and phenotypically. There were moderate positive correlations between successive liveweight measurements. There were small negative genetic correlations between the liveweight and ultrasonic backfat measurements, but small to moderate positive phenotypic correlations. There was a fairly strong negative genetic relationship between birthweight and muscle depth, although subsequent marking and weaning weights were positively genetically correlated with muscle depth (0.17 and 0.30 respectively). Finally, the fat and muscle depth measurements were positively phenotypically correlated, but the genetic correlations were small and negative. The standard errors of the estimates of phenotypic correlations ranged between 0.002 and 0.02, and for the genetic correlations they ranged between 0.01 and 0.28.

Tables 2.8 and 2.9 show estimates of heritability and phenotypic correlations calculated for the two different rearing environments, inbye and hill. There were no significant differences in heritability estimates between rearing types for liveweights and muscle depth, but the estimate of heritability for average backfat thickness was twice as large for inbye-reared compared to hill reared lambs (0.24 and 0.12 for inbye and hill reared lambs respectively). However, these estimates were not significantly different from each other. The estimates for the individual fat depth measurements for inbye reared lambs ranged from 0.15 to 0.28, and those for hill reared lambs ranged from 0.09 to 0.12. The phenotypic variance of average fat depth for hill reared lambs was higher than that of inbye reared lambs

(0.0065 cm² and 0.0047 cm² respectively). The correlation between weaning weight and fat depth was also reduced in the hill environment. These two subsets of data were too small to allow reliable genetic correlations to be estimated.

Table 2.8 *Estimates of heritabilities† and phenotypic correlations‡ for growth and ultrasonic measurements for hill reared lambs§*

	BWT	MMT	WWT	AVFD	MD
BWT	0.14(0.07)	0.48	0.34	-0.05	0.04
MWT		0.06(0.05)	0.64	0.28	0.36
WWT			0.15(0.09)	0.17	0.32
AVFD				0.12(0.08)	0.34
MD					0.26(0.11)

† On the diagonal. Standard error of heritability estimates shown in brackets.

‡ Above the diagonal. Standard errors of phenotypic correlations ranged from 0.02 to 0.03.

§ Number of lambs = 759. A key to abbreviations is given in Table 2.7.

Table 2.9 *Estimates of heritabilities† and phenotypic correlations‡ for growth and ultrasonic measurements for inbye reared lambs§*

	BWT	MMT	WWT	AVFD	MD
BWT	0.08(0.05)	0.51	0.39	0.09	0.13
MWT		0.04(0.03)	0.64	0.26	0.37
WWT			0.14(0.07)	0.32	0.41
AVFD				0.24(0.09)	0.36
MD					0.26(0.09)

† On the diagonal. Standard error of heritability estimates shown in brackets.

‡ Above the diagonal. Standard errors of phenotypic correlations ranged from 0.01 to 0.03.

§ Number of lambs = 1143. A key to abbreviations is given in Table 7.

Discussion

There is a dearth of information on body weight and *in vivo* body composition in sheep under UK hill farming conditions. It is important that such relationships between carcass and other traits are estimated and fully understood, in order that meaningful breeding programmes incorporating carcass attributes can be designed. The results reported here are from an experiment designed for these purposes.

In the present study, the decreasing importance of the maternal component with lamb age to around 0.1 for all measurements at weaning is in line with the findings of Atkins (1986), also working with Scottish Blackface sheep.

The low heritability estimates (less than 0.1) for pre-weaning weights are also in line with those of Atkins (1984, 1986), although the estimate for liveweight at weaning was higher in this study (0.14) than in his study (0.05) and that of Atkins & Thompson (1986) (0.08). Atkins' estimates were obtained with the same breed, at similar ages, reared under similar environmental conditions and with no nutritional supplementation. Waldron *et al.* (1992) reported a higher heritability estimate for liveweight of grass-reared Romney and Romney cross lambs (0.27, at an average age of 205 days). This is more in line with other liveweight heritability estimates which ranged from 0.23 to 0.38, with sheep offered nutritional supplementation at some stage in their growth phase (Mavrogenis, Louca and Robinson, 1980; Barillet, Bibé, and Bioux, 1982; Simm, Young and Beatson, 1987 (review); Young, 1989; Bishop, 1993; María, Boldman and Van Vleck, 1993). The higher heritability estimates for the pasture-based studies may in part be due to better quality grazing than that of the present study.

The selection criterion of the two Roslin Institute selection lines (described above) was dominated by fat depth. As selection reduces genetic variation, within-line heritability estimates will normally be reduced. As the rams used in

this study were themselves selected from two established selection lines, the heritabilities for fat depth in this study have been under-estimated as no prior selection was assumed (Bishop *et al.*, 1996). Therefore, the heritability estimates for ultrasonic backfat measurements of between 0.15 and 0.18 for all lambs were lower than that of 0.23 estimated by Waldron *et al.* (1992) and also that of 0.25 from Fennessy *et al.* (1992), (with Coopworth lambs reared on grass and clover swards also in New Zealand). The heritability estimates were also lower than published heritability estimates for ultrasonic backfat measurements, with animals given nutritional supplementation (see the review by Simm *et al.*, 1987). However, the pattern between rearing locations remains the same, with higher heritabilities for inbye versus hill reared lambs.

When backfat heritability estimates were calculated according to rearing location, those for inbye-reared lambs were on average twice that of hill reared lambs. The former were well within the range of estimates cited by Simm (1992) at a constant age, however the average fat depth heritability for hill reared lambs was low (0.12). Lambs reared on the hill had a slightly lower additive genetic variance of 0.00078 cm², compared to 0.00113 cm² for inbye reared lambs. Conversely, hill-reared lambs had a larger environmental variance of 0.00572 cm² compared with 0.00357 cm² for inbye-reared lambs. This shows that the harsher rearing environment (hill) has inflated the error variance, which partly explains the low ultrasonic backfat heritability estimates. This may have important implications for improvement programmes in harsh environments, with the objective of reducing fat levels. A further explanation for low estimates in this study (and the comparable study by Atkins, 1986) could be due to them having been calculated at a relatively early stage of the lambs' maturity, with the latest measurements taken at approximately 0.4 of mature size. In other studies, heritabilities were calculated when animals were proportionally over 0.5 of mature live weight (Young and Simm, 1990; Waldron *et al.*, 1992; Bishop 1993; Cameron & Bracken, 1992).

The heritability estimate for muscle depth in the present study was within the range of published estimates, although at the lower end of the scale. The heritability estimates were consistent for both rearing types in this study, and appear not to have been influenced by the harsh environment, unlike those for subcutaneous fat. This is perhaps due to muscle maturing earlier than fat, and also the fact that it was not a selection criterion in the two sire lines.

The estimates of negative genetic correlations between muscle depth and fat depths are not in accordance with estimates at a constant age published by Bouix, Bibé and Lefevre (1982) (with muscle area); Young and Simm (1990); Henningsson and Malmfors (1992) and Bishop (1993). However, the negative genetic correlations were in agreement with findings of Wolf, Smith, King and Nicholson (1981), Cameron and Bracken (1992) and Waldron *et al.* (1992). The latter found negative partial genetic correlations between all lean indicator traits and dissected fat weight (although at a constant weight). In a UK study comprising 10 ram breeds and three ewe breeds, Pollot *et al.*, (1994) explain that at a constant fat cover, animals with higher fat depths had poorer genetic potential for conformation and muscle depth. It was not possible to estimate genetic correlations between traits according to rearing types due to insufficient data. However phenotypic correlations for both rearing types showed positive relationships for all traits, with the exception of birthweight and ultrasonic backfat measurements, where correlations were all small and negative for hill reared lambs.

Estimates of phenotypic correlations between liveweight at weaning, backfat and muscle depth measurements were well within the range of estimates reported by Simm *et al.* (1987), Cameron & Bracken (1992) (from a review of the literature) and Young (1989) (from analysis of a selection experiment).

The results of this study show that selecting animals for divergent subcutaneous backfat levels when they are reared under non-limiting nutritional conditions does result in their offspring (reared in *extensive* conditions) being divergent in backfat thickness also. The results clearly show how important the environmental components are in affecting the growth and body composition of hill, in particular those reared on the hill rather than on improved pasture inbye. However, if it is assumed that the heritability estimates for fat depth are known without error, genetic improvement of carcass characteristics is a feasible option, although annual progress would be slower (by approximately 40%) for hill reared lambs than lambs reared on improved pasture (based on phenotypic variance of 0.0065 and 0.0047 cm² and heritabilities of 0.12 and 0.24 for hill and inbye-reared lambs respectively).

Chapter 3

Genetic parameters for carcass traits and lamb growth

Introduction

Improving carcass quality of hill lambs would increase the financial viability of hill farms, and make them more competitive and less vulnerable to fluctuations in hill farming subsidies. In the UK, lamb carcasses are graded at the abattoir according to an assessment of their fat cover (fat class) and muscularity (conformation). For example, 30% of all lambs in the UK fall into the category R3L (MLC, 1999). The following grid shows the scales for these carcass quality traits. The target grades for lambs are E, U, R, 2 and 3L (the shaded area shown on the grid).

		Fat class					
Conformation	1	2	3L	3H	4L	4H	5
E							
U							
R							
O							
P							

Usually, UK abattoirs penalise lamb carcasses which fall outwith the target fat class of 2-3L, because of the need to trim excess fat from the carcass before it can be sold. Carcasses with conformation score 'E' or 'U' also usually qualify for a higher price per kg than lambs graded 'R' or below. To date, carcass traits have not been incorporated into selection objectives for hill sheep. Firstly, this is because of an absence of reliable estimates of genetic and phenotypic parameters, in the relevant breeds, for carcass characteristics and associated traits which may be used as selection criteria, e.g. ultrasonic measurements. Secondly,

little is known about the relationships between carcass characteristics and other traits relevant to breeding goals for hill sheep.

The consequences of reducing fatness are of particular concern, because of its assumed importance for survival, pregnancy and subsequent lactation in the ewe. However, whilst there is a clear need to genetically improve the carcass characteristics of hill lambs, this is only part of a broader selection goal. Other traits relevant to the multi-purpose role of hill sheep, including their ability to survive and produce lambs in harsh environments, must also be addressed.

The aims of this Chapter are threefold: i) to investigate whether or not selection for divergent fatness (using ultrasound techniques) in animals reared under *intensive* conditions results in different fatness of the carcasses of their progeny when reared under *extensive* conditions; ii) to compare carcasses of lambs sired by rams from two genetic lines selected for divergent carcass fatness, slaughtered according to commercial finishing criteria and iii) to estimate heritabilities, phenotypic and genetic correlations for carcass and growth traits.

Materials and methods

Management of animals

The lambs used in this study are those described in Chapter 2, i.e. they were sired by Blackface rams from the two divergent selection lines (FAT line and LEAN line), out of unselected dams of the same breed. Measurements taken on these lambs at weaning through to slaughter are reported here. Weaned male lambs (which had been reared extensively) were brought together from both farms in August of each year, and managed as one flock on SAC improved lowground pastures at the Bush Estate. They were fed on silage aftermath until November of each year, and subsequently given access to swedes *ad libitum*, supplemented by an average of 0.4 kg per day of a concentrate ration containing proportionately

0.16 crude protein, and 10.8 MJ ME, per kilogram of dry matter. Lambs were weighed and condition scored fortnightly, and selected for slaughter at a target condition score of 3, by the same person on all occasions.

Pre- and post- slaughter measurements

Traits measured at weaning were: weaning weight (WWT), ultrasonic muscle depth (MD) and average fat depth (AVFD). A pre-slaughter weight (SLWT) was taken on average 6 hours after removal from grass. The lambs were slaughtered approximately 13 hours later. In addition, traits measured at slaughter were: pre-slaughter condition score (CS), cold carcass weight (CCWT) and killing out proportion (KÖ). Cold carcass weight was recorded approximately 24 hours post-slaughter, and KO was calculated as CCWT/SLWT. Age at slaughter (AGE) was calculated for each lamb. In addition, all carcasses were scored by the Meat and Livestock Commission (MLC) classifier on duty at the abattoir for assessments of subcutaneous fat (MLC FAT) and conformation (CONF). Since the interval between MLC fat classes is not equal, data were transformed to their corresponding estimated subcutaneous fat proportion before analysis: 1=0.04, 2=0.08, 3L=0.11, 3H=0.13, 4L=0.15, 4H=0.17 and 5=0.20 (Kempster *et al.* 1986). MLC conformation class was coded as E=5, U=4, R=3, O=2, and P=1.

Carcass dissection data were available on 997 lambs. Two hundred and twenty four left side dissections were made, representing proportionally about 0.2 of the carcasses in each sire progeny group. This proportion of lambs was chosen based on the formula of Cook, Jones and Kempster (1983), as it is the optimum number of full and partial carcass dissections, given finite monetary resources. The sides were separated into eight joints (breast, chump, end-neck, leg, loin, mid-neck, scrag and shoulder) as described by Cuthbertson, Harrington and Smith (1972). For the remainder of lambs slaughtered, the shoulder joint alone was dissected. Each joint was dissected into lean, fat (subcutaneous and intermuscular) bone and waste components. The shoulder joint was chosen as the sample joint to dissect

from all lambs because of the reported high correlation (0.9) between the lean content of the shoulder and the carcass (Cook *et al.*, 1983).

Traits derived

The dissected components of interest are weights and proportions of lean tissue (LEAN), subcutaneous fat (SUBFAT), intermuscular fat (IFAT), total fat (ALLFAT) (=SUBFAT + IFAT) and bone (BONE). Regressions were used to predict whole body composition, as suggested by Conniffe and Moran (1972). Specifically, shoulder data from the side dissection animals were used to derive prediction equations to best describe total carcass weight and weights and proportions of lean, subcutaneous fat, intermuscular fat and bone. The equations derived were then used to estimate predicted carcass weight and weights and proportions of total carcass lean, total carcass subcutaneous fat, total carcass intermuscular fat, total carcass fat and total carcass bone.

The prediction equations used are in **Appendix 1**, and the R² values, and residual standard deviations for predicted carcass components are shown in **Appendix Table A1**.

Statistical analysis

The analyses were done on the carcass and slaughter data adjusted to three 'end points': i) a constant dissected subcutaneous fat weight, ii) a constant age at slaughter, and iii) a constant cold carcass weight. Adjustments to constant subcutaneous fat and cold carcass weight were made by linear regression, and adjustment to a constant age was by quadratic regression. Genetic line means for carcass composition were derived from actual dissected proportions of shoulder joint tissues. Heritability estimates were obtained for both actual and predicted dissected carcass traits. As they were almost identical, heritability estimates for actual dissected shoulder tissue weights are reported here. As the lambs were selected for slaughter at a constant condition score, an estimate of subcutaneous

fat cover in the live animal, results from a constant fat weight measured in the carcass are likely to be the most relevant here. Although results from data adjusted to the other two 'end points' are intuitively more appealing because they are measured objectively, they must be interpreted with care. In practice, UK farmers select animals for slaughter according to a combination of liveweight and fatness, depending on market signals. The data were analysed initially using the GENSTAT package (Lawes Agricultural Trust, 1983) to identify significant sources of variation, using regression. GENSTAT residual maximum likelihood (REML) was then used to calculate fixed effect means. The main effects fitted were sire selection line (LEAN line or FAT line), dam age (2, 3+4 or 5+ years), success of castration (fully castrated, or cryptorchid males, i.e. males with one visible testicle, n=52) (MALE), and grazing code (GRAZ), where grazing code accounted for farm, birth type, rearing type and year. For each of the three 'end points', the relevant factor was also fitted as a covariate. Finally, sire was fitted as a random effect, nested within line. Prediction equations were derived using regression techniques in the GENSTAT statistical package.

Price per lamb was compared between genetic lines at a fixed MLC fat class (and transformed to an estimated subcutaneous fat proportion), adjusted for MALE, with ^oday of slaughter fitted with a quartic regression coefficient, as linear, quadratic, cubic and quartic terms were all significant, but higher order terms were not. Again, sire was fitted as a random effect, nested within line.

Within-line univariate heritabilities and multivariate genetic and phenotypic correlations were estimated for all traits using multivariate REML techniques (REMLPK; Meyer, 1985), fitting a sire model and the fixed effects described above. The fitted pedigree included all genetic relationships between the sires, but all ewes were assumed to be unrelated as their pedigrees were not known. The REMLPK algorithm was assumed to have converged when the difference in the variances of the log likelihoods of successive iterations was less than 10^{-6} .

Results

Least square means and phenotypic standard deviations for liveweight at weaning, average fat and muscle depths, slaughter characteristics and dissected shoulder components from all lambs are presented in Table 3.1.

In Figure 1, the MLC fat classification scores of lambs from the FAT or LEAN genetic lines are compared. Chi-square tests showed a significant difference between the two lines ($\chi^2 = 9.3$, $p < 0.01$) in fat scores. More lambs from the LEAN line fell into category 2, and more lambs from the FAT line fell into category 3H, despite there being no difference between the two lines in the condition score prior to slaughter. When the MLC fat scores were transformed to the linear fat scale described above, to describe biological differences, the difference between the two lines was not significant. There were no differences between the two lines in conformation score, as shown in Figure 2.



Table 3.1 *Least square means and phenotypic standard deviations (s.d.) for all measured traits*

Trait	Mean	s.d.
Number of observations	925	
Weaning weight (kg)	28.5	3.36
Average ultrasonic fat depth (cm)	0.21	0.074
Ultrasonic muscle depth (cm)	1.77	0.192
Pre-slaughter condition score	2.90	0.40
Pre-slaughter liveweight (kg)	38.2	3.65
Age at slaughter (days)	247	48.7
Killing out proportion	0.453	0.019
MLC estimated subcutaneous fat proportion	0.112	0.015
MLC conformation score (E=5)	2.60	0.50
Price received (£)	31.4	4.76
<i>Dissected shoulder proportions</i>		
Subcutaneous fat	0.136	0.028
Intermuscular fat	0.156	0.019
All fat	0.292	0.037
Lean	0.538	0.032
Bone	0.164	0.013

Figure 1 MLC Fat class
1991 and 1992 born male lambs

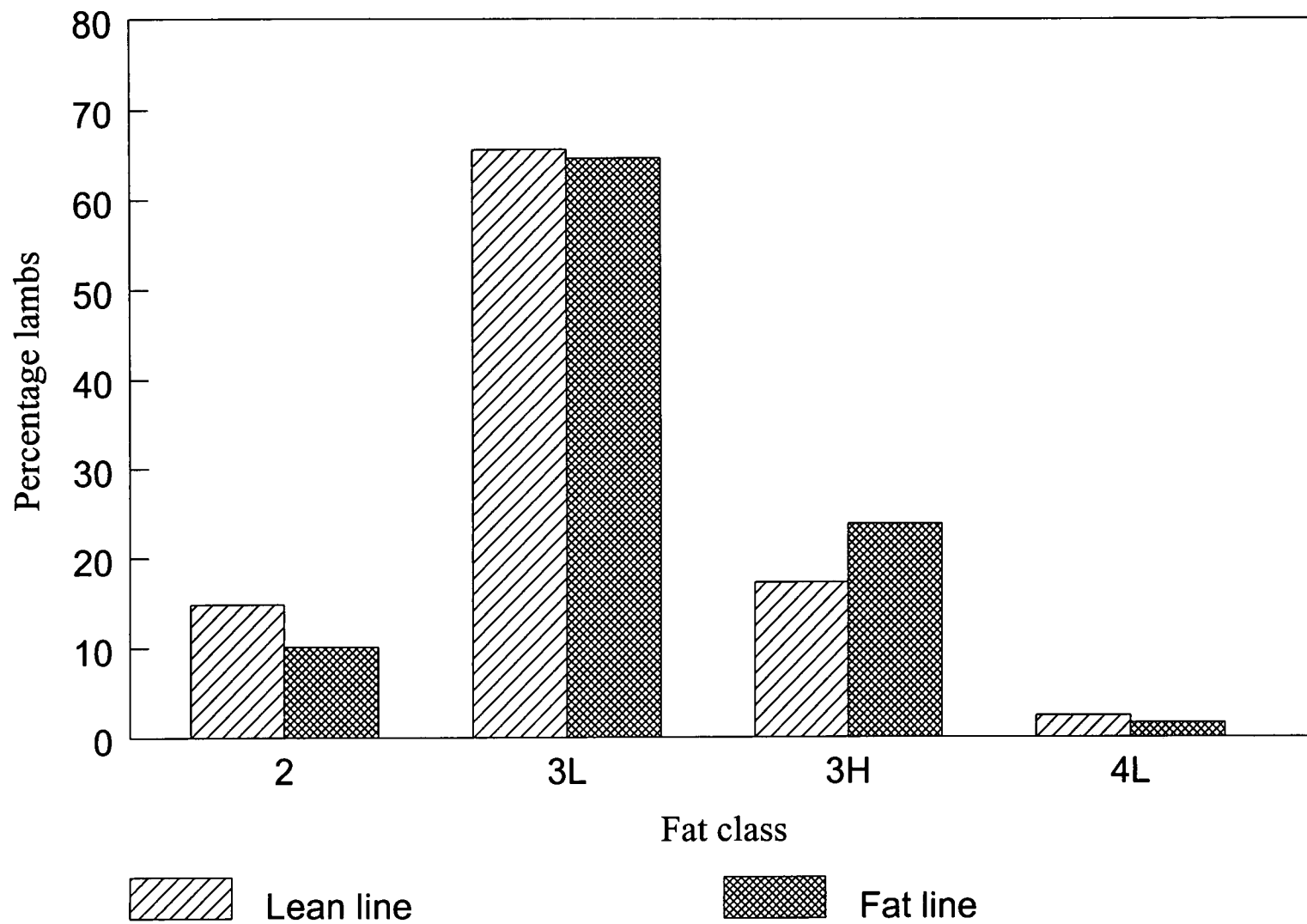
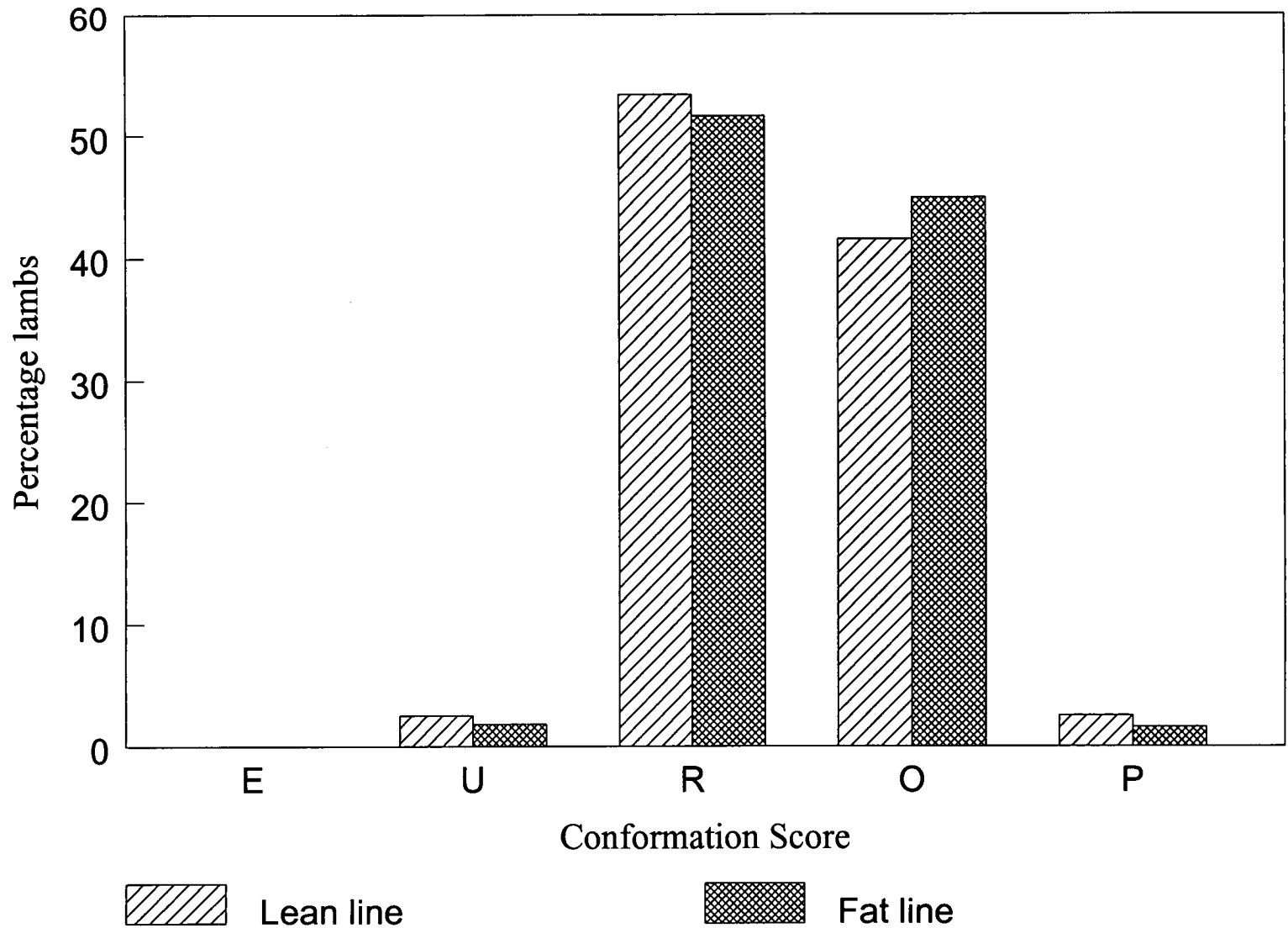


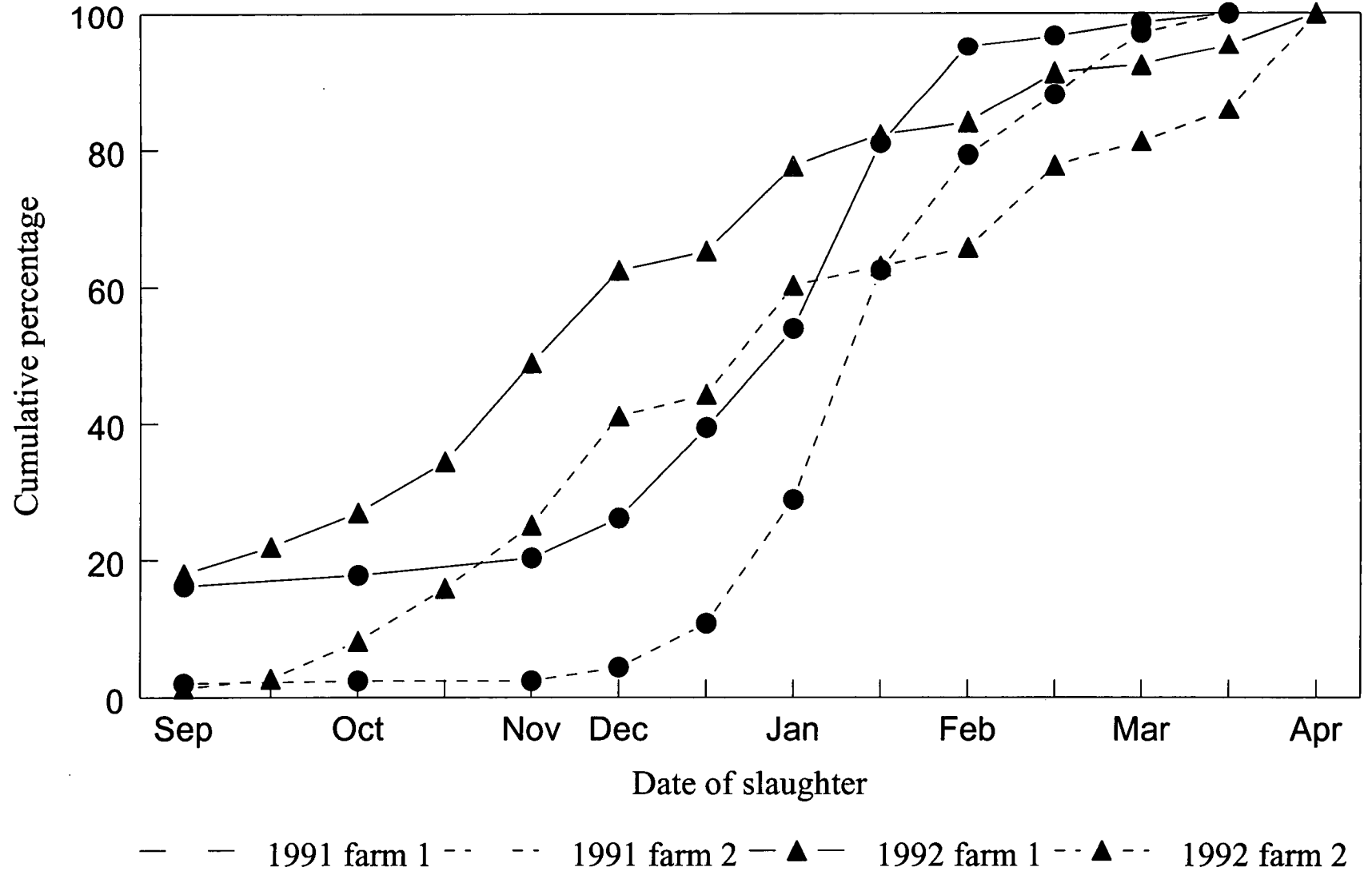
Figure 2 MLC Conformation score
1991 and 1992 born male lambs



Environmental influences

Important environmental effects on lamb performance are described in Chapter 1. In general, the influence of dam age on slaughter and dissection traits was less important than in traits measured earlier in life; lambs from two year old ewes were lighter at slaughter than lambs from 3-5 year old ewes (37.68 kg vs. 38.42 kg); cryptorchid lambs were classified leaner (MLC FAT 0.1078 Vs 0.1132), were heavier (39.82 kg vs 36.17 kg), took longer to finish (259.7 days Vs 234.5 days) and had a lower killing out proportion than fully castrated lambs (0.4488 Vs 0.4552). Differences between farms for most traits reflect the difference in mature live weight of ewes of about 10 kg, and the severity of the environment in which the lambs were reared, which was harsher on farm 2 than farm 1. Farm differences were greater than differences between years, although both were significant for most traits. Figure 3 shows farm differences in the cumulative proportions of lambs drawn for slaughter. It illustrates how lambs from the different farms performed in both finishing seasons in the time taken to reach slaughter. Despite being managed as one group post-weaning, lambs from farm 2 took approximately one month longer to finish than lambs from farm 1 in both years.

Figure 3 Slaughter pattern according to farm



Comparison between Lines

Table 3.2 shows least square means for carcass traits from lambs of the two selected lines (LEAN) and (FAT) corrected to a constant dissected fat weight. LEAN line lambs were 850g heavier pre- slaughter (SLWT), and produced carcasses which were 340g heavier (CCWT), than lambs from the FAT line. They also tended to have better conformation scores. Lean line lambs had a slightly poorer killing out proportion, and took an average of 1.4 days longer to reach slaughter. The tendency for LEAN line lambs to be heavier than FAT line lambs from *actual* shoulder dissection data became significantly different for *predicted* half carcass weight (line difference = 0.36 ± 0.17 kg). Predicted line differences are more robust estimates (due to a greater sample size) than those calculated from actual carcass dissections.

Table 3.3 shows results adjusted to the same cold carcass weight for lambs from LEAN and FAT lines. LEAN line lambs had significantly lower dissected subcutaneous and total fat proportions, more lean and more bone than FAT line lambs. Despite having the same condition score prior to slaughter, they were also classified significantly leaner by MLC.

Table 3.2 *Sire line means and differences in carcass characteristics compared at a constant dissected subcutaneous fat weight†.*

Trait	LEAN	FAT	s.e.d
No. obs.	429	496	
SLWT (kg)	38.38	37.53	0.442
CS	2.893	2.885	0.011
AGE (days)	247.0	245.6	6.203
CCWT(kg)	17.27	16.93	0.200
CONF (E=5)	2.583	2.494	0.046
KO	0.45	0.45	0.002
<i>Dissected shoulder proportions ‡</i>			
IFAT	0.1560	0.1541	0.0019
LEAN	0.5411	0.5413	0.0023
BONE	0.1660	0.1653	0.0012

† See Appendix 1 for all abbreviations. ‡ Dissected shoulder joint only

Table 3.3 *Sire line means and differences in carcass characteristics compared at a constant cold carcass weight†*

Trait	LEAN	FAT	s.e.d.
No. obs.	429	496	
CS	2.890	2.893	0.007
AGE (days)	240.3	238.0	0.007
KO	0.448	0.451	0.002
MLC fat	0.109	0.112	0.001**
CONF (E=5)	2.509	2.476	0.044
<i>Dissected shoulder proportions ‡</i>			
SUBFAT	0.1291	0.1413	0.0029**
IFAT	0.1557	0.1554	0.0019
ALLFAT	0.2847	0.2966	0.0039**
LEAN	0.5425	0.5357	0.0030*
BONE	0.1675	0.1640	0.0014*

† See Appendix 1 for all abbreviations. ‡ Dissected shoulder joint only. * p<0.05, **p<0.01

Table 3.4 shows results adjusted to a constant age. When lambs were compared at a constant weight, there was little difference in the age at slaughter, so it follows that there would be little difference in the live and carcass weights of the

lambs when compared at a constant age. Again, the most consistent results were seen in the fat measurement comparisons. These show that the LEAN line lambs had significantly less subcutaneous and total fat than the FAT line lambs. As in the previous analyses, there was no difference between the intermuscular fat levels between the two lines, but LEAN line lambs did have greater lean and bone proportions than FAT line lambs.

Table 3.4 *Sire line means and differences in carcass characteristics compared at a constant age†.*

Trait	LEAN	FAT	s.e.d.
Number of observations	428	496	
SLWT	38.31	37.96	0.360
CS	2.895	2.897	0.007
CCWT	17.29	17.29	0.162
MLC fat	0.1108	0.1136	0.0014*
CONF	2.585	2.550	0.045
KO	0.452	0.456	0.0022
<i>Dissected shoulder proportions ‡</i>			
SUBFAT	0.1313	0.1428	0.0030**
IFAT	0.1566	0.1562	0.0019
ALLFAT	0.2878	0.2991	0.0040**
LEAN	0.5409	0.5347	0.0032
BONE	0.1655	0.1620	0.0013*

† See Appendix 1 for all abbreviations. ‡ Dissected shoulder joint only. * $p < 0.05$, ** $p < 0.01$

Price differences

Comparing prices received for the carcasses between the two lines is clouded by the seasonal price fluctuations experienced during the finishing period. Lamb prices tend to rise after the summer, reaching a peak in the following spring. Once these seasonal price fluctuations had been accounted for however £0.57 per lamb extra was received for the LEAN line lambs than for the FAT line lambs. This is approximately £0.20 lower than the anticipated sum, based purely on the

difference in carcass weight between the two lines, and ignoring the leaner fat class scores of the LEAN line.

From regression analyses, the main traits affecting price received per carcass were cold carcass weight and day of slaughter (fitted as a quartic effect because of seasonal price fluctuations) which together accounted for proportionately more than 0.80 of the variation in price. When fat and conformation class were included in the regression model, the total variance accounted for increased to only 0.83. A further multiple regression analysis was undertaken on the residual values, after slaughter day had been accounted for. Cold carcass weight alone explained 0.50 of the residual variation, and together with fat and conformation score, accounted for 0.62 of the residual variation. Dissected carcass proportions and condition score prior to slaughter had only a very small influence.

By drawing lambs to a target condition score equivalent to fat class 3L, we might expect the difference in fatness between the two sire lines to be very small, and the proportion of variation in price explained by differences in fatness, also to be very small. Conversely, drawing lambs at a constant live weight would reduce the apparent influence of live weight on price, and increase the variation explained by carcass fatness.

Heritability Estimates

Heritabilities of the slaughter and carcass traits estimated at a constant dissected subcutaneous fatness are presented in Table 3.5. **Appendix** Table A2 shows equivalent results for the other two end points. All the estimates tend to be low to moderate, but in general, bone and slaughter weight have the highest heritabilities, and intermuscular fat, conformation and condition score have the lowest. As the correction for subcutaneous fatness will have removed some genetic variation in intermuscular fat, this may partly explain the low heritability for this trait. The heritability estimates range from 0.09 for

conformation score, to 0.36 for pre- slaughter weight and bone measurements, and 0.39 for cold carcass weight. Some fluctuation in values is seen according to the end point.

Table 3.5 *Heritability estimates (s.e.) for traits adjusted to a constant dissected shoulder subcutaneous fat weight*

Trait	h^2
WWT†	0.20 (0.10)
AVFD†	0.22 (0.10)
MD†	0.20 (0.10)
SLWT	0.36 (0.13)
CS	0.10 (0.04)
AGE	0.34 (0.12)
CCWT	0.39 (0.14)
MLC fat	0.13 (0.08)
CONF	0.09 (0.07)
Shlderwt	0.28 (0.11)
IFAT	0.10 (0.07)
LEAN	0.27 (0.11)
BONE	0.36 (0.13)

† See Appendix for all abbreviations.

‡ End point correction not fitted

Heritability estimates for MLC fat and conformation scores, and condition score prior to slaughter, (all subjective measurements) are low, and similar at each end point. Heritability estimates for predicted carcass traits were almost identical to heritability estimates for actual carcass traits shown in Table 3.6, compared at a constant subcutaneous fat weight. This was also the case for traits compared at the other two end points, with the exception of bone estimated at a constant cold carcass weight (0.24 ± 0.10 , Vs 0.16 ± 0.18) for BONE and PBONE, respectively. These estimates are shown in **Appendix** Table A3.

Table 3.6 *Univariate heritability estimates (with s.e.) using data from shoulder and predicted carcass traits, compared at a constant dissected subcutaneous fatness*

Trait	Shoulder joint	Predicted total carcass
Weight†	0.28 (0.11)	0.28 (0.11)
Intermuscular fat weight	0.10 (0.07)	0.15 (0.08)
Lean weight	0.27 (0.11)	0.27 (0.11)
Bone weight	0.36 (0.13)	0.34 (0.13)

† Shoulder joint weight compared with predicted carcass weight

Correlation Estimates

Estimates of phenotypic and genetic correlations adjusted to a constant dissected subcutaneous fat weight are summarised in Table 3.7. **Appendix** Tables A4 and A5 show equivalent results for the other two end points. Most phenotypic correlation estimates are robust, with no standard errors greater than 0.04. However, there are large standard errors for several genetic correlations at all three end points. This is particularly the case where one or both traits have low heritabilities, and it limits the interpretation of many correlations.

The correlation estimates between ultrasonic measurements made at weaning and carcass and slaughter characteristics were moderate to low. The phenotypic correlation estimates (r_p) between average fat depth, and dissected subcutaneous fat are 0.26 and 0.30 at a constant cold carcass weight and constant age respectively. The estimates of genetic correlations between the same traits, at the same end points, are unreliable due to the large standard errors.

The phenotypic and genetic relationships between price and several carcass components are interesting. Obviously, the relationship between price and carcass weight is positive, and very strong. But this is also exacerbated by the fact that lamb prices per kg liveweight increased throughout the lamb finishing period, so older (heavier) lambs made more money. At a constant cold carcass weight,

moderate negative phenotypic (-0.32), but strong negative genetic (-0.78) correlations are seen between MLCFAT and price. The relationships between CONF and price are less clear. Conformation score is supposed to be an indicator of muscularity. However, it is not strongly favourably correlated with muscle depth, which is also an indicator of muscularity.

Table 3.7 *Estimates of heritabilities, genetic and phenotypic correlations† between lamb growth, live measures of body composition, pre- and post- slaughter characteristics at a constant dissected shoulder subcutaneous fat weight.*

Shlderwt	0.28	0.54	0.96	0.82	0.79	0.20	0.07	0.88	0.73	-0.12	0.20	-0.13	-0.05	0.58
	.11	.02	.00	.01	.01	.03	.04	.01	.02	.03	.03	.04	.04	.02
Intermusc. fat	0.71	0.10	0.38	0.25	0.30	0.13	0.19	0.45	0.29	0.04	0.14	-0.03	-0.01	0.27
	.20	.07	.03	.03	.03	.03	.03	.03	.03	.04	.03	.05	.04	.03
Lean	1.00	0.81	0.27	0.79	0.78	0.21	0.04	0.87	0.73	-0.14	0.17	-0.13	-0.04	0.58
	.00	.19	.11	.01	.01	.03	.04	.01	.02	.04	.03	.04	.04	.02
Bone	0.91	0.56	0.88	0.36	0.81	0.12	-0.05	0.80	0.68	-0.17	0.28	-0.11	-0.03	0.48
	.06	.31	.08	.13	.01	.04	.04	.01	.02	.04	.04	.04	.04	.03
Slterwt	0.93	0.42	0.94	0.90	0.36	0.18	0.04	0.89	0.74	-0.18	0.28	-0.06	-0.02	0.49
	.05	.31	.05	.06	.13	.03	.04	.01	.02	.02	.03	.04	.04	.03
Conf	0.37	-0.14	0.48	0.40	0.44	0.09	0.18	0.29	0.29	0.04	0.00	-0.03	0.09	0.19
	.35	.48	.35	.36	.33	.07	.04	.03	.03	.02	.04	.04	.04	.03
MLC Fat	0.39	0.37	0.40	0.26	0.14	0.19	0.13	0.14	-0.03	0.15	0.01	0.08	0.08	0.04
	.33	.41	.32	.34	.34	.44	.08	.04	.04	.04	.04	.04	.04	.04
CCWT	1.00	0.77	0.99	0.85	0.88	0.44	0.29	0.39	0.81	-0.12	0.20	-0.10	-0.03	0.62
	N/C	.20	.01	.08	.06	.35	.28	.14	.01	.04	.04	.04	.04	.02
Price	0.85	0.59	0.84	0.72	0.92	0.62	-0.06	0.89	0.32	-0.23	-0.03	-0.12	-0.16	0.77
	.09	.28	.09	.14	.06	.32	.31	.06	.12	.03	.04	.04	.04	.01
CS	-0.69	-0.60	-0.64	-0.57	-0.69	-0.42	-0.09	-0.73	-0.87	0.10	0.02	-0.01	0.02	-0.19
	.15	.25	.23	.21	.16	.38	.38	.21	.14	.04	.04	.04	.02	.04
WWT	0.21	0.02	0.19	0.14	0.18	-0.06	0.17	0.07	-0.11	0.06	0.20	0.36	0.55	-0.35
	.32	.40	.30	.32	.31	.46	.34	.31	.32	.39	.10	.03	.03	.03
AVFD	-0.46	-0.25	-0.45	-0.47	-0.38	-0.64	0.24	-0.45	-0.41	-0.08	-0.41	0.22	0.35	-0.27
	.27	.37	.28	.26	.28	.42	.32	.25	.27	.32	.29	.10	.03	.04
MD	-0.31	-0.28	-0.26	-0.28	-0.35	-0.37	-0.58	-0.41	-0.54	-0.97	0.67	-0.06	0.20	-0.40
	.31	.39	.32	.31	.30	.48	.27	.29	.26	.02	.20	.36	.10	.03
AGE	0.56	0.57	0.54	0.50	0.67	0.43	0.15	0.67	0.84	0.95	-0.37	-0.22	-0.94	0.34
	.20	.28	.20	.22	.17	.37	.31	.15	.09	.09	.27	.29	.08	.12

† Heritability estimates on the diagonal. Genetic correlation estimates (and standard errors) below the diagonal. Phenotypic correlation estimates (and standard errors) above the diagonal

Discussion

This study has demonstrated that selection for divergent subcutaneous fatness under intensive feeding conditions results in progeny which are also divergent in subcutaneous fat, when reared under extensive conditions. This observation was first seen at weaning (discussed in Chapter 2), when lambs born from LEAN line sires had significantly less subcutaneous fat measured ultrasonically than lambs born from FAT line sires. After slaughter, LEAN line lambs were classified leaner than FAT line lambs by MLC, even though they were selected for slaughter at a condition score of 3. When results were adjusted to a constant fatness to reflect this end point, no difference in dissected lean proportion between the two lines was seen and it is possible that LEAN line lambs were incorrectly assessed prior to slaughter (despite there being no difference in the condition score recorded.) The difference in fatness between the two lines seen at weaning and at slaughter was verified by results from carcass dissection at a constant carcass weight and constant age, which showed that LEAN line lambs had less subcutaneous fat than FAT line lambs. These results indicate that body composition in lambs reared in hill situations can be manipulated through genetic selection. The design of this experiment follows what actually happens, to a certain extent, in the hill sheep breeding community. Hill farms in more favourable locations produce rams for selling to other hill farms, often in harsher environments. Frequently, these rams receive supplementary feeding and are reared on good quality pasture. Once sold, these rams are normally managed on hill pastures of poorer quality than those on which they were reared. The results from this trial are therefore particularly relevant for the UK hill sheep breeding industry.

Adjusting data to compare lambs from LEAN and FAT sires at three end points at slaughter enables the effects of such divergent selection to be assessed on a large number of traits, although results at a constant cold carcass weight and constant age must be interpreted cautiously, since slaughter was actually at a target

constant fatness. It is also appropriate to compare animal performance using data adjusted to three different end points because objective selection decisions are based on parameters estimated at a given end point. It may appear inappropriate for the end point in this trial to be constant fatness, when differences between genetic lines in fatness are under investigation. However, under commercial conditions, lambs are normally selected for slaughter at an acceptable level of fatness, and therefore commercial carcass grades are available for each lamb slaughtered. Other carcass characteristics, such as carcass weight and age at slaughter, are then the indicators of performance. These are important for hill lamb producers, as payment is based on a combination of weight and fatness, and to a lesser extent, age of lamb.

The information on the traits affecting price received per lamb from the regression analyses is interesting. The timing of slaughter and weight of lamb at slaughter appear to have an overriding influence on the price obtained. The 'quality' traits had a minor influence in comparison. However, it must be recognised that by selecting animals to a constant body condition score to ensure the majority of lambs would fall into the 'normal' grades, limits the variation seen in fatness and hence the price differentials per kg received per lamb are reduced. If lambs had been selected for slaughter at a constant weight, undoubtedly a greater proportion of variation in price would be explained by differences in fatness.

Table 3.8 summarises heritability estimates from previously published papers, mainly from grass-based finishing systems. None of the estimates reviewed are specifically from hill or mountain breeds, although most references are for work done in Australia or New Zealand, and therefore use sheep genotypes adapted to extensive management systems.

Table 3.8 Summary of published heritability estimates

Trait	h^2 (\pm s.e.)	End point	No. of sires and breed	Reference†
<i>Fat Depth</i>				
5-9 months	0.01± .03	Fixed age	161 / Poll Dorset	1
10-13 months	0.18± .07	Fixed age		
14-18 months	0.28± .15	Fixed age		
205 days	0.23	Fixed age	60 / Romney 40 / Romney X	2
5-9 months	0.11± .05	Fixed live weight	161 / Poll Dorset	1
10-13 months	0.33± .09	Fixed live weight	161/Poll Dorset	
14-18 months	0.29± .16	Fixed live weight	161 / Poll Dorset	
	0.25	Fixed age	10 / Coopworth	5
	0.33	Fixed live weight	20 / Southdown	4
	0.28± .08	Fixed live weight	130 / Hyfer	6
	0.22± .08	Fixed age	130 / Hyfer	6
7 months	0.38± .03	Fixed live weight	125 / Coopworth	7
<i>Muscle Depth</i>				
5-9 months	0.15 ± .05	Fixed live weight	161 / Poll Dorset	
10-13 months	0.15± .06	Fixed live weight	161 / Poll Dorset	1
14-18 months	0.19± .12	Fixed live weight	161 / Poll Dorset	
	0.38	Fixed age	60 / Romney 40 / Romney X	2
<i>Muscle Width</i>				
	0.63	Fixed age	60 / Romney 40 / Romney X	
<i>Pre-slaughter live weight</i>	0.31± .12	Fixed age	79 / Swedish Pelt sheep	3
<i>Carcass weight</i>	0.17± .10	Fixed age	79 / Swedish Pelt sheep	
<i>Dressing proportion</i>	0.05± .09	Fixed age	79 / Swedish Pelt sheep	
<i>Fat score</i>	0.21± .11	Fixed age	79 / Swedish Pelt sheep	
<i>Subcutaneous fat (mm)</i>	0.20± .11	Fixed age	79 / Swedish Pelt sheep	
<i>Dissected lean</i>	0.08± .09	Fixed age	79 / Swedish Pelt sheep	
<i>Dissected fat</i>	0.15± .10	Fixed age	79 / Swedish Pelt sheep	
<i>Dissected bone</i>	0.26± .11	Fixed age	79 / Swedish Pelt sheep	

†(1) Gilmour, *et al.*, (1994). (2) Waldron *et al.*,(1992). (3) Henniñgsson and Malmfors, (1995). (4) Solis-Ramirez *et al.*, (1993). (5) Fennessy *et. al.*,(1992). (6) Fogarty *et al.*,(1994). (7) Morris *et al.*, (1997).

Most estimates of heritability of liveweight at slaughter and cold carcass weight in this study are within the range of published estimates for these traits for lambs reared on pasture. However, the published estimates for carcass weight are based on hot carcass weight, and none of them have been calculated at a constant fat level. The slight differences amongst estimates according to the end point of the analysis can be partly explained by the different interpretation of what are superficially the same traits at differing end points. For example, fat weight adjusted for liveweight is roughly equivalent to fat percentage, and liveweight adjusted for age is essentially lamb growth rate. It is interesting to note that heritability estimates for pre- and post-slaughter weights are considerably higher when measured at a constant fatness.

Heritability estimates for carcass composition are comparable to those cited in the literature, with the exception of bone, which is higher than several estimates quoted in the literature for pasture-based rearing systems.

The genetic correlations between ultrasonic measurements taken at weaning, and dissected carcass tissue traits are clearer at a constant age or carcass weight than at a constant fatness, where they are negative. The large standard errors for the estimates of genetic correlations for these traits limit the interpretation of this result, but may be explained in part due to the long finishing period the animals took to reach slaughter. During this long finishing period lamb growth rate was not constant, and fluctuated between periods of slow (or negative), and positive growth rate. It would be beneficial to re-estimate these parameters both on a larger data set, or with an improved pedigree structure, and also for lambs which had a shorter finishing period to obtain more reliable estimates of genetic correlations.

Some of the results from this work do not fit well with industry expectations. As the main influences on price received per lamb are shown in this study to be the carcass weight and date of slaughter, then stronger price signals are required to influence the improvement of carcass quality through decreasing fatness and improving conformation. Higher premiums are paid by abattoirs for carcasses with better conformation. Yet the results here show that the heritability of conformation score is low, and it will be a difficult trait to change through within-breed selection. In addition, results comparing animals at a constant fatness show that the phenotypic and genetic correlations between conformation score and live ultrasonic measurements at weaning are unfavourable, and those between conformation score and MLC fat class are positive, indicating that fatter carcasses will have better conformation. These are confusing messages which are likely to persist, unless abattoirs adopt an alternative to the current visual assessment of conformation.

Some of the information provided in this study will be used to incorporate carcass characteristics into an index of overall merit for hill sheep, together with indicators of maternal performance. The results from these analyses demonstrate that some components of body composition are under significant genetic control in hill sheep, and that it is possible to alter them under extensive rearing conditions.

Chapter 4

Breeding goals and economic values for hill sheep.

Introduction

In most livestock production systems, profitability depends on several different animal characteristics, rather than a single trait. The use of selection indexes to identify animals of high genetic merit for several traits is widely accepted as being highly cost effective (Wade and Goddard, 1994, Banks, 1994, Simm *et al.* 1997). For terminal sire sheep breeds (meat breeds) in the UK, identifying breeding goals for genetic improvement using selection indexes is reasonably straightforward, as improving carcass weight and quality are the main priorities for breeders of these sires. For example, the selection index currently being used by the major terminal sire breeds in the UK via the Signet performance recording scheme, incorporates live weight and ultrasonic measurements of fat and muscle, as predictors of carcass lean and fat weights (Simm and Dingwall, 1989).

For hill sheep, the breeding goals are less clear. This is because hill flocks supply flock replacements for use in this, and in other sectors, and they produce lambs destined for slaughter. Hill sheep must be adapted to their harsh environment such that they survive and rear their own lambs with minimal human intervention. The productivity of such hill flocks is closely related to the grazing quality of the hill and the amount of improved pasture available, which in turn is largely determined by climate and topography. The breeding goals currently used by UK hill sheep flocks via Signet, are a combination of lamb growth, mature size, litter size and maternal ability. The desire to incorporate predictions of carcass merit has led to some hill flocks using ultrasonic measurements on a selected number of animals, as predictors of carcass merit in addition to the traditional maternal index. To date, these measurements are not combined into an overall index score.

With regard to hill farm environment and management, three typical hill farm types have been defined as intensive, semi-intensive and extensive (Eadie 1985). Extensive hill sheep farms are characterised as having colder, wetter environments,

little improved grassland, low stocking densities, and with sheep performance at the poorer end of the spectrum. As a result, these farms usually sell all surplus lambs not required as replacements as 'store lambs', on to other farms to be finished for slaughter. The intensive (or 'upland') hill sheep farms lie at the other extreme. These farms have higher productivity, would normally have the infrastructure to 'finish' all those lambs for slaughter which are not required as replacements or to be sold for further breeding, and they occupy drier and less hostile hill areas. Semi-intensive hill farms lie between the two farm types mentioned above.

Despite hill farm systems varying considerably, the objectives of farms within this sector are arguably the same: to produce breeding females capable of surviving, and rearing progeny with high carcass value, in adverse climatic conditions. However, it is possible that the economic value of each component of the breeding goal might differ considerably for the three farm systems, largely as a result of the differing levels of productivity and the physical constraints of the farms themselves.

Few studies have considered a 'whole farm' approach to derive relative economic values for sheep on grass-based farming systems (Amer *et al.*, 1999; Wang and Dickerson, 1991). This is largely because of the difficulty in predicting incremental costs and benefits in a grazing situation, as a result of marginal changes in, say, an increase in the number of twin lambs compared to singles, or from a decrease in the number of replacements required as a result of improving longevity. Such changes have a significant impact on the value of genetic improvement in hill environments, where the real limitations of grass production can only be overcome by purchased inputs, renting additional grazing, or by a reduction in the number of other livestock carried on the farm.

The value of constructing bio-economic models for estimation of economic values is that more detailed and mechanistic understanding of the interface between breeding and production is possible (Harris and Newman, 1994). In addition,

attention to the inter-relationships between mature size, weaning weights and post weaning growth rate can be made, and allowances can be made for the known non-linear relationships among them (Koots and Gibson, 1998a,b). In addition, constraints such as fixed feed available from pasture and fixed amount of output (e.g. milk under quota limitations) can be incorporated to make the economic values closer to their true values in production systems (Harris and Freeman, 1993, Groen, 1989). Visscher *et al.* (1994) advocate that defining the size of an enterprise may be more useful when deriving economic weights, e.g. they derived economic values for dairy traits with fixed feed supply.

The objectives of this Chapter are to describe the method by which economic values were derived for a combination of carcass and maternal characteristics for UK hill sheep flocks using a 'whole farm' approach, and to show how these economic values vary between different production systems as a result of differences in the physical constraints of farm size, pasture availability and quality, and the biological limits of the sheep themselves. The effects of variation in market prices on economic values for the major costs and returns were explored by price sensitivity analyses.

Methods

General Approach

A model was developed to simulate the three farm types described above (extensive, semi-intensive and intensive) to derive economic weights for breeding goal traits tailored to each of the three farm systems. The model simulates a flock of 100 ewes over a time period of 10 years. Assumptions are made for typical production levels, and these are inputs to the model. The model then calculates the numbers of each class of stock on the farm at any point in time. The nutritional requirements of each stock class throughout the year are determined, together with the ability of the farm to meet these requirements, and the variable costs associated with production. Economic values are then derived by first calculating the change

in flock gross margin following a unit change in the trait of interest, with the performance of the other goal traits held constant. These values are then multiplied by discounted gene expressions of the trait, to account for the different timing and frequency of expression of genetic improvement in each of the goal traits. For example, improvements in longevity can be expressed only once in a ewe's life, whereas improvements in litter size are expressed earlier and several times. The discounted gene expressions are then summed over 15 years to obtain the final economic values.

The model

Hill farm type and feed availability

A detailed Hill Grazing Management Model (HGMM) to predict seasonal changes in the quantity and quality of dwarf shrub- and grass- dominated vegetation types commonly found in the hill areas of the UK, has been developed and described by Armstrong *et al.* (1997a). The dry matter production is predicted from each different vegetation type, after adjusting for temperature zone, altitude, rainfall, rainfall retention and fertiliser use. Seasonal changes in the quantity and digestibilities of the offtake by ewes and lambs are then determined according to the numbers and live weights of each class of stock grazing the hill. This model provided the inputs of hill grass availability and offtake by sheep (Armstrong *et al.*, 1997b). These results were then fed into the 'whole farm' simulation model described in this chapter, to provide the foundation for the development of the three model farm types, from which economic values were determined.

All three farm types were assumed to have a 100 ewe purebred Scottish Blackface breeding flock, but to differ significantly in the proportion of hill and inbye land, quality of hill pasture and hence hill stocking rate, to reflect the three main hill types described earlier. The hill pastures on all three farms were assumed to be heather (*Callunus*) based. To avoid changing too many variables, all three base farms were assumed to be within a single Climatic Zone (that which covers

Northumberland, the Southern Uplands and Perthshire). However the vegetation mix and therefore its overall grazing quality were changed between the three farm types. The Intensive farm with the best 'summer' hill has a proportion of good quality *Festuca Agrostis* pasture in addition to heather, which itself includes a high proportion of *Festuca Agrostis* within it. The other two farm types had less *Festuca Agrostis* within the heather plant communities, and had *Nardus* pasture as the main grassland area with relatively low proportions of good quality plant species within it. The areas of heather were set by examining the level of utilisation of pioneer heather by successive runs of the HGMM, and fixing on an area which gives an annual utilisation rate of proportionally 0.20, which is widely accepted as a sustainable level of grazing utilisation (A. McDonald, personal communication). Thus the overall quality of grazing, the digestibility of vegetation consumed, declines from intensive to extensive, even though the available land area increases. Appendix II provides the areas of each plant community type, used to provide the base data for the hill pastures for each farm type.

Most hill farms have a range of pastures in their enclosed paddocks ('inbye') ranging from high quality, recently reseeded pasture to wetland of low agricultural value. It was assumed that the improved pastures comprised reseeded perennial ryegrass, because credible data on production and responses to nitrogen are available for this grass species. This provides a satisfactory mechanism to balance animal requirements with pasture availability. However, it does tend to underestimate the inbye area compared to the typical hill farm, whose inbye areas are rarely so uniformly productive. Thus the intensive farm model uses 5 hectares of high quality inbye pasture to carry some 45 twin-rearing ewes and produce a significant quantity of silage, a slightly smaller but more productive area of improved pasture than commonly seen on hill pastures.

For each farm type (intensive, semi-intensive and extensive), a 'baseline' farm was created on which grazing resources and animal requirements were in balance with

typical levels of feed and fertiliser to improved pastures. Inevitably, due to the complexity and variability of hill farm systems and of hill pastures, these baseline farms are unique. Using the HGMM, it is possible to estimate offtakes of digestible dry matter for a set of pasture types. Intake of the sheep is restricted, in practice, by residual availability of pasture as the season progresses and by the capacity of ewes to digest the poor quality diet.

Feed requirements

Using equations based on AFRC (1993), the model calculates the requirements for total feed energy (in units of metabolisable energy) of sheep to reflect their changing physiological needs for pregnancy, for loss and re-gain of body weight in winter, for the net costs of lactation and changing body weight in the summer. In addition, it then takes into account the different productive capacities and nutritional values of pastures of different types and in different seasons. These pastures offer different opportunities for sheep to meet their dietary requirements depending upon their relative abundance and upon the availability to the animal of digestible matter. This allows the costs of changes in animal performance (e.g. due to selection) to be estimated by modifying animal nutrient requirements throughout the year.

Differing energy concentrations of the diet also affect the energetic requirements of the animal itself, as sheep on low quality diets have higher requirements for energy than those on higher quality diets, due to greater loss of heat and methane during digestion (ARC, 1980). In addition, the model reflects the movement between different sectors of the farm of ewes and of the other non-productive sheep (lambs, weaned lambs, draft ewes, rams and replacement ewe lambs).

Using the digestibilities of the predicted offtakes from the HGMM, it is possible to calculate the energy requirements of each ewe for each month of the year. This differed according to whether ewes are on the hill or on inbye, and according to

their physiological status. Lamb energy requirements are also calculated accounting for the energy coming from milk (part of the ewe's energy requirement) and that coming from grazing. Feed requirements are not fixed as they interact with body weight change and the lamb (and conceptus) weights (AFRC 1993). By including data on these latter factors it is possible to identify the difference between pasture energy available on the baseline farm, and that necessary to meet the combined demands of maintenance, pregnancy and weight change (usually negative or neutral in winter).

Matching feed availability with requirements

Table 4.1 shows the main management differences between the three model farms. Together with the numbers of sheep in each class of stock, they formed the base from which feed requirements were determined. Differences between the food energy available and that required were converted into supplementary feed energy requirements and then into monetary value. As the sheep in the baseline model were already receiving supplementary feed, marginal changes in requirements were allocated to extra supplementary feed alone. In practice, some of the change could be met in the short term by changes in the utilisation of semi-natural vegetation. However, any change in utilisation of grass and heather in one season can have long term impacts on future productivity (Grant *et al.*, 1982), which will impact on both future pasture availability and animal performance. Therefore, additional requirements were assumed to be met entirely from supplementary feed. Appendix III shows details of how each component of animal requirements was calculated, and the assumptions made in the model to determine energy requirements throughout the year.

Table 4.1 *Characteristics of the main distinctions between the three model hill farms*

	Intensive	Semi-Intensive	Extensive
No. ewes in flock	100	100	100
No. lambs reared/ewe	1.21	1.05	0.89
Hectares hill	22	40	80
Hectares reseed	5	3	1
Proportion inbye	0.23	0.075	0.01
Lamb weights	singles > twins	singles = twins	twins > singles
Weight of ewe	57 kg	53.5 kg	50 kg
<i>Management</i>			
Mating	All ewes inbye	0.30 inbye	All ewes on hill
Mid pregnancy	All ewes on hill	All ewes on hill	All ewes on hill
Late pregnancy	All twin + 0.2/single inbye	All twin inbye	All twins inbye
Lambing	All inbye - singles for ave. 20 days	Twins inbye + singles for ave.15 days	Twins inbye
Lactation	Twins inbye	Twins inbye	Twins inbye
Post weaning	Lambs + cast ewes inbye 2 months. All ewes to hill. Hoggs - inbye 1 month then to wintering or shed	Lambs + cast ewes inbye 2 months. All ewes to hill. Hoggs - inbye 1 month then to wintering or shed	Lambs + cast ewes inbye 1 month. All ewes to hill. Hoggs - inbye 1 month then to wintering or shed
Lamb destination: non-breeding lambs	All lambs finished	0.5 finished, 0.5 sold as stores	All lambs sold as stores

Improved grassland

The methodology for estimating marginal changes in costs due to changes in animal state and location during summer on improved grassland is less complex. Summer grass production is estimated using the equations of Doyle and Lazenby (1984), corrected for annual production using the approach described by Armstrong *et al.*, (1997b). Altitude and climatic zone were corrected for using the methodology of Lance (1984) and using the corrections described by Doyle and Edwards (1986) to change monthly production. It was then assumed that 80% of this grass production was available, being the maximum utilisation of perennial ryegrass achievable by sheep (Sibbald *et al.*, 1987). The energy supply from the utilisable grass production was then compared with that required by the sheep using the improved pasture area. Then either the area of land available, or the fertiliser inputs, were adjusted until utilisable production met requirements in all months. Precise relationships between fertiliser nitrogen supply and grass production were incorporated into the equations used to calculate total grass production (Doyle and Lazenby, 1984). By modifying these inputs, production could be made to equal or exceed requirements in all summer months. This fertiliser input is the main mechanism for deriving the economic cost of changes in animal requirements as a consequence of changing the size of ewes, the size or number of lambs, and the ratio of twins to singles. However, responses to increased fertiliser inputs are finite, and farmers rarely exceed certain upper limits. In the models developed here, the maximum input of fertiliser N was set at 150 kg N/ha. This provides an upper limit on the amount of grass that could be produced by the farm's own inbye land. However, if requirements still exceeded this availability, then an extra area of land of the same pasture quality and productivity was assumed to be rented in the summer. This is common practice for UK hill flocks.

Grassland sheep systems are constrained by spring and autumn grass production but usually have a surplus of grass in mid season (Maxwell *et al.*, 1985, Treacher, 1990). This grass is available for conservation. Increasing grass production by

using more fertiliser to meet the demands of the sheep in spring, increases the total annual production of grass and, in particular, the surplus grass available in mid season. So, as well as a direct cost due to more fertiliser, there is also a benefit of extra conserved forage. This extra forage has a value which is subsequently deducted from the increased production costs. The net grassland cost is therefore calculated as the cost of fertiliser application of N (plus appropriate P and K), less the gross margin value of the conserved forage if sold at market value (SAC, 1997). The converse argument follows for reduced demands for grass by the sheep system. This is illustrated in Figures 4 and 5.

Figure 4: Energy requirements by sheep on hill, and energy supplied by grazing - difference in winter is the supplementary feed requirement

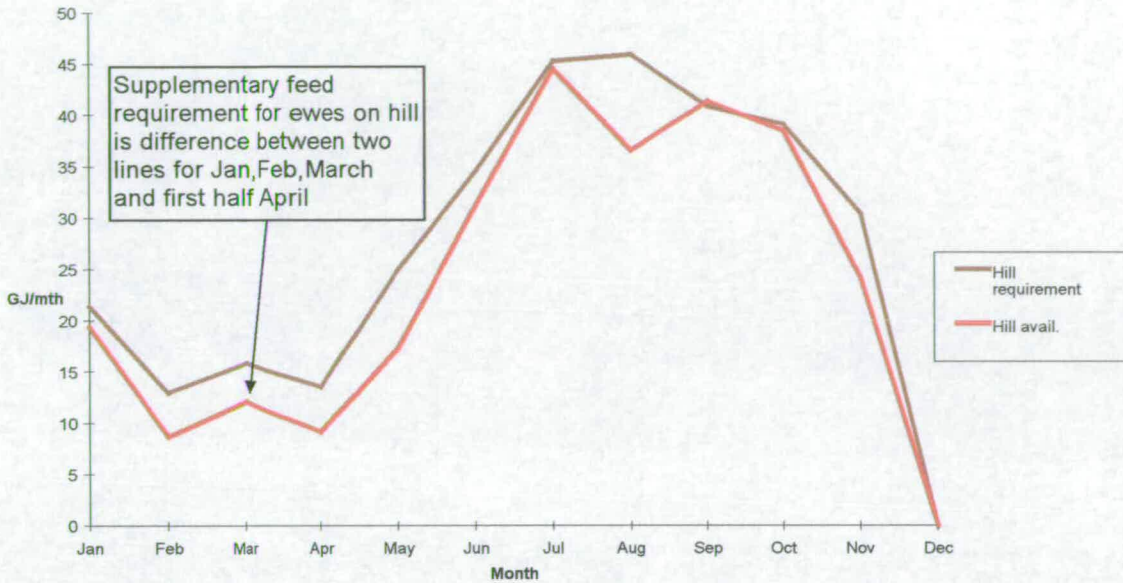
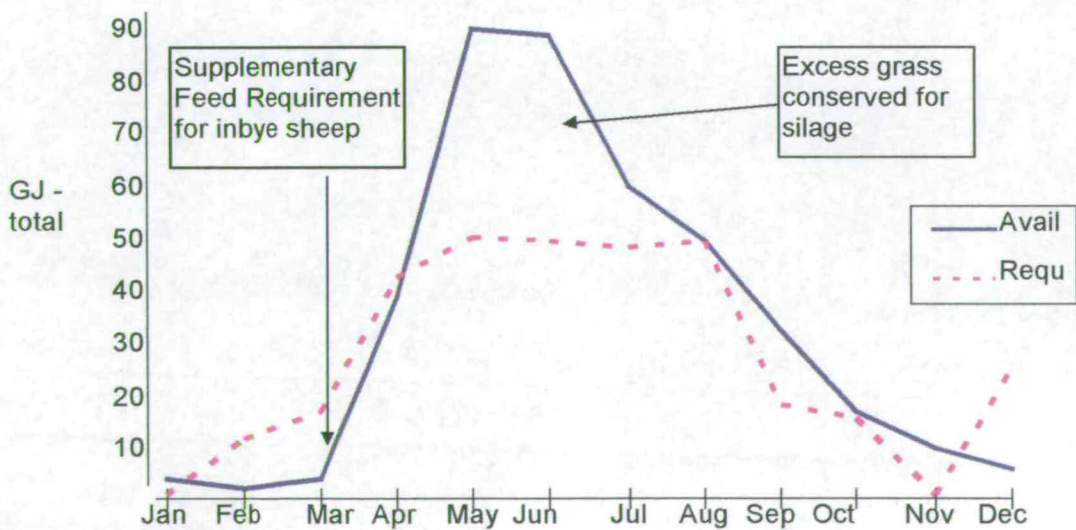


Figure 5: Inbye pasture for intensive farm type showing both winter feed deficit and matching grass supply, to equal or exceed animal requirements in May to August by applying the appropriate fertiliser Nitrogen



Flock structure

The Markov Chain

The core of the model developed here uses Markov chain methodology (Agrawahl and Heady, 1972) to generate the flock structure and replacements needed according to the assumptions made about ewe survival and productivity. Markov chains have been used frequently in agricultural research since the 1960s (Jenkins and Halter, 1963) to model the economics of milk production, and to solve animal replacement problems in both the dairy and the pig sectors (reviews by Arendonk, 1984; van der Wal and Wessels, 1985, White and White 1989; Kristensen, 1993), and to estimate age distributions in herds of beef cattle under different culling strategies (Azzam *et al.*, 1990; Koots and Gibson, 1998a). Markov chains have recently been used to establish the economic values of conception rate in dairy cattle (Boichard, 1990; Stott, Veerkamp and Wassell, 1999) and for health, functional and other traits in dairy cattle (Reinsch and Dempfle, 1998). To my knowledge, no studies have been published using Markov dynamic programming techniques for the derivation of economic values for sheep.

The essence of the Markov chain approach is that farms are dynamic systems; the transition of an animal from one state to another is described by the independent probability of reaching the second state. In the hill sheep model for example, the probabilities of the number of ewes in each age group 'surviving' until the following production year are computed, and a series of matrices are used to derive the ewe age structure and number of lambs born alive per ewe, according to given assumptions of fertility for each age group. The model runs across a 10 year time span, after which the data produced from the 'steady' state of the Markov Chain are integrated into the rest of the sheep system calculations. In this way, the complex, long term effects of different litter sizes, barren rates, ewe and lamb survival rates on the number of replacements available and required can be encapsulated in a single gross margin.

Hill flocks in Scotland normally sell or cull breeding ewes from the flock after they have reared four lamb crops (when they are 6 years old). This age structure was incorporated into the Markov chain, where each age group of ewes was represented by a row vector of states $\mathbf{S}(a)_{t=0}$ where a represents the number of ewes in each age group 1-6 at time $t=0$. The number of ewes in $t=1 \dots 10$ years depends on the matrix of transition probabilities \mathbf{P} , which describes the probability of survival from the state described by row i at time t , to the state described by column j at time $t+1$. As \mathbf{P} is fixed for all values of t , the Markov Chain is therefore static. The assumptions of survival rate in each age group were based on data from 1990 to 1996 from the two SAC experimental hill flocks representing two extreme hill farm systems.

The assumptions of the proportions of productive ewes (excluding barren and ewe deaths prior to lambing) and litter size were defined by diagonal matrices, also fixed for all values of t . \mathbf{N} = a matrix of the proportion of productive ewes per age class on the diagonal, and zeros on the off-diagonal, and \mathbf{L} = matrix with litter size per ewe age category on the diagonal, and zeros on the off-diagonal. The chain is then defined as

$$\mathbf{S}(a)_{t+1} = \mathbf{P} \mathbf{S}(a)_t$$

and

$$\mathbf{N} \mathbf{L} \mathbf{S}(a)_t$$

gives the numbers of lambs born for each age group (and thus a flock average) and the number of replacements needed each year.

The steady state of the Markov Chain is reached before $t=10$, and the final population structure was used in the standard expected gross margin for comparative purposes. It provides information on the optimal flock structure, litter size and replacement rate on which the model flock performance is based. Figure 6 shows a schematic description of the \mathbf{P} , \mathbf{N} and \mathbf{L} for the intensive farm system. The

input data for the matrices for the other two farm systems are summarised in Table 4.2.

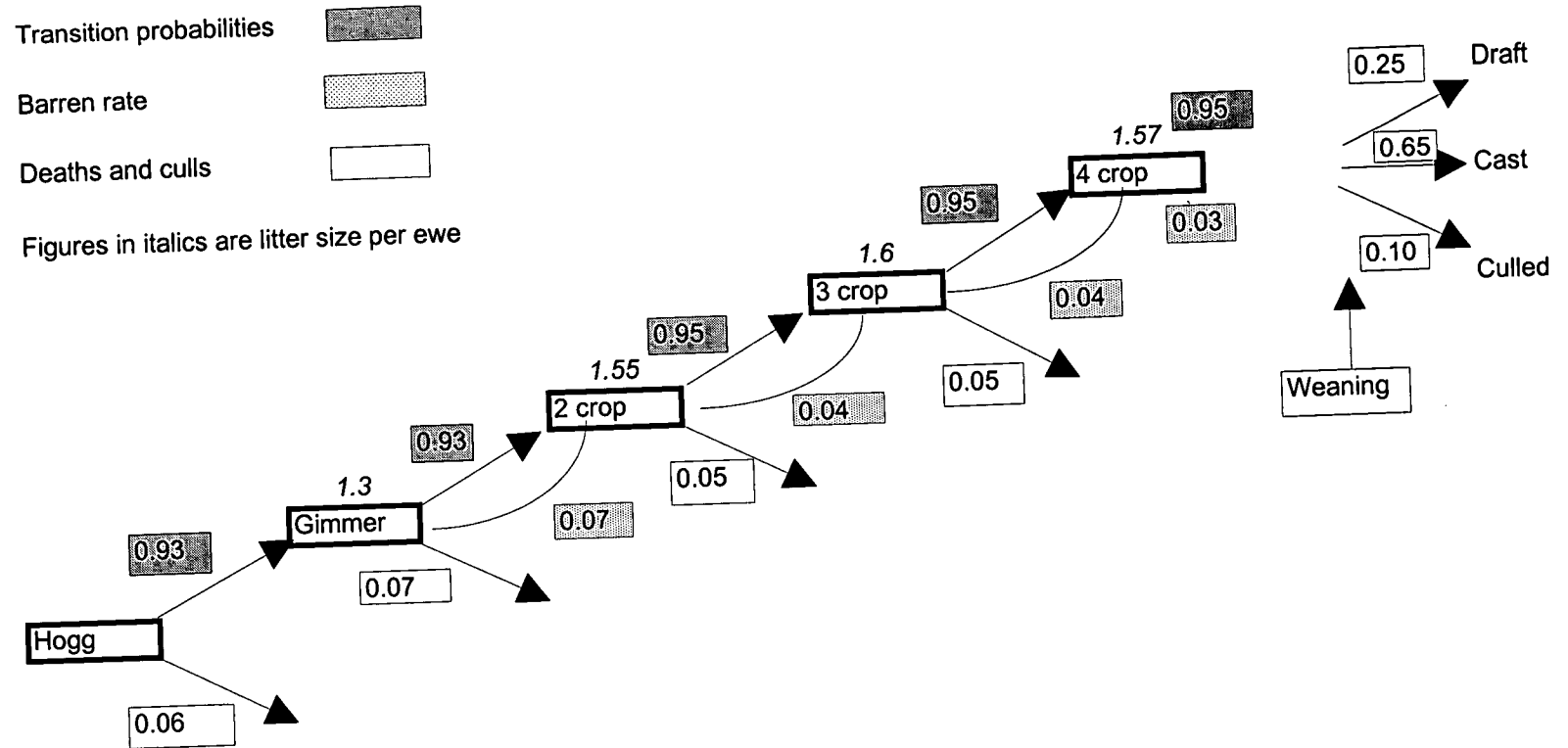
Table 4.2 *Markov input data for semi-intensive and extensive farm systems*

Proportions of ewes in 100 ewe flock†			
Ewe age	Transition probabilities (P‡)	Non-productive proportion (NP)	Litter size (LS)
<i>Semi-intensive</i>			
1(replacements)	0.92	1§	0
2	0.92	0.1000	1.05
3	0.94	0.0817	1.36
4	0.94	0.0750	1.44
5‡	0	0.0750	1.44
<i>Extensive</i>			
1(replacements)	0.92	1	0
2	0.91	0.1117	0.80
3	0.93	0.0950	1.20
4	0.93	0.0873	1.25
5	0	0.0863	1.25

†including ewe replacements. ‡ Proportions of ewes 'surviving' to the next age group For example, proportionately 0.93 of 3 year old ewes remain in the flock to become 4 year old ewes in the extensive farm system. § No ewe lambs are mated. † All 5 year old ewes are culled or sold before the following breeding season, i.e. when they would be 6 years old at mating.

Figure 6

Schematic description of Markov chain probabilities for the intensive farm system



Extension of model using data derived from the Markov chain

The data derived from the Markov chain formed the basis for the ewe age structure, replacement rate and number of lambs, and were combined with lamb survival and performance data. These data provided the total flock performance for each farm, which in turn was used to calculate farm income from sales of lambs, cast ewes and wool, and corresponding variable costs of production (veterinary, medicine, feed, ewe-lamb ('hogg') wintering, haulage, shearing and forage costs). The model simulated credible farm production systems to produce gross margins comparable to industry standards (SAC, 1997). The factors influencing productivity included ewe mature size, lamb survival, lamb birth type, lamb sex, proportion of single versus twin lambs kept for breeding (in turn affecting lamb weights at weaning and carcass weights), lamb growth rate, lamb weights (weaning weight and carcass weight), and proportion of non-replacement animals sold as 'store' lambs or fattened for slaughter. (Store lambs are live lambs sold for further growing and finishing (or fattening), usually to farms with surplus grass or other cheap source of feed). The algorithms for the computation of more complex influences on productivity (number of ewes lambing for each litter size according to defined flock averages, lamb live weights and carcass weights) are shown below.

Lamb birth types

The number of single, twin and triplet births was determined from the following equations:

$$\text{Singles} = 3 - 2.5\mu + 0.5\mu^2 + 0.5\sigma^2$$

$$\text{Twins} = 4\mu - 3 - \mu^2 - \sigma^2$$

$$\text{Triplets} = 1 - \text{proportion single} - \text{proportion twin}$$

where μ = mean number of lambs born per ewe lambing (lambing %) and σ^2 = variance of lambing %. These equations were derived by solving the **expectations** for the mean and variance of litter size (Bishop, pers. comm.) A coefficient of

variation of 0.36 (Fogarty,1985) was assumed, giving $\sigma^2=(0.36 \mu)^2$.

The proportion of lambs lost prior to being sold was assumed to be 10% for all single lambs, across all three farm types. Twin lamb death rate was assumed to be 15% and that for triplets 30%.

Lamb live weight and carcass weight

Lamb weights were derived from the same principles summarised by Amer *et al.*, (1997) using a form of the Gompertz (1825) growth equation, to express lamb weights at a given time according to their potential (as defined by their mature weights under non-limiting conditions). The additional multiplier, *Mx* allows for limiting growth conditions, and has been used to derive lamb weights appropriate for each farm system modelled. The equation used in the model is as follows:

$$W_x = A * \exp (-\exp(G - B_{t_2-t_1}))$$

where:

W_x = lamb weight,

A = mature weight,

$G = \ln (-\ln (bwt/A))$,

$B = 0.0365/A^{0.73} * M_x$,

M_x = proportion of potential growth achieved, and

t_2-t_1 = time from birth to weaning (or from weaning to slaughter for slaughter weight.)

The values of M_x were altered for each farm system to produce lamb weights typical for each system, and based on average weights from SAC experimental farms. Live weights were determined in this way for single male lambs, and a set of constants was used to derive weights for single females and for twins and triplets of both sexes (see Table 4.10). Carcass weights were derived by scaling the assumed live weight by a constant killing out proportion of 0.43.

Once the numbers of lambs of each birthtype, sex and live weight were computed, the numbers of each class of stock on the farm were used to predict the pasture requirements and utilisation for feed throughout the year, as described above. A flow diagram to describe the sheep system is shown in Figure 7. Together with Figure 8, this shows how the animals' requirements and pasture production are linked together.

Figure 7

Hill sheep model: Overview of flow of information

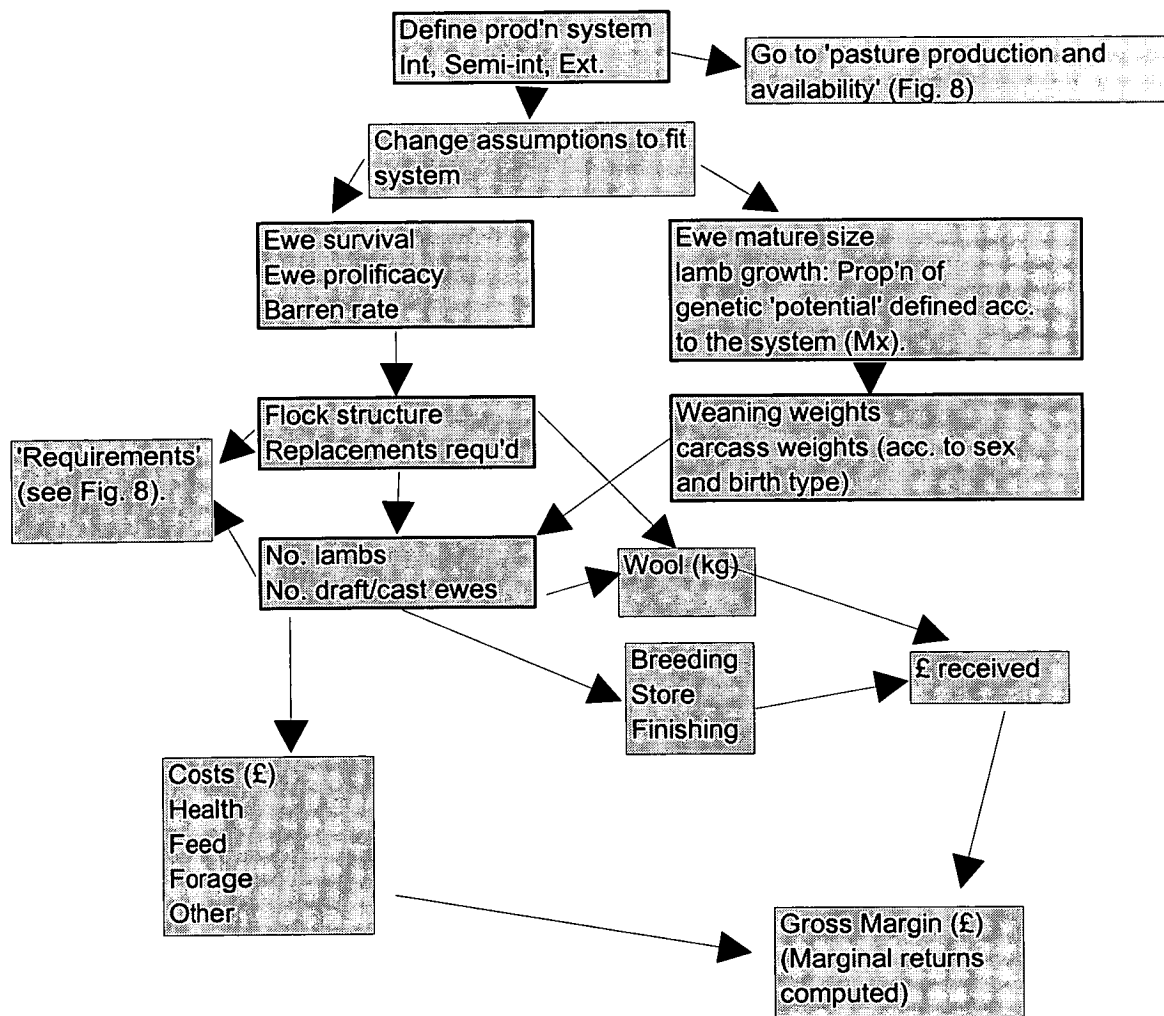
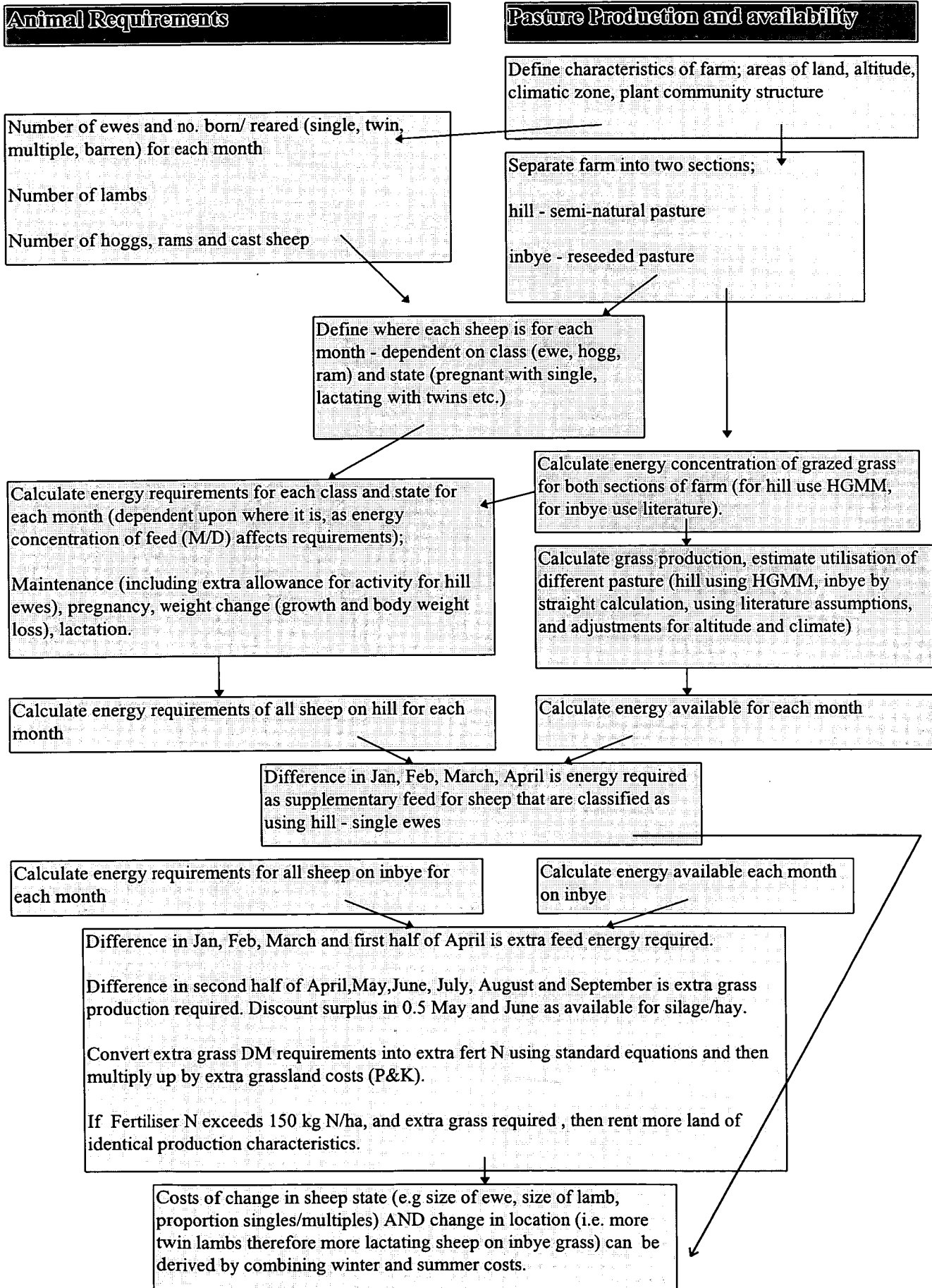


Figure 8

Links between animal nutritional requirements and pasture production



Lamb finishing

The three farm types considered differ widely in the destiny of lambs produced. It is assumed that intensive hill farms sell all non-breeding stock for slaughter, the extensive farms sells all non replacement animals as store lambs, and the semi-intensive farms sell 50% for store, and 50% for slaughter. However, as weaning is an important milestone in all three systems, this point in time is used to compare the farm types. The intensive and semi intensive models treat lamb finishing as a separate enterprise and the gross margin from this enterprise is then incorporated into the overall gross margin figure.

Ewe sales

After rearing 4 lamb crops, mature ewes are divided into three categories:

- i) 'draft' ewes, which fall into acceptable standards suitable for selling on for further breeding. These ewes are defined as still having 6 central incisor teeth together and both sides of their udders are normal.
- ii) 'cast' ewes are not suitable for further breeding in general, as they do not meet requirements for draft ewes. These ewes are either fattened and sold directly from the farm of origin, sold to other farms for fattening or sold directly to meat processors.
- iii) Cull ewes are not suitable for either breeding or fattening, and are culled directly from the flock after weaning.

The proportion of all 4 crop ewes falling into each category was assumed to be the same for each farm system, although the absolute number in each category differed due to the assumptions of flock structure. The proportions of draft, cast and cull ewes used in the model were based on results of a postal survey of Blackface breeders, in addition to results from the two SAC experimental hill farms.

Derivation of economic values

It is a principle of deriving economic values for breeding goals, that they are the effect of marginal changes, and are calculated assuming that all the other traits in the breeding goal are held constant. The fact that goal traits are associated with each other is dealt with, in the calculation of index weights, through the correlations among them. Economic values were calculated firstly by increasing and decreasing each goal trait by one genetic standard deviation (with all other goal traits held constant) except where realistically smaller increments were appropriate. This reduces the risk of economic values for different traits differing because of the scale of the change evaluated. Often the financial benefits of increasing the trait differ in magnitude from the financial penalties of decreasing the trait. This is the case for carcass fat class where the benefits of increasing leanness are smaller than the penalties of increasing fatness. Also, the benefit of increasing longevity differs slightly from the penalty of decreasing it. This is because different numbers of ewes in each age group have different litter sizes, and hence there are small differences in gross margin calculations. To overcome this, the relative economic weight was then plotted against the increment in the trait value, above and below the trait mean. The economic weight is then defined as the slope (tangent) of this line, at the population mean, i.e. the first derivative of the quadratic line connecting the three points. This economic weight is valid for the current levels of performance. In the case of the REV for the number of lambs reared, it is clear that as the mean level of performance increases, for example due to genetic progress, the economic weight is not linear. In this case, economic values should be re-evaluated and altered if necessary.

With the exception of carcass fat and conformation, the EVs for the goal traits were calculated using the whole farm model. A full explanation of how EVs for fat class and conformation score were calculated is given below. All EVs were subsequently multiplied by a combined frequency of expression (discount factor) to account for genetic improvements in traits being expressed at different times by a different

number of animals, and to discount expected future returns to net present values (NPV).

Sensitivity Analyses

The sensitivity of the economic values to changes in the main sources of returns (prices of store and finished lambs, draft ewes, cull ewes, and wool) and the major costs of production (lamb finishing feed, ewe feed and fertilizer) were investigated. Each price was changed by proportional increments of ± 0.5 around the prices used in the base models. New 'base' gross margins were calculated after each single price change, and before any genetic change in each goal trait was made. The same unit change (increment) in each goal trait as that used to derive the economic value of the trait was used, and 'new' economic values then calculated from the difference between the new gross margin after the genetic change, and the new base gross margin, for each of the ten goal traits and fourteen price changes.

Breeding goals

Ten breeding goal traits were considered for inclusion into selection indexes for hill sheep. The definitions of each goal trait, their importance in hill sheep breeding systems, their influence on other components of the farm system, and methods of computing the economic values are described below.

Ewe Traits

Mature size

Pre-mating liveweight was chosen to represent a single measure of mature body weight. For economic value calculations, it was assumed that any differences among ewes for this trait were maintained throughout the year, and throughout the lifetime of the ewe. The mature weight for rams was assumed to be proportionally 0.4 higher than ewe mature weight (Hammond, 1932). The benefits from increasing mature size are heavier offspring, higher litter size, increased cull ewe value and

heavier fleece. The converse is true for a decrease in mature size. As lamb weights, litter size and fleece weight are dealt with in their own right as goal traits, the only direct benefit of heavier ewes was evaluated as increased cull ewe value.

The costs of having heavier ewes are the extra feed costs, reduced forage availability and consequential reduction in stocking density (which the model computes as an additional cost for rented grazing.) The latter is not immediately apparent for a small increase in mature size, but after a number of years of selection, some re-structuring of the farm may be necessary to accommodate larger ewes. The costs of having heavier ewes are calculated annually, whereas the benefits of higher cull ewe value are only received once in a ewe's lifetime. The model assumes that of the number of ewes available after their 4th crop, 25% are sold as draft ewes, 65% as 'cast' ewes, and 10% are culled directly. The payment for draft ewes is on a per head basis (regardless of mature size), and that for cast ewes is on a carcass weight basis. Prices used in the model for draft ewes were the average price per head received in 1997 from a total of 20,547 draft Blackface ewes sold at two major draft ewe sales in Scotland. The price for cast ewes per kg used in the model is the average price paid in 1997 by a leading cull ewe buyer and processor, as such information is not collected nationally through the normal price reporting channels (to MLC).

Longevity

Longevity can be defined as the age of a ewe when it leaves the flock. It is affected by a combination of ewe death ('involuntary culling') and culling ('voluntary culling') rates, and affects the number and cost of replacements required to maintain the flock size. The consequence of improving longevity results in:

- i) increased average age of the flock by keeping ewes longer, and therefore reducing the number of replacements required each year (more ewe lambs to sell, but reduced cull ewe value), and
- ii) having more ewes available for sale at the end of their 4th lamb crop, with an

increase in the number of ewes suitable for drafting versus sale as cast, in addition to a reduction in the number of replacements required.

The converse is true for a decrease in longevity. The reduction in death and cull rates for all ewe age groups (including hogs), and a reduction in the number of replacements required contribute to improved flock profitability. A reduction in veterinary and medicine costs is computed due to a lower number of replacements being kept, rather than from having healthier ewes *per se*. A non-financial benefit is also seen because of a reduction in demand for hill grazing, which would be cumulative over time, although this marginal change is not taken into account in the model. (Hence the true economic value for longevity may be higher than the value calculated from the model.)

The costs of improved longevity are higher feed costs from keeping a mature ewe versus a hogg, higher feed costs from increased lambing percentage, and a lower wool clip value from mature versus hogg fleece. Again, the costs of improving longevity occur annually, whereas the benefits are received only once in a ewe's lifetime. A constant barren rate was assumed for each farm model. The proportion of animals within each age group which became productive ewes the following year was increased in the Markov chain model. An increase in the ratio of draft vs. cast ewes is used in the model to calculate the benefits of improved longevity, along with the marginal increase in lamb production from the older age structure.

Number of lambs reared

This was defined as the number of the ewe's own lambs reared until weaning. (Credit is given to ewes which foster lambs via 'average lamb weaning weight' (see below)). It is influenced both by the litter size born and survival rate of lambs. Changes in litter size alter the proportions of ewes rearing litters of singles, twins and triplets, which in turn influences both the number of lambs sold and the costs and revenues of lambs sold per ewe lambing. If good quality grazing is not limited,

flocks with low numbers of lambs reared have a higher economic value for increasing litter size compared to flocks which already have a higher number of lambs reared. For farms with a low proportion of improved pasture, increasing the number of lambs reared may be less desirable because extra grazing is needed (which is usually rented) to cope with increases in the number of multiple lambs reared.

The proportion of ewes having singles, twins and triplets, and the survival rates of each were determined using the equations and assumptions described above. Table 4.3 shows the values used for each farm model. Changes in the number of lambs reared were made by increasing litter size for each ewe age group in the Markov chain calculations, whilst holding survival rates for each birth type constant. The benefit of increasing the number of lambs is higher financial return from the sale of more lambs.

The costs of increasing the number of lambs reared are mainly feed, forage and extra veterinary and medicine costs. Feed to meet requirements in late pregnancy usually has to be bought in, increasing the cost of having twin-bearing ewes. The background to the forage calculations is described above, but the model assumes any increase in the demands for grass above that provided from a maximum input of 150 kg nitrogen per hectare is met by rented grazing.

Table 4.3 *Proportions of ewes having singles, twins and triplets for each farm system*

	Proportion ewes	No.lambs	Proportion lost	No. lost	No. available
<i>Intensive</i>					
Singles	0.5209	48.665	0.10	4.866	43.798
Twins	0.4583	85.616	0.15	12.842	72.774
Triplets	0.0207	5.817	0.30	1.745	4.072
<i>Semi-intensive</i>					
Singles	0.6935	63.530	0.10	6.353	57.177
twins	0.3023	55.381	0.15	8.307	47.074
triplets	0.0042	1.165	0.30	0.349	0.815
<i>Extensive</i>					
Singles	0.8909	80.541	0.10	8.054	72.487
Twins	0.1066	19.275	0.15	2.891	16.384
Triplets	0.0024	0.658	0.30	0.197	0.461

Lamb loss

Lamb loss is defined as the number of lambs a ewe 'loses' from birth to weaning, including lambs fostered off. Specifically, it is the number of lambs born (including dead lambs) minus the number of lambs reared. Identifying animals which have lambs, but do not rear them, is important in any flock but is particularly important in hill flocks. Improving (decreasing) lamb losses is the most efficient way to achieve marginal increases in the number of lambs reared, because there are no additional winter feed costs compared to increasing lambing percentage.

The benefit of reducing lamb losses is increased number of lambs available for sale after weaning. The additional grazing and medicine costs associated with higher lamb numbers is included in the calculations. The percentage of lamb deaths after birth was increased and decreased by 1% and 2% for singles, twins and triplets for each farm system. The economic value was then computed by the method described above.

Maternal component of weaning weight

Maternal weaning weight is defined as the average weight of lambs weaned, including lambs fostered on, adjusted for the sex and birth rank of the lamb. The importance of this trait is to identify ewes with higher milk supply, measured indirectly through the weight of lambs weaned.

The costs of increasing this trait were calculated by increasing ewe milk supply to meet the same proportion of lamb requirements as that before the incremental change in weaning weight. For example, twin ewes inbye on the extensive farm produce on average of 2.25 litres of milk per day (AFRC, 1993) at the peak of lactation in early June, which meets 57% of lambs' requirements. Increasing average lamb weaning weight by 0.5 kg required an increase in milk production to 2.29 litres per day at this stage of lactation. A marginal (1kg) increase in fertiliser was required to meet the additional ewe energy requirement for this extra 0.04 litres /day.

The benefits of ewes with higher milk production are heavier lambs at weaning. For store lambs, this equates directly to higher lamb value. For finishing lambs, this means a shorter finishing time to achieve the same carcass weight, with a consequent reduction in lamb finishing feed costs.

Fleece weight

In the UK, the main influences on wool price within a breed are fleece weight and freedom from contamination (vegetable, sprays etc.). Although the quality of fleeces (in terms of kemp and grey fibres) affects price, there is no consistent trend in prices across years paid for these qualities (due to inconsistencies in the world demand for carpet versus mattress type wools), and the premiums for improved quality are smaller than those for the fleece being free from contamination. Hence economic values were derived for fleece weight only.

There are no direct costs associated with increasing fleece weight, as there is no strong evidence to suggest there are significant increases in feed requirements with improved genetic potential for wool production at a constant ewe body weight (Binnie and Clarke, (1992), Clarke and Rae, (1997), Elliott and Johnson, (1976), Morris, (1980)). The benefit is the additional revenue from extra weight of fleece sold. The absolute economic value for fleece weight is similar for each farm type, although relative to other traits considered within each farm system, it is higher on the extensive farm than the intensive.

Lamb traits

Weaning weight (direct)

This is defined as the weight of lamb at a constant weaning age. In general, heavier lambs at weaning are more valuable because either a shorter finishing time is required before they reach slaughter (assuming the same mature weight, these animals are at a later stage of maturity), or they reach a heavier carcass weight at the same degree of maturity (i.e. point at slaughter). Whether a farm sells lambs as stores, or finishes them on farm, heavier weaning weights are beneficial. The cost of heavier lambs at weaning are higher pre-weaning feed cost. In the past, this has always been difficult to quantify because of the interactions with seasonal grazing management. However, the models developed here make it possible to do this calculation.

The economic values of heavier weaning weights, for lambs finished to slaughter weights, were calculated at a constant carcass weight for the intensive and semi intensive farm types. In this way, double counting the benefits of heavier weaning weights, heavier carcasses and heavier mature ewes is avoided. Also, the economic values between farm systems are assessed on an equitable basis. The benefits to the store producer are simply heavier weaning weights and hence greater lamb value. The benefits to the semi-intensive and intensive farm system are the saving in feed costs from a reduced number of days to slaughter. The costs for each system are

computed as extra fertiliser requirements, marginal increments for administering antihelmintics ('dosing') heavier lambs before weaning, and (for the semi and intensive systems) the additional 'cost' of buying heavier lambs back into the farm to finish. The converse is true for a reduction in weaning weight.

Carcass weight (CW)

The benefit of heavier carcasses is greater value per lamb. The costs of heavier carcasses are the feed costs incurred from extra time required to finish lambs to a heavier weight, and thus extra post-weaning demands on grazing.

Calculation of the benefits of heavier carcasses was made at a constant weaning and mature weight within each system, to avoid double counting the benefits and costs of having heavier weaning weights and higher mature weights. Carcass weight was increased (or decreased) by one genetic standard deviation. The number of extra days to finish (at the same pre-increment growth rate) was subsequently multiplied by the daily cost of finishing lambs.

The average market price for the marketing season August to December from 1993 through to 1997 (217.43 pence per kg of carcass weight) was used in the model.

Carcass conformation score and fat class

Under the current price structure in the United Kingdom, MLC conformation score and MLC fat class influence lamb price to a much lesser degree than the weight of carcass, or the time of marketing (Conington *et al.*, 1998). Improving fat and conformation at a fixed weight do not have associated costs or benefits on other components of the sheep farming system (or at least within-breed improvements by traditional selection are unlikely to have any major impact) with the exception of a very small reduction in feed cost, following selection for reduced fatness.

A different approach was required to derive EVs for these traits because they are

categorical and have prices based on thresholds. EVs were calculated using a method described by Hovenier *et al.* (1993). This method accounts for traits with an intermediate optimum, with thresholds below or above which penalties occur. A threshold subroutine with mean of zero, and standard deviation of 1, was written (Amer, pers comm., 1998) using Mathcad 6.0 (1995) to calculate the underlying fat and conformation distributions from the price schedule (Table 4.4) and proportions of lambs falling into each category (Table 4.5). Fat class data were transformed to their corresponding estimated subcutaneous fat proportions (ESF%) before analysis: 1=0.04, 2=0.08, 3L=0.11, 3H=0.13, 4L=0.15, 4H=0.17 and 5=0.20 (Kempster *et al.*, 1986). Penalties and premiums for fat and conformation were calculated independently, i.e. the premiums and penalties for fat class were calculated at a constant conformation score and carcass weight, and those for conformation score at a constant fat class and carcass weight. Three increments above and below the population mean were derived from the Mathcad subroutine to provide marginal premiums or penalties after each change.

Price premium/penalties for fat class and conformation score were collated from the average of 6 separate pricing schedules operating in 1998 (see Table 4.4.) The proportions of lambs in each fat class and conformation class cell were based on data from 992 lamb carcasses classified from lambs from two SAC experimental hill farms born in 1991 and 1992 (Table 4.5.) Together, these data provided information to determine the independent weighted premiums and penalties of fat and conformation scores, and the original 'base' threshold values for the derivation of each economic value.

Table 4.4 *Price premiums (p/kg) and penalties according to fat class and conformation score*

	1	2	3L	3H	4L	4H	5
E	-30.0	+9.93	+9.9	+0.05	-17.5	-36.7	-48.3
U	-30.8	+7.4	+7.43	-0.78	-17.5	-36.7	-48.3
R	-31.6	+1.5	+2.38	-2.6	-17.5	-36.7	-48.3
O	-38.3	-5.1	-2.6	-13.66	-31.67	-36.7	-48.3
P	-43.3	-43.3	-43.3	-43.3	-43.3	-43.3	-48.3

Table 4.5 *Proportion of animals falling into each fat and conformation class*

	1	2	3L	3H	4L	4H	5	Total
E	0	0	0	0	0	0	0	0
U	0	0.002	0.0151	0.004	0	0	0	0.0212
R	0	0.0292	0.3438	0.129	0.0131	0.002	0	0.5171
O	0.001	0.0907	0.2792	0.0625	0.005	0	0	0.4385
P	0.0233	0	0	0	0	0	0	0.0232
Total	0.0243	0.122	0.6381	0.1955	0.0181	0.002	0	1

Fat Class

The average premiums and penalties for fat class at a constant conformation score are shown in Table 4.6. Each penalty/premium for fat class is the product of each column of price premiums with the overall ("total") proportion of lambs in each conformation score. The proportions of animals falling into each fat class before and after each incremental change are also shown in Table 4.6, together with the new economic values for each change. These economic values (EV new - EV old) were regressed on the incremental change, and again, the first derivative (tangent) taken as the economic value.

Table 4.6 *Proportions of lambs in each fat class at a constant conformation class, following different magnitudes of incremental change*

Fat class	Penalty / premium (p/kg)	Starting proportion	Incremental changes (underlying standard deviations)					
			leaner 0.05	leaner 0.1	leaner 0.15	fatter -0.05	fatter -0.1	fatter -0.15
			New proportions					
1	-40.66	0.0243	0.027	0.031	0.034	0.022	0.019	0.017
2	-0.89	0.122	0.131	0.14	0.149	0.114	0.105	0.098
3L	0.661	0.6381	0.641	0.642	0.642	0.634	0.629	0.623
3H	-8.5043	0.1955	0.183	0.172	0.16	0.208	0.221	0.233
4L	-36.853	0.0181	0.016	0.014	0.013	0.02	0.023	0.025
4H	-41.649	0.002	0.001705	0.00145	0.00123	0.00234	0.00273	0.003184
EV		-3.089	-3.028	-2.992	-2.982	-3.174	-3.284	-3.418
EV _{new} - EV _{old} (p/kg)			0.061	0.097	0.107	-0.085	-0.195	-0.329

Costs of increasing fat class

To calculate the costs of increasing fat class, the data were classified according to % dissected lean and % dissected (subcutaneous + intermuscular) fat for each fat class category, before and after genetic change. The overall proportions of fat and lean were then determined (weighted by the proportions of animals falling into the fat classes), before and after genetic change. The weighted percent lean and percent fat according to the proportion of animals falling into the fat classes before improvement was 53.96% lean and 28.89% fat. After improvement, this became 54.134% lean and 28.707% fat. This results in a difference of 0.174% lean and -0.183% fat. As a consequence of increasing lean proportion by 0.01, costs reduced proportionately by 0.0052 (Appendix IV).

As the costs of increasing lean by 1% are reduced by 0.52%, the penalty of increasing fatness is reduced marginally by 0.005 (i.e. multiplied by 0.995). The tangent is £-0.02 per kg carcass weight. The base EV for fat class for the intensive farm model is hence:

Base REV = (tangent (price/kg) x no. lambs x carcass weight x fat cost)/ rescaling factor

$$= [(-0.02 \times 89.23 \times 17.04 \times 0.995) / \sqrt{\sigma_p^2}],$$

where σ_p^2 is the phenotypic variance, and 0.995 adjusts for costs of increasing fatness, explained above. This translates to -£20.00 per increase in ESF%, for a 100 ewe flock.

Conformation score

The economic value for improving conformation was calculated in the same manner as for fat class, although it was assumed that there were no costs associated with changing the shape of the animals. However, as we have already assumed

animals are evaluated on the underlying normal scale, the economic value is not rescaled back to conformation score units.

The average premiums for conformation at a constant fat class, the proportions of animals falling into each conformation score before and after each incremental change, and the new economic values for each change are shown in Table 4.7. The premiums/penalties for conformation are the product of each row of Table 4.4 with the overall ('total') proportion of lambs in each fat class.

The tangent is £0.052 per kg carcass weight. The base EV for conformation score for the intensive farm model is hence:

$$\begin{aligned}\text{Base EV} &= \text{tangent (price/kg)} \times \text{no.lambs} \times \text{carcass weight} \\ &= 0.052 \times 89.23 \times 17.04 \\ &= \text{£ } 79 \text{ per } 100 \text{ ewe flock.}\end{aligned}$$

The results show that the premium for an increase in a unit conformation score is roughly equivalent to the penalty for increasing fatness by a whole fat class (as each fat class represents 4 ESF% units).

Table 4.7 *Proportions of lambs in each conformation class at a constant fat class according to the magnitude of incremental change.*

Conformation	Penalty/ Premium (p/kg)	Base Proportions	Incremental changes (underlying standard deviations)					
			Better conformation			Poorer conformation		
			0.05	0.1	0.15	-0.05	-0.1	-0.15
			New proportions					
E	6.4376	0	v small	v small	v small	v small	v small	v small
U	4.367	0.0212	0.024	0.027	0.03	0.019	0.017	0.015
R	0.9959	0.5171	0.534	0.551	0.567	0.5	0.482	0.464
O	-6.5272	0.4385	0.421	0.404	0.387	0.456	0.472	0.489
P	-43.37	0.0232	0.021	0.018	0.016	0.026	0.029	0.033
EV		-3.261	-3.007	-2.762	-2.526	-3.525	-3.799	-4.085
EV new - EV old (p/kg)			0.254	0.499	0.735	-0.264	-0.538	-0.824

Geneflow

Genetic improvements in different traits are expressed at different times by different numbers of animals. For example, a change in litter size is expressed by females over the age of two every year, a change in fleece weight is expressed by females over the age of one every year but a change in longevity is only expressed once in the animals' lifetime. Accounting for the flow of genes across time through the flock overcomes this problem when deriving economic values. Again, gene flow (or Markov Chain) methodology (Hill, 1974) was used in this study to count the expression of genes across years. Expressions of different traits were calculated using a programme in GENSTAT (Lawes Agricultural Trust, 1983) written by S. Bishop (pers. comm., 1998), which used matrices to describe the flow of genes through the population. The total number of expressions in each category of traits (defined below) was achieved by multiplying the vector of gene distribution each year (for 15 years) by a vector describing the expression of the trait category by each age class. An explanation of how the expression of genes in the flock was derived is described below.

Ram lambs selected in year 1 to be used as the sires of next year's lamb crop are genetically superior for the following categories of traits: (i) lamb performance, (ii) maternal performance, (iii) wool and mature weight, (iv) longevity. Their genetic superiority in each of these categories is expressed in the following ways:

Lamb performance traits

These traits are expressed once only by all year 1 lambs destined for slaughter. In addition, half of the genetic superiority expressed once by slaughter progeny of daughters is accounted for, but this occurs from years 3 to 6. A quarter of the genetic superiority expressed once by slaughter grand-progeny of females, from years 5 to 12, etc. are included.

Maternal traits

Litter size, lambs lost, maternal weaning weight.

Litter size, lambs lost and maternal weaning weight are expressed by 1-crop ewes in year 3, 2-crop ewes in year 4, 3-crop ewes in year 5, and 4-crop ewes in year 6. Thus, each ewe gets up to 4 opportunities to express maternal traits, but each year only a proportion of the flock is expressing the genetic superiority resulting from selection and use of a particular ram lamb. In addition, half of the genetic superiority expressed by 1, 2, 3, and 4 crop ewes which are daughters of base year females, in years 3 to 6 are included.

Wool and mature weight

These are the same as maternal traits, but their expression starts 1 year earlier.

Longevity

Longevity is expressed once only per ewe during her lifetime in the flock and it is assumed to be expressed at the mean flock age.

Discounting

Economic benefits promised in the distant future are perceived to be of lesser value than benefits immediately available. Future benefits are commonly discounted to take account of this time effect. Assuming a discount rate of x (e.g. 5%), then future benefits occurring in year t are scaled by $1/(1+x)^t$ to express them as current values.

To compare all trait categories in an equitable way, the expressions of the benefits were counted across years, discounted appropriately and then summed to get a total net present value (NPV) coefficient. The discount factors multiplied by the economic value of each goal trait show the value of each goal trait over a 15 year time horizon expressed as NPVs. The NPV coefficients are the same for all lamb performance traits at 1.6164, and maternal traits at 1.3323. As measurements of

wool and mature weight occur once per year, the NPV coefficient for these traits is 1.3769. Longevity is expressed only once in the animals' lifetime and hence it is lower at 0.3032. The NPV coefficients were then multiplied by the economic values calculated from the farm model to obtain the Net Present Economic Values.

Results

Properties of the modelled farms

The herbage production and offtake data from the HGMM for the intensive farm model are shown in Table 4.8. The same data for the other two models are shown in Appendix V. These data form the base from which the energy available for all classes of stock during each month are derived, to determine supplementary feeding requirements.

The equilibrium flock structure for all age groups and the number of productive ewes for the three farm systems derived from the Markov chain are shown in Table 4.9. One of the features of the Markov chain is that the 'optimal' flock structure evolves after several years, irrespective of the original number of animals in each age group.

Table 4.8 *HGMM data: Intensive farm*

	Jan	Feb	Mar	Apr	May	June	Jly	Aug	Sept	Oct	Nov	Dec
Production	341.89	396.69	952.58	1740.7	6918.0	17299.3	29417.8	6702.79	1946.53	1571.11	892.55	514.13
Total offtake (kg)	2597.4	1140.4	1438.9	911.66	1618.4	2970.0	4263.6	3546.7	4031.3	3853.8	2772.6	0
Digestibility of organic matter (DM)	0.4755	0.4840	0.53627	0.6394	0.6808	0.6702	0.6649	0.6575	0.6532	0.6362	0.5553	0
ME value = OMD * 0.157	7.46	7.59	8.42	10.04	10.69	10.52	10.44	10.32	10.25	9.98	8.72	8.09
Total ME offtake per month (gj/month)	19.39	8.66	12.11	9.15	17.29	31.25	44.51	36.61	41.34	38.49	24.17	0

Table 4.9 *Equilibrium flock structure per 100 ewe flock*

Ewe Age	Intensive		Semi-intensive		Extensive	
	Proportion	No. Productive	Proportion	No. Productive	Proportion	No. productive
1	0.226	0	0.230	0	0.232	0
2	0.214	25.060	0.216	25.186	0.218	25.213
3	0.198	24.015	0.199	23.745	0.200	23.550
4	0.188	22.934	0.188	22.551	0.187	22.268
5	0.174	21.404	0.168	20.127	0.163	19.368

The main differences between the three farm types are seen in these initial performance data and form the base for the gross margin calculations. The gross margins produced from the model for the three farm types are consistent with acceptable performance indicators for each category of hill farm (SAC, 1997), as shown in Appendix VI. Details of lamb weights derived from the model, and the major performance indicators for each farm system are shown in Table 4.10. The data provide a comprehensive summary of differences between the three sheep farm systems in the key areas of productivity, and provide the background to explain the differences seen in the gross margin calculations for each farm system. Results from the model show that the value of lambs from higher litter sizes is usually lower than that of single lambs, although this depends on the environment in which they are reared. Hill farms with poor quality hill grazing can easily rear twins on improved inbye land to heavier weights than single lambs reared on the hill (Conington *et al.*, 1995), and this is reflected in the results in Table 4.10.

Table 4.10 *Performance data of model farms*

	Intensive	Semi-intensive	Extensive
Ewe Characteristics			
No ewes	100	100	100
Mature ewe weight (kg)	57	53.5	50
Ewe death + cull rate (%)	6.7	8.0	9.0
Barren	4.61	6.06	7.00
Non-productive (including 0.25 of deaths before lambing)	6.59	8.39	9.60
Ewes lambing	93.41	91.61	90.39
No. Lambs per ewe to tup	1.40	1.20	1.00
No. Lambs per ewe lambing	1.51	1.31	1.11
No. Lambs reared per ewe	1.21	1.05	0.89
No. Lambs reared per ewe lambing	1.29	1.15	0.98
Proportion draft : cast ewes sold†	0.25 : 0.65	0.25 : 0.65	0.25 : 0.65
Proportion single : twin females kept for breeding	0.30: 0.70	0.50 : 0.50	0.85 : 0.15
Lamb characteristics			
Lamb losses:single @ 10%	4.866	6.349	8.054
Lamb losses:twin @ 15%	12.842	8.319	2.891
Lamb losses:triplet @ 30%	1.745	0.349	0.197
Lambs for sale or keep	120.64	105.09	89.33
Lambs kept for breeding: (females)	29.4	29.8	30.9
Lambs sold store	0	36.39	57.13
Lambs sold fat	87.83	36.39	0
Single male birthweight (kg)	4.1	4.0	3.9
Twin male birthweight (kg)	3.96	3.7	3.4
Triplet male birthweight (kg)	3.6	3.0	2.7
Weaning weight: single males (kg)	30.7	28.01	26.33
Weaning weight: twin males (kg)	29.29	28.01	27.83
Weaning weight: triplet males (kg)	28.29	27.01	26.83
Weaning weight (all lambs) (kg)	28.89	27.05	25.66
Weaning wgt (non-breeding stock) (kg)	29.19	27.42	26.17
Mean age at weaning (days)	119	119	119
Post weaning growth rate (g/day)	120	120	-
Mean carcass weight (kg)	17.03	16.54	-
Mean age at slaughter (days)	218	214	-
Mx weaning weight†	0.85	0.828	0.8
Mx slaughter weight	0.638	0.654	-
Killing out % (lambs)	0.43	0.43	0.43

† Percentage of potential growth achieved for weaning weight .

‡ 10% of 4 crop ewes are culled after weaning.

Economic Values

Economic values, discount factors and Net Present Values for all 10 goal traits, and for the three farm systems are shown in Table 4.11. In general, the economic values for the intensive farm are higher than those in the less intensive farming systems although the comparison is different for different traits. From these results, it appears that a farming system which has fewer constraints to production such as pasture quality and availability, benefits more from genetic improvement than farms less able to cope with the extra demands on the farm system. In addition, taking increments above and below the mean for each trait has shown that economic values are *not* linear, so the EVs calculated reflect more closely the biology of sheep themselves and seasonality of pasture availability in the hill areas of Britain. In the case of number of lambs reared on an extensive farm, the non-linearity in economic value is particularly extreme. There is a benefit to small increases in litter size. However, this benefit tails off and becomes a net loss as the lamb number increases above an extra 0.3 lambs/ewe. Clearly, in such a situation, the economic weight for the trait depends on both the current population mean, and the increment of the change in performance of the trait considered. For the intensive farm, the benefits of increasing the number of lambs reared do not increase at a linear rate beyond 1 standard deviation. These results are shown in Figures 9 and 10.

Investigating changes in economic values over a wide range of litter sizes has illustrated that there are 'optimum' increments for some traits, beyond which the economic value declines. This implies that diminishing marginal returns from genetic improvement will be apparent at least for the extensive farm system. The economic benefit of increasing the number of lambs reared in the extensive farm situation is negative when the increase in the number of lambs reared is too large, because the cost of additional inputs outweigh the benefits of extra returns. This means that the performance of breeding flocks should be regularly evaluated, and if necessary, the economic values re-calculated to reflect the true level of performance

of the flock. This would more accurately reflect the economic impact of continuing to select for such traits when farm resources are limited.

Table 4.11 *Economic Values for the three farm systems, discount factors and the discounted Net Present Values for each goal trait.*

Trait	Economic Values (£ per 100 ewe flock)			Discount Factor	Net Present Economic Values (£ per 100 ewe flock)		
	Extensive	Semi-intensive	Intensive		Extensive	Semi-intensive	Intensive
Mature weight (/kg)	-10.37	-13.57	-11.84	1.3769	-14.278	-18.68	-16.30
Longevity (/ day)	5.42	6.19	6.82	0.3032	1.642	1.877	2.067
No. reared (/ % incr) †	16.94	17.46	27.08	1.3323	22.57	23.27	36.08
No. lost (/ 1% incr) ‡	-22.04	-27.02	-31.99	1.3323	-29.37	-35.99	-42.62
Maternal weaning wt (/kg)	50.28	52.67	54.09	1.3323	66.99	70.17	72.06
Fleece weight (/kg)	122.3	122.59	122.06	1.3769	168.4	168.8	168.1
Weaning weight (/kg)	43.88	50.21	55.02	1.6164	70.92	81.15	88.93
Carcass weight (/kg)	-	20.00	76.29	1.6164	-	32.33	123.31
Fat class (/ESF%)§	-	-7.897	-19.95	1.6164	-	-12.76	-32.25
Conformation (/unit)	-	31.322	78.897	1.6164	-	50.62	127.53

† For example, increasing no. lambs weaned per 100 ewe flock from 120 to 121.

‡ For example, increasing the number of lambs lost per 100 ewe flock from 13 to 14%

§ For example, increasing estimated subcutaneous fat from 10 to 11%.

Figure 9

**Change in gross margin as the number of lambs reared increases :
extensive farm**

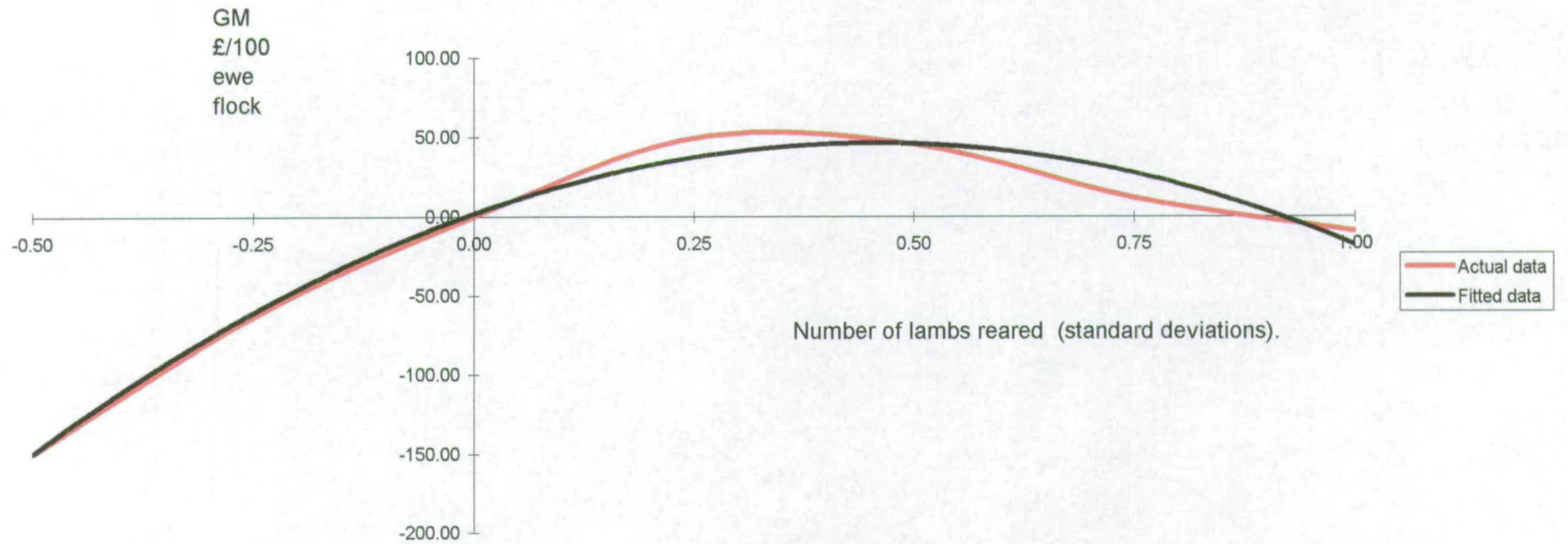
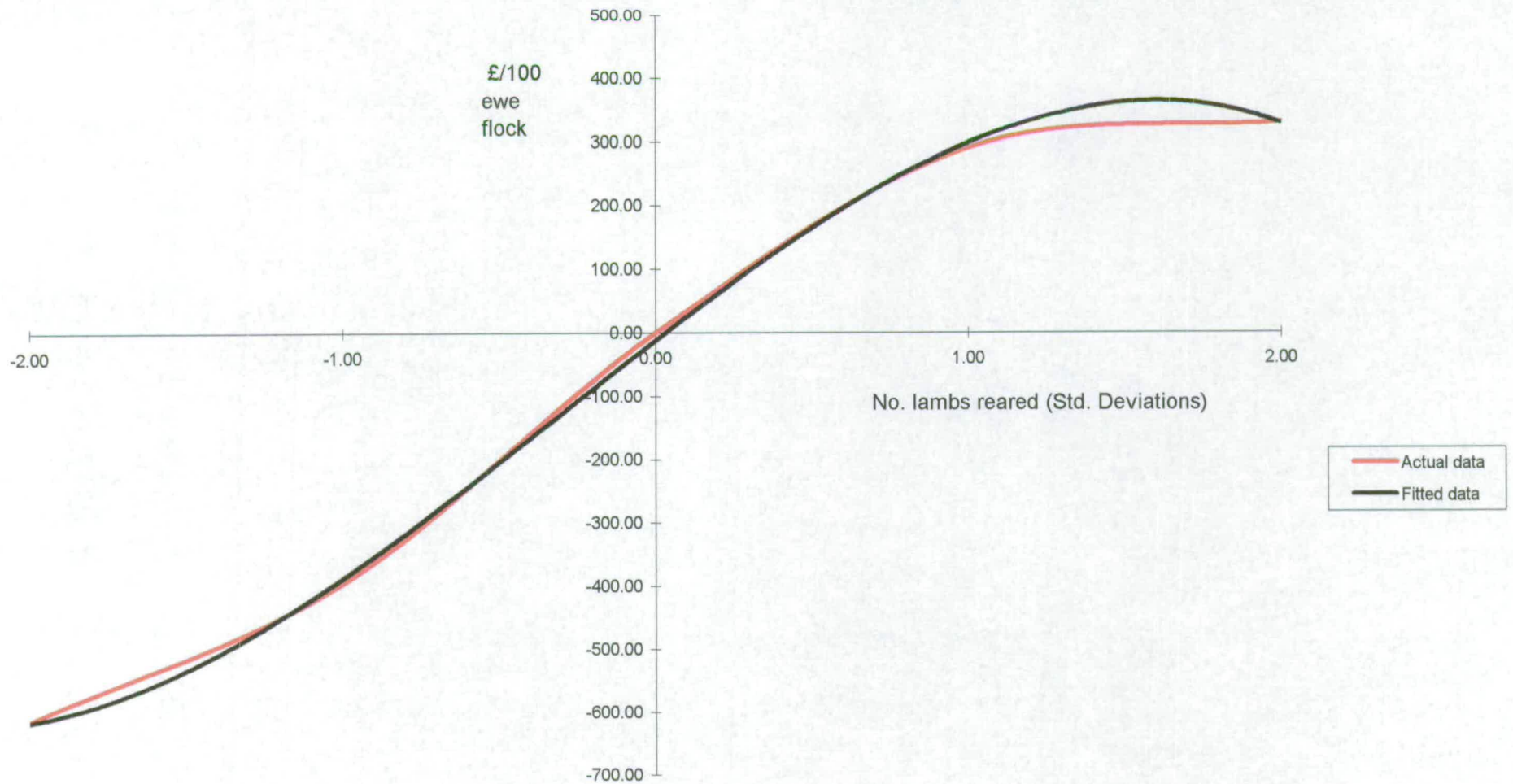


Figure 10
Change in the number of lambs reared as gross margin increases:
Intensive farm



The economic values reflect the importance of maternal characteristics of purebred hill sheep as well as carcass traits, however, improving fleece weight in hill sheep is not considered a priority in the current economic climate in the UK. Indeed, long fleeces are strongly selected against (phenotypically) in some strains of Blackface sheep, not just because of the practical difficulties of having long-fleeced sheep on snow-covered ground in winter, but also because of the perception that a shorter fleeced Blackface has a better carcass, and is therefore more valuable. Including fleece weight in the breeding goal may be more important to producers of other hill breeds, such as the Cheviot or Shetland, or to flocks with lower than average lamb production. However, wool is produced each year by every adult sheep, and is highly correlated with mature size. This means that allowing mature size to increase will result in a correlated increase in fleece weight. Compared to the other goal traits, the relative economic value of fleece weight is more important in the extensive flock than the intensive flock, although the absolute value is the same. Although commonplace in New Zealand and Australia, measuring fleece weight in the UK is likely to be unpopular with breeders because of the perceived low value of the fleece itself, and the extra effort involved at clipping time to record the fleece weights.

The negative values for mature size on all three farming systems indicate that there are no direct benefits of having heavier ewes on hill farms. However, mature weight is positively correlated both phenotypically and genetically to live weight at weaning. This has a high economic value, so it is possible that results from index calculations will show that mature weight increases as a result of selecting for heavier lambs at weaning.

In the breeding goal described here, the emphasis has moved away from improving litter size (as in more conventional breeding programmes). Instead, two breeding goal traits to minimise the numbers of lambs 'lost', and maximise the number of lambs reared have been included. This will ensure that high-performing dams will

be selected which have the ability to rear and nurture lambs. This will lead to more sustainable breeding goals for hill sheep, which are frequently noted for suffering some of the highest neonatal losses in the sheep industry in the UK.

Sensitivity analyses

The sensitivities of the economic values to changes in prices of major inputs and outputs for the intensive and extensive farm types are shown in Tables 4.12a and 4.12b. In general, the economic values are robust to fluctuations in prices which do not have a significant impact upon, or which are not directly related to the trait in question. For example, the economic value for mature weight for the intensive system are within 97% of the original economic value for changes in prices for lambs, wool, lamb finishing feed and fertiliser. However, it decreases or increases by 29% when the price of cast ewes is reduced or increased by 50%. The same pattern can be seen for ewe feed prices. The economic value of mature weight is less negative (by 66%) when the cost of ewe feed decreases by 50% to £0.074 per MJ. The negative economic value for carcass weight when the price of lambs is very low, shows that increasing carcass weight is only profitable if a corresponding reduction in finishing costs is made. These results infer that unless one of the major component prices changes dramatically, the economic values are stable. If prices do change significantly, then new economic values will be required.

Table 4.12a *Sensitivities of REVs to price changes for the Intensive farm*

			Lambs reared /100	Lambs lost /100	Mature weight	Longevity	Fleece weight	Maternal wwt	Direct wwt	Carcass weight	
Revised prices (± 50% original prices)			Original REVs	27.083	-31.99	-11.843	6.817	122.06	54.09	55.02	76.29
			Revised REVs								
Lamb price (£/kg)											
1.1 (slter),0.45(store)†			8.888	-13.15	-11.85	4.398	124.06	50.25	51.45	-11.44	
3.3(slter),1.35(store)			45.28	-50.42	-11.85	9.233	124.06	57.65	58.59	164.05	
Draft ewes	£ / ewe	23	27.08	-31.59	-11.5	6.44	124.06	59.07	57.30	76.29	
		70	27.16	-31.78	-11.85	7.172	124.06	54.09	57.30	76.29	
Cast ewes	p / kg	0.25	27.08	-31.78	-15.32	6.243	124.06	54.09	57.30	76.29	
		0.75	27.08	-31.78	-8.38	7.39	124.06	54.09	57.30	76.29	
Wool	p / kg	0.48	27.08	-31.78	-11.85	6.814	61.01	54.09	57.30	76.29	
		1.44	27.08	-31.78	-11.85	6.818	186.06	54.09	57.30	76.29	
Ewe feed	p / MJ	7.37	25.79	-31.07	-4.05	6.864	124.06	51.01	49.37	76.29	
		22.5	28.43	-32.52	-20.03	6.765	124.06	57.33	60.93	76.29	
Lamb finish feed	p / lamb / day	0.25	29.79	-34.52	-11.85	7.176	124.06	30.83	31.76	130.40	
		0.75	25.27	-29.96	-11.85	6.577	124.06	69.61	70.53	40.24	
Fertilizer											
N21,P20.5,K11.5			31.50	-32.23	-11.58	6.937	124.06	56.06	58.62	76.29	
N63,P61.5,K34.5			22.63	-31.33	-12.03	6.695	124.06	52.13	51.42	76.29	

† prices are p/kg dead weight for slaughter lambs, and p/kg live weight for store lambs

Table 4.12b *Sensitivities of REV's to price changes for the Extensive farm*

			Lambs reared /100	Lambs lost /100	Mature weight	Longevity	Fleece weight	Maternal wwt	Direct wwt	
Revised prices (\pm 50% original prices)			Original REV's	16.94	-22.04	-10.37	5.42	122.3	50.06	43.88
			Revised REV's							
Lamb price:										
1.1(slater),0.45(store) †			-4.58	-10.41	-10.37	3.82	124.41	24.77	18.54	
3.3(slater),1.35(store)			-21.1	-33.62	-10.37	6.85	124.41	75.33	69.23	
Draft ewes	£ / ewe	23	16.94	-22.02	-10.37	4.96	124.41	50.06	43.88	
		70	16.95	-22.02	-10.37	5.69	124.41	50.06	43.88	
Cast ewes	p / kg	0.25	16.94	-22.02	-13.64	4.83	124.41	50.06	43.88	
		0.75	16.94	-22.02	-7.09	5.83	124.41	50.06	43.88	
Wool	p / kg	0.48	16.94	-22.02	-10.37	5.33	62.23	50.06	43.88	
		1.44	16.94	-22.02	-10.37	5.33	186.62	50.06	43.88	
Ewe feed	p / MJ	7.37	14.51	-22.02	-6.29	5.38	124.41	48.54	43.88	
		22.5	19.48	-22.02	-17.88	5.28	124.41	53.48	43.88	
Lamb finish feed‡		0.25								
p/ lamb / day		0.75								
Fertilizer:										
N21,P20.5,K11.5			18	-22.10	-10.29	5.61	124	50.84	47.75	
N63,P61.5,K34.5			15.89	-22.13	-10.45	5.05	124	48.99	39.93	

† prices are p/kg dead weight for slaughter lambs, and p/kg live weight for store lambs. ‡Not applicable for Extensive farm system (store lamb production).

Discussion

By using a 'whole farm' approach, this Chapter makes a significant contribution to the calculation of economic values for hill sheep breeding programmes. Including estimates of available energy supply and uptake for sheep from hill and mountain pastures, together with that from reseeded (or improved) grassland provides a base from which to define the limitations to genetic improvement in harsh environments. Modelling the extremes of hill farm systems has illustrated the degree to which different farm systems are able to accommodate the changes as a result of genetic improvement. This flexible, multi-disciplinary model has facilitated detailed sensitivity analyses of changes in the major costs and returns of the sheep farm systems. Such an integrated approach is recognised as being more detailed than using single profit equations to derive economic values, because it operates at the interface between genetic improvement and animal production systems (Harris and Newman, 1994). Weller (1994) lists the disadvantages of simulation models as being i) lack of generality, as the results are only applicable to the sample populations modelled, ii) they do not account for changes in REV's due to selection, and, iii) they only apply if the data are available to develop the model. In this study, the lack of generality has been addressed by deriving economic values appropriate for three different production systems within the hill sheep breeding sector, representing the extremes of such farm systems. As the REV's were taken as the first derivative after unit increases and decreases for each trait, non-linearity was accounted for and, implicitly, changes due to selection are indeed accounted for. Most of the data have been generated from the two SAC experimental flocks and assumptions were therefore limited to only a few variables.

The results of the model show that the main influences on overall productivity are lamb output (number of lambs reared) and the weight of these lambs at the point of marketing, as for most sheep enterprises in the UK (MLC, 1998). The model also shows that genetic improvement in harsh environments is likely to be of greater benefit to farms with fewer constraints to improvements in production such as

better quality pasture or a higher ratio of improved grassland to hill pasture. In the derivation of economic values for ewe prolificacy for different farm and production types in New Zealand, Amer *et al.*, (1999) also found that economic value for litter size depends on the mean level of flock prolificacy and farm location.

This study has shown that there is an intermediate optimum economic value for improving the number of lambs reared for the extensive farm system. Beyond this, an increase in the number of lambs reared results in decreasing marginal economic values. Detailed analyses of theoretical 'optimum' performance levels could be examined for each goal trait. Such analyses would provide further insight to determine 'suggested limits' for individual farm systems. This would facilitate the tailoring of economic indexes for hill breeds to suit different farming systems operating in different environments. In Australia, where there are large environmental differences between flocks, personalised breeding objectives are made for individual Merino breeders using OBJECT, a computer programme which predicts likely rates of genetic progress for alternative selection criteria and economic values, to help breeders with selection decisions (Atkins *et al.*, 1994). In the UK, different indexes are largely confined to different breeds, which in turn largely represent different geographical areas. However, results from this study show that economic values can differ according to different farms and farming systems with the same breed.

The model was designed using a purebred Scottish Blackface sheep farm as a base for the three farm systems. Using data typical for their own production systems, economic values for other major hill breeds such as the Cheviot (North Country and South Country), Shetland, Welsh Mountain, Beulah Speckleface and Swaledale could be produced with some modifications to the model.

Chapter 5

Multi-trait selection indexes for UK hill sheep

Introduction

Until relatively recently, only a small proportion of UK hill sheep flocks were engaged in performance recording. For the last two decades, the total number of lambs from hill breeds recorded per year has fluctuated between 5000 and 8800, (Signet, 1999). This represents proportionally less than 0.01 of the total number of lambs from hill breeds born each year. The reasons for such a low level of participation in genetic improvement of production traits in purebred hill flocks probably include the physical difficulty of pedigree recording in extensive conditions, lack of knowledge of the potential benefits of genetic improvement programmes, emphasis on aesthetic qualities, and the perception that the environment has an overriding influence on attempts to improve sheep performance. Some hill breeds have no flocks registered with Signet, the organisation which carries out performance recording and genetic evaluations for the sheep industry in the UK.

The introduction of sheep quotas in the UK in 1992 has imposed an upper limit to the number of sheep eligible for subsidy. Improving performance of sheep through increased output must therefore come from improved productivity. This can be achieved by temporary means such as management or nutrition, but improvement of production through genetic selection is permanent. As more hill flocks now lamb either indoors or in enclosed paddocks, the physical difficulties of recording, in particular identifying a lamb to its dam at birth, can be overcome.

The selection indexes currently used by the hill sector combine mature size, lamb growth, litter size and maternal ability (an indication of a ewe's milking ability). Most hill flocks have adopted the index derived for the first Welsh Mountain Group breeding scheme, CAMDA.

As purebred hill lambs tend to fall at the poorer end of the carcass quality scale

used in the UK (Conington *et al.*, 1998), there is considerable scope for improving carcass traits from hill lambs as well as maternal traits. An index derived by Simm and Dingwall (1989) has been used successfully for terminal sires in the UK. This incorporates measurements of lamb weight, ultrasonic fat depth and muscle depth to predict carcass lean and fat weights. Some hill flocks have used both the maternal index and the terminal sire index on their flocks in a two-stage selection process. However, to date, there is no overall breeding value combining either carcass and maternal traits, and no EBVs for traits associated with improved health, longevity or welfare.

The objective of this Chapter, therefore, is to derive selection indexes for purebred hill sheep incorporating carcass and maternal traits, including traits which contribute to the overall sustainability of increased performance in hill ewes. As the hill sector in the UK is diverse, three indexes will be described in this Chapter to reflect the extremes of hill production systems, as reported in Chapter 4. These are: i) intensive, where all surplus lambs not required for breeding are finished for slaughter, ii) extensive, where all surplus lambs are sold as stores, and where physical constraints such as hill pasture quality and limited improved pasture for twin-rearing limit genetic improvement, and iii) semi-intensive, which is intermediate between the two extremes, and where farms finish some lambs and sell others as stores.

Results from the investigation of the selection indexes will explore whether responses to selection are similar in the three production systems, which traits contribute the most to the indexes, and which could be dropped from the index without affecting responses in other traits. The accuracy of the indexes, and the predicted economic returns from selection using the indexes are examined. The extent to which the results from the index calculations are altered due to changes in both economic values and heritabilities of key traits are investigated through systematic sensitivity analyses.

Methods

A selection index can combine information from an individual's own and relatives' phenotypic performance for multiple traits into an overall score. It is an effective way of selecting breeding stock when several traits are being evaluated. Currently, the most effective way of implementing multiple trait selection is through Best Linear Unbiased Prediction (BLUP). This method predicts the genetic merit of animals whilst simultaneously estimating environmental effects. However, BLUP alone does not answer many of the questions raised by the implementation of selection in breeding programmes. For example, it does not directly predict the economic benefit of selection over a number of years from breeding programmes based on the results of BLUP, nor does it easily predict responses to selection in individual traits. Evaluating selection indexes which mimic BLUP will i) determine how each trait contributes to selection, ii) determine which traits are important, and which can be safely dropped from the index, iii) calculate the expected genetic change in each trait with selection and iv) determine the overall accuracy of selection. This Chapter describes predicted results from selection indexes, using information from a fixed number of relatives of several classes to mimic the outcome of BLUP. For each selection index, predicted results from a simple index were computed as well, with information recorded only on the candidate for selection or its dam. In all instances, the simple index predicted lower responses in goal traits with lower accuracies than comprehensive indexes and so the results are not included in this Chapter.

In order to obtain the results from index evaluation, information is required on goal traits, measured (index) traits, genetic parameters for these, relative economic weights for goal traits, expected information from relatives, selection intensity and generation interval.

Definition of the breeding goal and measured traits

It is useful to think of indexes in two parts, the breeding goal, which is a list of the traits we want to improve, and the index traits, which is a list of traits which we can measure and select on. The two need not be the same. For instance, if the goal includes carcass traits, we cannot measure them directly on animals available for selection, so we rely on ultrasonic measurements and/or measurements of carcass composition of relatives.

Ten breeding goal traits have been evaluated for their inclusion into the selection indexes. They include *maternal* and *lamb* traits. Definitions of each trait, and why they are important are given in Chapter 4. To achieve the goals, nine index traits are considered. The goal and index traits are shown in Table 5.1. Pre-mating liveweight is used as the indicator of mature size, and average weight of lambs weaned ('maternal weaning weight') as the indicator of weaning weight as a trait of the ewe.

Table 5.1 *Breeding goal and index (measured) traits*

Breeding Goal Traits	Index Traits
<i>Ewe Traits</i>	<i>Ewe Traits</i>
Mature weight (Mat wt)*	Pre-mating live weight
Longevity (age at culling) (Long)	Age at culling
Lamb loss† (Ndead)	Lamb loss from birth to weaning† ^a
No. lambs reared (litter size at weaning) (Nrear)	Litter size at weaning‡
Maternal weaning weight (MWW)	Average weight of lambs weaned§
Fleece weight (Fleece)	Fleece weight
<i>Lamb Traits</i>	<i>Lamb Traits</i>
Lamb weaning weight (direct) (WWT)	Ultrasonic fat depth (Fatd)
Carcass fat class (Fatcl)	Ultrasonic muscle depth (Musd)
Carcass conformation class (Conf)	Weaning weight
Carcass weight (CWT)	

* Abbreviations in brackets. † No. lambs lost to weaning (including dead at birth, lambs fostered/taken off).

†^a including lambs born dead, ‡ own lambs only, § including weight of lambs fostered on.

Genetic Parameters

In order to calculate the properties of the selection indexes, genetic and phenotypic parameter estimates (heritabilities and correlations) are required for goal and index traits. The univariate heritabilities, means, standard deviations and repeatabilities of the traits used in index calculations are shown in Table 5.2.

The genetic and phenotypic correlations used in the index calculations are shown in Table 5.3. Phenotypic correlations between carcass traits and all other traits were not required for the index calculations, so these are not shown. These estimates are a combination of unpublished estimates from data generated from the two SAC experimental hill flocks described in Chapter 2, as well as published literature estimates. The same parameters were used for each selection index. Parameter estimates are assumed to be known without error, and assumed not to change over time. For example, no reduction in variances from selection due to the Bulmer effect (Bulmer, 1971) are assumed.

Table 5.2 *Heritabilities (h^2), means, phenotypic standard deviations (σ_p) and repeatabilities (r) used in the index calculations.*

Trait	h^2	Mean	σ_p	r
Mature wt (kg)	0.44	59.4	5.28	0.49
Longevity (days)	0.08	1756	378	N/A
Fleece wt (g)	0.54	1.82	0.506	0.613
Maternal weaning wt (kg)	0.01	29.16	5.384	0.058
No reared (lambs/ewe)	0.13	1.35	0.454	0.21
Lamb loss (lambs/ewe)	0.05	0.24	0.497	0.085
Ave Fat depth (mm)	0.24	1.998	0.598	N/A
Muscle depth (cm)	0.28	1.763	0.202	N/A
Lamb weaning wt (kg)	0.22	27.79	3.52	N/A
Fat class (ESF%)	0.11	11.14	1.529	N/A
Conformation score (units†)	0.07	3.00‡	0.974	N/A
Carcass weight (kg)	0.29	16.75	1.94	N/A

N/A Not applicable. It is assumed that a store lamb producer would not benefit directly by changes in carcass traits.† Threshold units on the underlying normal distribution scale.

‡ The mean value of 3 for conformation score is transformed to 0 on the underlying normal scale.

Table 5.3 *Correlations† between breeding goal and index traits.*

	Mat wt	Long	Fleece	MWW	Nrear	Ndead	Fatd	Musd	WWT	Fatcl	Conf	CWT
Mat wt	1	0.19	0.24	0	0.65	0.17	0.008	0.63	0.62	0.15	0	0.68
Long	0.073	1	0.37	0	0.27	-0.59	0.053	0.15	-0.28	0.053	0	0
Fleece	0.22	0.041	1	0	0.13	-0.16	0.33	0.18	0.12	-0.31	0	0
MWW‡	0	0	0	1	0	0	0	0	0.20	0	0	0.20
Nrear	0.22	-0.028	-0.12	0	1	-0.12	0.13	0.40	0.52	-0.14	0	0.10
Ndead	0.074	-0.099	0.28	0	-0.42	1	-0.17	-0.047	0.48	-0.16	0	0.05
Fatd	0.13	0.053	0.26	0	0.13	0.098	1	-0.19	-0.051	0.16	-0.32	-0.30
Musd	0.30	0.038	0.20	0	-0.068	-0.12	0.33	1	0.40	-0.54	-0.40	0
WWT	0.46	0.042	0.22	0	0.16	0.079	0.49	0.31	1	0.19	0.01	0.36
Fatcl	-	-	-	-	-	-	-	-	-	1	0.19	0.26
Conf	-	-	-	-	-	-	-	-	-	-	1	0.44
CWT	-	-	-	-	-	-	-	-	-	-	-	1

†Genetic correlations above the diagonal, phenotypic below. ‡ Maternal (average) weaning weight.

Economic Values

Relative economic values are required for each breeding goal trait. They were derived using a whole farm model approach for each farm system, described in Chapter 4. All economic values have been expressed on a 'per 100 ewe flock' basis, and differ for each farm system. The index calculations in this paper are based on the assumptions that relative economic values remain constant over the range of variation likely to occur for different traits, and they do not change over time.

Index calculations

The selection index used the following assumed data structure for lamb traits:-

- i. a measurement on the lamb itself
- ii. a measurement on the dam of the lamb
- iii. a measurement on 60 paternal half-sibs of the lamb
(given the lamb, dam and paternal half-sib information, knowledge of the sire performance contributes negligible information).

For traits measured on the dam (ewe) of the lamb:-

- i. measurements on the ewe itself
- ii. measurements on the dam of the ewe
- iii. measurements on 15 female paternal half-sibs of the ewe

It is assumed that for each female in this set, each trait has an average of **two** recordings (in separate parities) except for predicted longevity, which only has one measurement. This data structure mimics that for an average animal subjected to multi trait BLUP analyses in the selection flocks, once selection has been underway for several years. It is important to note that the 'maternal' traits are being predicted for the lambs who are candidates for selection, rather than for their dams.

The selection index calculations were done using programmes written by Bishop (Pers. comm.) using Genstat (1983), and based on index theory by Cunningham (1969). The index matrices and vectors were:-

X = vector of measured variables for each index trait

v = vector of economic weights for the goal traits

$b = b_1 \dots b_n$, is a vector of weighting factors to be used in the index

$P = m \times m$ matrix of actual covariances between the measured traits X . In this case, P has dimensions of 27 x 27, as the 9 traits are measured on three groups of animals.

$G = m \times n$ matrix of genetic covariances between the m measured variables and the n traits in the breeding goal. The dimensions of this matrix are 27 x 10.

$C = n \times n$ matrix of genetic covariances between the goal traits, (a 10 x 10 matrix).

D = selection differential on a standardised normal distribution

The general index equation is:

$$b = P^{-1}Gv$$

the variance of the index is:

$$b' Pb$$

The expected monetary returns from a single round of selection using the index are:

$$D \sqrt{b' Pb}$$

and the accuracy of the index is:

$$\sqrt{\frac{b' Pb}{v' Cv}}$$

One round of selection on the index will produce $D\sigma_i$ units of change in the index, and therefore a vector

$$D \frac{b'G}{\sqrt{b'Pb}}$$

of units of change in each trait.

To derive the annual progress in each trait, a selection differential (D) of 1 and generation interval of 2.5 was assumed. The contribution of each index trait to the selection objective was calculated by measuring the reduction in the efficiency of the index, the correlation between the true breeding value and the index after each trait was individually dropped from the index.

Sensitivity Analyses

The sensitivity of the index to changes in the economic values proportionally 0.5 above and below the base values was investigated. Each goal trait was changed individually, and the effects on the expected genetic progress in all the goal traits, and the accuracy of the new index were determined. The changes in economic values necessary to alter expected progress in the desired direction for mature size and number of lambs reared are also reported. This was achieved by substituting different economic values for these traits in the programme until responses in the desired direction were obtained.

As heritability estimates for ultrasonic fat depth and weaning weight differ according to the environment in which lambs are reared (Chapter 2), the sensitivity of the index to changes in these heritabilities was investigated. All sensitivity analyses were performed using the intensive farm system as a model.

As well as sensitivity analyses for changes in economic values and heritabilities, some alternatives to the indexes are proposed. These alternatives which might be appropriate for some, but not all, hill breeds were investigated for the intensive farm system. The aim was to investigate the consequences of: i) excluding fleece weight from the breeding goal, ii) leaving fleece weight *in* the breeding goal but

not measuring it, and iii) using fat and muscle measurements on the ewe, rather than on all lambs. The different parameters used for exploring this last option are shown in Table 5.4.

The last option would provide more flexibility for the producer for management purposes, in particular for farms where lambs are relatively immature at the time of ultrasonic measurements, and show little variation in fat depths; it would also be a cheaper alternative to scanning all lambs.

Table 5.4 *Correlations† between breeding goal and index traits for index calculations using fat and muscle measurements on ewes‡.*

	Mat wt	Long	Fleece	MWW	Nrear	Ndead	Fatd	Musd	WWT	Fatcl	Conf	CWT
Mat wt	1	0.195	0.245	0	0.646	0.173	-0.096	0.274	0.623	0.148	0	0.676
Long	0.073	1	0.373	0	0.271	-0.586	0.053	0.146	-0.279	0.053	0	0
Fleece	0.219	0.041	1	0	0.129	-0.158	-0.139	0.091	0.125	-0.313	0	0
MWW	0	0	0	1	0	0	0	0	0.200	0	0	0.200
Nrear	0.219	-0.028	-0.122	0	1	-0.118	0.128	0.402	0.517	-0.144	0	0.100
Ndead	0.074	-0.099	0.284	0	-0.419	1	-0.175	-0.047	0.480	-0.159	0	0.050
Fatd	0.360	0.081	0.123	0	0.128	0.098	1	-0.103	-0.051	0.160	-0.319	-0.300
Musd	0.433	0.062	0.173	0	-0.068	-0.121	0.474	1	0.402	-0.536	-0.400	0
WWT	0.464	0.042	0.218	0	0.162	0.079	0.020	0.153	1	0.189	0.010	0.365
Fatcl	-	-	-	-	-	-	-	-	-	1	0.190	0.258
Conf	-	-	-	-	-	-	-	-	-	-	1	0.440
CWT	-	-	-	-	-	-	-	-	-	-	-	1

† Heritabilities for fat depth and muscle depth used are 0.24 and 0.39 respectively; phenotypic standard deviations 1.8mm and 0.29cm respectively, and repeatabilities 0.157 and 0.397 respectively.

Results

Progress in goal traits

Predicted annual progress in each goal trait for the three farm types is shown in Table 5.5. Traits which consistently improve, regardless of production system, are longevity, fleece weight, the number of lambs lost from birth to weaning and lamb weaning weight. Mature weight and number of lambs reared to weaning are predicted to increase in all three production systems, although predicted responses are greatest for the intensive farm system.

Table 5.5 *Expected annual genetic change in each goal trait in the three farm systems.*

	Intensive	Semi-intensive	Extensive
Mature weight (g)	663	477	507
Longevity (days)	9.9	12.1	11.6
Fleece weight (g)	45.5	50.7	51.8
Maternal weaning weight (kg)	0.002 (negl)	-0.004 (negl)	-0.003 (negl)
No. Lambs weaned/ ewe	0.025	0.020	0.021
No. Lambs lost/ ewe	-0.005	-0.009	-0.008
Weaning weight (g)	169	75	96
Fat class (ESF%)	-0.043	-0.052	N/A
Conformation (units†)	-0.016	-0.019	N/A
Carcass weight (g)	24.6	-18.8	N/A

N/A Not applicable. It is assumed that a store lamb producer would not benefit directly by changes in carcass traits.

† Threshold units on the underlying normal distribution scale.

In general, proportional changes in lamb and carcass traits are lower than changes in the ewe traits. Lamb weight at weaning is predicted to improve, although the changes in carcass weight are smaller. Improvements in the reduction of fat class are predicted, although at the expense of conformation, which is predicted to decrease by a small amount.

Contribution of traits in the index

The importance of each measured trait in the overall index is shown in Table 5.6. The figures shown represent the genetic improvement obtained if a particular measurement was dropped from the index, compared to the genetic gain achieved by the full index. Therefore, the smaller the value the more important that measurement is, and the more it contributes to the index. For example, if mature weight is dropped from the intensive index, the overall rate of progress is predicted to be 77% of that possible from selection on the full index. The results show that mature size is the most important trait for all three indexes, and maternal weaning weight is the least important for all farm systems (due to the low heritability for this trait). It could be dropped from the index entirely with no effect on the expected responses. Most of the traits have a small effect on the index, and if removed individually, result in a reduction in the efficiency of the index of proportionally 0.01 to 0.03.

Table 5.6 *Relative contribution of each trait to the index, in the three production systems †.*

	Intensive	Semi-intensive	Extensive
Mature weight	0.77	0.85	0.89
Longevity	0.97	0.96	0.96
Fleece weight	0.94	0.91	0.91
Maternal weaning weight	1.00	1.00	1.00
No. Lambs weaned	0.98	0.99	0.97
No. Lambs lost	0.99	0.99	0.99
Fat depth	0.98	0.95	0.95
Muscle depth	0.89	0.88	0.87
Fat + muscle depths	0.88	0.85	0.83
Weaning weight	0.98	0.98	0.98

† The smaller the value, the more the trait contributes to the index. The efficiency of the index r_{TI} is the correlation between the index and the True Breeding Value. The data presented in the Table show the relative efficiency of the index, measured by the reduction in r_{TI} resulting from dropping each variable from the index (Cunningham, 1969).

Accuracy

The accuracies of the indexes are shown in Table 5.7. In general, when traits have low heritabilities, or breeding objectives conflict, the accuracy of the index is lower than if traits have higher heritabilities and are favourably correlated. Having many traits in the breeding goal increases the chance that some unfavourable correlations will exist among them. It is inevitable that a dual-purpose breeding programme will have more traits than a single purpose breeding programme, especially if additional traits such as reducing lamb mortality and increasing ewe longevity are included. This may explain why the accuracies are low.

Table 5.7 *Accuracy of selection for the comprehensive selection indexes in the three production systems*

	Intensive	Semi-intensive	Extensive
Comprehensive index	0.37	0.37	0.38

Monetary returns

Selection indexes provide the optimum distribution of emphasis among traits. They do not answer the question of whether breeding is economically justified. However, to help breeders answer that question, the annual expected monetary return from using the selection indexes can be determined. As the benefits from continuous genetic improvement are cumulative, these benefits become greater once several years of selection have been performed. The expected benefits from one year of selection for a 100 ewe flock are £363, £267 and £248 for the intensive, semi-intensive and extensive farms respectively, using the economic weights which describe returns over a 15 year time horizon. Table 5.8 shows the expected discounted benefits across time, assuming no reduction in variation of these traits. Although implicit from the economic values, these figures confirm that the potential to improve farm efficiency is greater for the more intensive hill

farms.

Table 5.8 *Projected discounted monetary returns (£) from continuous genetic improvement for 100 ewe flock*

Year	Intensive	Semi-intensive	Extensive
1	363	267	248
5	1671	1576	1127
10	2986	2890	2011
20	4822	4727	3245
30	5950	5854	4003

Sensitivity Analyses

Proportional changes of ± 0.5 of the economic value of each goal trait were made to investigate the sensitivity of the intensive farm system index. The results for the expected progress in goal traits from these sensitivity analyses are shown in Table 5.9. The majority of the changes in economic values result in proportional changes of less than ± 0.10 in responses for mature size, longevity, fleece weight, maternal weaning weight, fat class and conformation score. However, changes in the economic values for the number of lambs weaned, number of lambs lost, and to a lesser extent, weaning weight and carcass weight, (shown in italics in Table 5.9), resulted in greater fluctuations in responses for most of the traits, except responses in fleece weight, fat class and conformation score. The greatest change in predicted response was seen in carcass weight, when the economic values for the number of lambs reared and number of lambs lost were altered. The expected responses for carcass weight increased almost threefold from 0.06 kg to 0.18 kg after a decrease in the negative economic value for the number of lambs lost, from £-426 to £-213. When the economic value for the number of lambs lost was changed to £-639, expected progress in carcass weight decreased by proportionally 0.77 to -0.048 Kg. Increasing the economic value for the number of lambs weaned from £361 to £541 resulted in a twofold increase in expected response in carcass weight. A decrease in the economic value for the number of

lambs weaned to £180, resulted in a proportional change in response in carcass weight of 0.94, to -0.58 kg.

The accuracies of the indexes with the different economic values are also shown in Table 5.9. In general, they are similar to the optimum index (0.37), but when the economic value for number of lambs lost is -£213, the accuracy rises to 0.42, the highest accuracy of all. When the economic value for mature size is -£24.5, the accuracy goes down to 0.34, the lowest accuracy.

The effects of increasing the magnitude of the negative economic value on mature size to constrain its increase was investigated. Table 5.10 shows the expected progress in each trait and the accuracy of the index when the economic value is -£100 and when it is -£141. When the economic value for mature size is -£100, mature size still increases, but at a lower rate than in the original index, being 263g per annum, instead of 663g per annum. However, responses in carcass weight, weaning weight, maternal weaning weight, fat and conformation are all predicted to decrease, and the accuracy is 0.30. When the economic value for mature size is -£141, response in this trait per annum is predicted to be -27g, with correspondingly large decreases in carcass and weaning weights and maternal weaning weight, but with a significant improvement in the number of lambs lost. The accuracy of this index is reduced to 0.29.

Table 5.9 *Sensitivities of expected responses† and accuracies of the index, to changes in economic values*

		Mat wt	Mat wt	Long	Long	Fleece	Fleece	MWW	MWW	Nwean	Nwean	Ndead	Ndead
EV (£/100 ewe flock)	Original response	-24.46	-8.155	310.05	103.2	252.1	84.05	108.0	36.00	541.2	180.4	-639.4	-213.1
Mat wt (kg)	1.557	1.504	1.605	1.465	1.650	1.539	1.575	1.562	1.552	1.729	1.157	1.194	1.849
Longevity (days)	24.9	25.7	24.3	27.4	22.0	25.2	24.8	24.8	25.2	20.5	32.0	30.9	16.3
Fleece (kg)	0.1137	0.115	0.112	0.116	0.110	0.118	0.110	0.114	0.114	0.108	0.119	0.116	0.102
MWW (kg)	0.004	-0.001	0.002	-0.005	0.006	0.000	0.001	0.001	0.000	0.009	-0.015	-0.015	0.018
no.wean /ewe	0.0619	0.061	0.063	0.059	0.065	0.062	0.062	0.062	0.062	0.067	0.049	0.051	0.069
no.lost / ewe	-0.0119	-0.013	-0.011	-0.015	-0.008	-0.012	-0.011	-0.011	-0.012	-0.005	-0.023	-0.023	0.002
WWT (kg)	0.4228	0.393	0.451	0.343	0.512	0.418	0.428	0.430	0.416	0.561	0.146	0.154	0.696
Fat (ESF%)	-0.1081	-0.109	-0.107	-0.118	-0.095	-0.111	-0.105	-0.107	-0.109	-0.081	-0.152	-0.135	-0.070
Conf (units)	-0.0402	-0.041	-0.040	-0.042	-0.038	-0.041	-0.040	-0.040	-0.041	-0.035	-0.048	-0.050	-0.026
Carc wt (kg)	0.0614	0.049	0.074	0.035	0.092	0.053	0.071	0.063	0.060	0.125	-0.058	-0.048	0.181
Accuracy		0.337	0.382	0.373	0.376	0.381	0.368	0.374	0.375	0.395	0.342	0.352	0.422

† Expressed per generation. Data should be divided by 2.5, to obtain responses per annum.

Table 5.9 (Continued) Sensitivities of expected responses† and accuracies of the index, to changes in economic values

Economic value	WWT	WWT	Fat class	Fat class	Conf.	Conf.	Carc wt	Carc wt
	133.3	44.45	-48.37	-16.12	191.2	63.75	184.9	61.65
Mat wt (kg)	1.696	1.376	1.555	1.559	1.559	1.555	1.646	1.458
Longevity (days)	21.4	28.6	25.2	24.8	24.9	25.1	23.3	26.6
Fleece (kg)	0.110	0.115	0.114	0.113	0.113	0.114	0.107	0.120
MWW (kg)	0.009	-0.009	0.000	0.001	0.001	0.000	0.004	-0.003
no.wean / ewe	0.066	0.056	0.062	0.062	0.062	0.062	0.065	0.059
no.lost / ewe	-0.006	-0.018	-0.012	-0.011	-0.011	-0.012	-0.008	-0.015
WWT (kg)	0.549	0.276	0.419	0.427	0.429	0.417	0.488	0.354
Fat (ESF%)	-0.097	-0.119	-0.110	-0.107	-0.107	-0.109	-0.105	-0.111
Conf (units)	-0.036	-0.044	-0.041	-0.040	-0.039	-0.041	-0.037	-0.044
Carc wt (kg)	0.107	0.010	0.061	0.062	0.065	0.058	0.091	0.031
Accuracy		0.363	0.376	0.373	0.371	0.378	0.374	0.376
	0.371							

† All data should be divided by 2.5 to obtain responses per annum.

Table 5.10 *Effects of changing the economic value for mature weight on annual expected progress and accuracy of goal traits.*

	Original EV Mature weight = -11.8 (original index)	EV Mature wt = -100	EV Mature wt = -141
Mature weight (g)	664	264	-26
Longevity (days)	9.9	12.9	13.2
Fleece weight (g)	45.5	49	46
Maternal weaning weight (kg)	0.002	-0.007	-0.01
No. lambs weaned / ewe	0.025	0.015	0.007
No. lambs lost / ewe	-0.005	-0.012	-0.014
Weaning weight (g)	169	-16	-144
Fat class (ESF%)	-0.043	-0.043	-0.037
Conformation (units†)	-0.016	-0.015	-0.013
Carcass weight (g)	24.6	-48	-94
Accuracy	0.37	0.31	0.29

† Threshold units on the underlying normal distribution scale.

The sensitivity of the index to changes in the heritability for fat depth from 0.24 to 0.12 made little difference in the expected progress for each trait, with the greatest changes being for the predicted responses for carcass weight, increasing from 24g per annum to 31g. The heritability for weaning weight was then reduced from 0.22 to 0.11, and the predicted responses in most traits changed. In particular, the expected response in weaning weight almost halved from 169g to 93g per annum, and that for carcass weight halved from 24.5g to 12.6g. The results for these changes in heritabilities are shown in Table 5.11.

Table 5.11 *Effects of changing the heritability of fat depth and weaning weight on annual expected progress in goal traits.*

	Original index	h ² fat depth 0.12	h ² weaning weight 0.11
Mature weight (g)	664	682	582
Longevity (days)	9.9	9.9	11
Fleece weight (g)	45.5	45.2	46.6
Maternal weaning weight (kg)	0.002	0.006	0.002
No.Lambs weaned/ewe	0.025	0.024	0.023
No. Lambs lost/ ewe	-0.005	-0.004	-0.006
Weaning weight (g)	169	173	92
Fat class (ESF%)	-0.043	-0.043	-0.044
Conformation (units†)	-0.016	-0.015	-0.017
Carcass weight (g)	24.6	31	12.6
Accuracy	0.37	0.37	0.37

† Threshold units on the underlying normal distribution scale.

Index Options

Excluding fleece weight from the breeding goal

Improving fleece production is currently not a priority for breeders of some hill sheep breeds, in particular coarse wool breeds such as the Blackface. Including fleece weight in the breeding goal may therefore be an obstacle to uptake of these selection indexes. Index calculations were made for the intensive farm system excluding fleece weight from the breeding goal. The expected responses in goal traits as a result of leaving fleece weight out of the breeding goal are shown in Table 5.12. The results show that fleece weight will increase by proportionally 0.62 of the original response. This is due to the correlations between fleece weight and the other components of the breeding goal, in particular mature size. The predicted responses in carcass weight and maternal weaning weight have

increased by more than double that predicted for the original index although direct weaning weight is not predicted to increase. The differences in the other maternal traits are small, with a slightly lower response in lambs reared and lost, and a lower improvement in longevity. The incremental reduction of fat class has halved with this option, the annual discounted returns of £328 are £34 less than the original index, and the accuracy is 0.34 (compared to 0.37).

Not recording fleece weight (but retaining fleece weight as a goal trait).

The physical and financial effort of recording weight of fleece at clipping could be a barrier to its improvement. Including it in the breeding goal but not recording it, will give a more reliable estimate of the economic benefit of the index compared to excluding it altogether. The expected responses from selection on such a modified index are also shown in Table 5.12. The responses are very similar to those from taking fleece weight out of the goal altogether, and the annual discounted returns are higher, being only £22.50 less than the original index. The accuracy is reduced to 0.35.

The results from these two scenarios imply that there is a trade-off between responses in carcass and fleece weights, with responses in carcass traits being greater when fleece weight is left out of the breeding goal altogether.

Measuring fat and muscle on the ewe

Another modified index was investigated using ultrasonic measurements of fat and muscle from the ewes prior to tupping, instead of measuring lambs at weaning. The results from this index shift the emphasis of the index in favour of carcass traits, at the expense of some of the maternal traits. The expected responses are shown in Table 5.12.

Table 5.12 *Summary of predicted annual responses from the four selection strategies for the intensive farm system*

	Original index	Exclude fleece weight from breeding goal	Not measuring fleece weight (but remains in breeding goal)	Maternal ultrasonic measurements
Mature weight (g)	664	662	657	662
Longevity (days)	9.9	8.5	8.5	7.9
Fleece weight (g)	45.5	28.1	28.7	54.8
Maternal weaning weight (kg)	0.002	0.005	0.003	0.009
No. Lambs weaned/ewe	0.025	0.024	0.024	0.021
No. Lambs lost/ ewe	-0.005	-0.004	-0.004	0.001
Weaning weight (g)	169	167	165	221
Fat class (ESF%)	-0.043	-0.019	-0.021	0.015
Conformation (units†)	-0.016	-0.016	-0.017	0.007
Carcass weight (g)	24.6	56.8	51.1	131
Annual discounted returns (£)	363.2	328.5	340.5	322.9
Accuracy	0.37	0.34	0.35	0.33

† units expressed on the underlying normal distribution scale

This ‘carcass orientated’ index shows extra improvements in weaning weight, maternal weaning weight, carcass weight and conformation, whilst holding fat class and number of lambs lost more or less constant (with a tendency for them to increase). This index has an expected annual monetary benefit of £323. However, this index may be more practical and profitable to the industry, as it reduces the need to scan all of the lambs at weaning, and hence reduces costs.

Discussion

The results from this work show that multi-trait selection indexes can theoretically improve flock productivity and economic returns for UK hill sheep for a range of different production levels and production systems. Improvements in maternal characteristics including genetic selection for reduced lamb losses can be achieved with more modest improvements in lamb carcass traits. Lamb survival has been shown to be both repeatable and heritable (Atkins, 1980, Donnelly 1982, Haughey and George, 1982, Piper et al, 1982, Matos et al, 1994) and improving it would help to alleviate the seemingly intractable problem of perinatal mortality (Haughey, 1983). It is also more cost-effective to select ewes with the ability to rear more of their lambs, rather than increasing prolificacy *per se*. This is because the costs of supplementary feed for ewes carrying higher litter sizes during winter, would not be proportional to the increase obtained in the number of lambs weaned (as discussed in Chapter 4). Improving longevity has been documented as being important for livestock profitability, and evaluations of this trait are currently used in breeding programmes in the UK for dairy cows (Veerkamp *et al.*, 1996, Brotherstone *et al.*, 1997). This is the first time that it has been considered in the breeding goal for UK sheep. Improving longevity of the flock ensures that higher flock productivity will not be achieved at the expense of shorter ewe lifespan.

The use of these indexes is expected to lead to an increase in the mature size of the sheep. For some flocks, this may not be acceptable. However, improvements in lamb weaning and carcass weights, as well as the predicted economic returns, would perhaps be smaller if the increase in mature size was constrained through the use of a 'desired gains', or 'target production' index approach (Newman and Ponzoni, 1994; Gibson and Kennedy, 1990). The results in this study from applying a greater negative economic value on mature size, confirm that lamb

weaning weights and carcass weights may not increase, if mature size is

constrained even further.

Responses in lamb carcass traits are small, and for the semi-intensive farm system are in the 'wrong' direction (i.e. with a small reduction in carcass weight). This is difficult to comprehend, when the genetic correlation between mature size and carcass weight that was used was so high (0.68). As the differences between the expected responses of the three farm systems are solely a reflection of the differing economic values between them, then it follows that a favourable response in carcass weight for the semi-intensive system will be achieved only if the economic value for this trait is increased above the original value. The small responses in fat class, in the 'right' direction, and a small response in conformation in the 'wrong' direction, reflect the low heritabilities for these traits, positive genetic correlation between conformation and fatness, and the negative genetic correlations between the live ultrasonic measurements of fat and muscle depths, and the fat class and conformation scores measured post-slaughter. These latter correlations may seem erroneous, but in practice for hill lambs, the time-lag between the measurement of lamb body composition at weaning and when they are slaughtered means that well-grown, more mature lambs at weaning (measured at a constant time, and adjusted for age) are likely to reach the point for slaughter (at a constant condition score, an indication of fatness) sooner than the lighter, less mature lambs at weaning. The results from these indexes show that the importance of carcass traits for hill flocks in terms of genetic improvement is less than is generally perceived in the industry, due to the additional costs and inputs required to improve them.

As the traditional way of finishing lambs for slaughter allows lambs to continue to grow, average carcass weight increases with age, and hence older lambs at slaughter have heavier carcasses than their contemporaries who grew faster,

matured quicker, and were slaughtered sooner. Although fat class is predicted to improve (i.e. lambs will get leaner), conformation score is predicted to decline by a small amount. In practice, farmers may overcome this by keeping lambs longer to reach the desired level of finish (fatness).

The results from the index calculations show that the current industry payment structure for lamb carcasses is inadequate to provide clear signals to the farmer for reducing fatness in meat, in line with current Government objectives. This has also been discussed by Lewis *et al.* (1996) in an analysis of Suffolk x Mule (Bluefaced Leicester x Scottish Blackface) lambs. In this study, lambs sired by rams from a selection line designed to increase lean deposition with little change in fat deposition were compared with lambs from a control line (Simm and Dingwall, 1989): This study showed that conformation score improved with higher fat class scores (irrespective of differences in lean tissue) and that progress in reducing fat in market lambs would be slowed by the carcass assessment system currently in place.

The differences between the three farm types in the predicted progress in goal traits are interesting. The monetary returns and, in general, the economic values for all traits are smaller for the extensive than the other two farm systems, but the predicted responses in goal traits are not. The intensive index predicts greater progress in lamb production traits overall compared to the other two farming systems. This implies that greater emphasis is placed on maternal traits for more extensive, and lower production-level farms.

The alternative selection indexes described for the intensive hill farm situation explore the implications of i) a different breeding goal (dropping fleece weight) and ii) using a different strategy to meet the same goal (by not measuring fleece weight, or by using ewe ultrasonic measurements of fat and muscle). The former option is more likely to appeal to breeders whose returns from wool production

make up a much smaller proportion of total income than lamb sales, i.e. whose lamb output is at the higher end of the production spectrum.

Using indexes which predict less than optimum economic response may well be the most profitable, if the cost of implementation is less than that of the 'optimum' index. For example, measuring fat and muscle depths on the ewe instead of on the lamb removes the need to measure all lambs at, or just prior to, weaning. As weaning is normally in August for hill flocks in Scotland, and the major store and breeding lamb sales commence in September, lambs are frequently sorted into groups for slaughter, for store sales or for breeding at this time, so measuring them at this stages leaves too little time for evaluation and selection. Recording fat and muscle on lambs much earlier for many hill flocks is inappropriate as they may only gather lambs once or twice after lambing, and they may be too immature to have measurable variation in fatness. Using the index based on measuring fat and muscle on the ewe may well be the most cost-effective strategy. At £2.50 per scan, and based on the numbers of lambs reared for the intensive farm type (120), compared to the number of replacement ewes (29), the difference in cost between using the original index and that using measurements of fat and muscle on the ewe is £227. The predicted economic benefit of selection on this index is only £40 less than on that measuring fat and muscle on all lambs, so selection on the index would be more cost-effective.

The economic benefits from genetic improvement depend on the level of production of individual farms when embarking on genetic improvement programmes, together with the ability of the farm to accommodate increased productivity. In some instances, unrealistic breeding objectives, such as increasing the number of lambs reared beyond the capacity of the farm to provide suitable grazing, results in negative economic values and negative returns from genetic improvement in some hill situations (see Chapter 4). The results

highlight the need for a flexible approach to breeding objectives and breed

improvement in hill flocks to suit the farm production system and the physical limitations to genetic improvement. Such flexibility may well pave the way for a greater involvement by the hill sector in genetic improvement programmes.

The indexes described here are a first step towards improving sustainability and flock performance simultaneously, through genetic selection. By including 'lamb loss' in the breeding goal, the 'wastage' of lambs from birth to weaning will be minimised. Including longevity in the breeding goal will reduce ewe 'wastage' as ewes will live longer and fewer replacement ewes will be required. This Chapter demonstrates clearly that productivity and sustainability can be improved simultaneously. Implementation of the indexes described here will increase productivity whilst helping to keep the image of lamb as a natural product, and to maintain the acceptance of an increasingly discerning consumer.

In the future, other traits important for improved 'sustainability' of sheep systems, such as increasing resistance to parasites, decreasing lambing difficulty and improving maternal behaviour important for neonatal survival, could be considered for inclusion into wider breeding goals for hill sheep. Animal welfare could be improved through genetic selection by including some of these traits alongside conventional production traits. By so doing, the emphasis of livestock production will shift towards greater sustainability of the farming system. 'Agenda 2000' is likely to result in lower returns for production for sheep kept on hill farms. This means that the role of hill sheep in the future may well be altered towards maintaining the hill environment for other pursuits (conservation of bird populations, leisure activities, shooting etc.) rather than for sheep production *per se*. A selection index which identifies sheep which live longer, lose fewer lambs, are resistant to disease, have good maternal behaviour and few lambing problems, may well appeal to flock owners whose custodial role of hill environments is

likely to become increasingly important in the next century.

Chapter 6

Final Discussion and Conclusions

This thesis contributes to our knowledge and understanding of the genetics of hill lamb growth and body composition. It shows that traits conferring improved carcass composition are under substantial genetic control, and can be manipulated under extensive rearing conditions. Compared to lambs reared under non-limiting conditions, however, the hill environment plays a large part in determining growth rates and tissue deposition, resulting in lower heritabilities for these traits. The economic values derived for different production systems are lower for the extensive farm type than the intensive farm type, and show that potential economic benefits are greater for farm systems where production levels are already high. Sensitivity analyses showed that the economic value for ‘number of lambs reared’ is applicable for farms within specified production limits. Combining traditional maternal traits, ‘novel’ maternal traits, lamb growth and lamb carcass traits into indexes of overall economic merit results in positive economic returns for a range of hill farm types, and evaluation of these indexes show that progress in these traits is feasible from continuous selection.

Genetic parameters

The results from Chapter 2 report both an increase in direct heritabilities, and a decrease in the maternal component for lamb growth, with increasing lamb age. This corresponds to the findings of Atkins (1986), Nashölm and Dannell (1996), and Larsgard and Olesen (1998). These results also suggest (but require validation) that selection for maternal ability will not be made more efficient by including pre-weaning traits in the selection index in addition to direct selection for lamb growth. The low heritability estimates for pre-weaning weights correspond to other studies for sheep reared under extensive management conditions for Blackface (Atkins, 1984, 1986), Welsh Mountain (Aslaminejad *et al.*, 1999), Swedish Peltsheep (Nashölm and Dannell, 1996), and (mainly) Norwegian - Dala (Larsgard and Olesen, 1998).

Heritability estimates for ultrasonic backfat measurements were lower than the

majority of published estimates, in particular for lambs reared on the open hill. The heritabilities for backfat depths for inbye-reared lambs were on average twice that of hill reared lambs. Lambs reared on the hill had a slightly lower additive genetic variance than inbye-reared lambs, and conversely, hill reared lambs had a much larger environmental variance than inbye-reared lambs. This shows that the harsher rearing environment (hill) has inflated the error variance, which may partly explain the low heritability estimates for ultrasonic measurements of subcutaneous fat. The implications for genetic improvement of the harsh rearing environment, and the unique management system used in hill sheep farming have been discussed by Atkins (1994). The strategies which may be employed to overcome these difficulties for genetic improvement have been suggested by Bishop *et al.* (1996). In short, genetic improvement will be easier, the less limiting the environment in which the animals are reared. Attention must be made, however, to ensure that the environment in which breeding animals are reared and recorded is not too far removed from that in which their progeny are expected to perform and live.

Another explanation for the low heritability estimates in this study for fat depth could be due to them having been calculated at a relatively early stage of the lambs' maturity, at approximately 40% of mature size. Other studies estimated heritabilities when animals were over 50% of mature liveweight (Young and Simm, 1990; Waldron *et al.*, 1992; Bishop, 1993; Cameron & Bracken, 1992). The 'optimum' time for measuring animals' performance for genetic improvement is usually determined by a combination of management as well as genetic factors. For extensive rearing systems, the former usually presides due to the physical difficulties of gathering sheep, and this occurs usually once or twice from birth to weaning. The results from this study for lamb growth infer that measuring animals much younger than at weaning (which normally occurs at approximately 115 days of age), is likely to be less efficient. A similar age (105 days) has also been reported as being the minimum to predict direct genetic effects on lamb weights for Swedish Peltssheep (Nashölm, 1994).

The results show that selecting animals for divergent subcutaneous backfat levels reared under non-limiting nutritional conditions results in their offspring reared in extensive conditions also being divergent in backfat thickness, as determined by ultrasound. This has been discussed in some detail by Bishop *et al.* (1996). Despite the low heritabilities for ultrasonic fat depth, genetic improvement for carcass characteristics is a feasible option, although annual progress would be slower (by approximately 40%) for hill-reared lambs than lambs reared on improved pasture, because of a smaller amount of genetic variance. After slaughter, LEAN line lambs were classified leaner than FAT line lambs by MLC, even though they were selected for slaughter at a condition score of 3. When the animals were dissected, a significant difference in subcutaneous fat was seen between the two genetic lines. The three methods of comparing subcutaneous fat levels (ultrasound, carcass classification and dissection) reinforced the result that LEAN line lambs had significantly less fat than FAT line lambs, and showed that lamb body composition can be manipulated under extensive rearing conditions.

Comparing lambs from LEAN and FAT sires at three end points at slaughter enables the effects of such divergent selection to be assessed on a large number of traits. However, it must be emphasised that the data set is truly valid only for comparison at a fixed degree of fat, as results from the other end-points have been extrapolated, and should be treated with caution. It is appropriate and perhaps necessary to compare animals and estimate parameters at three different end points, because objective selection decisions are based on parameter estimates at a given end point. This gives animal breeders flexibility when deciding on appropriate parameters for inclusion into multi-trait breeding programmes. Flexibility should be incorporated into any large-scale genetic evaluation scheme to enable greater participation by breeders and allow farms with greater constraints for recording, or less scope for genetic improvement, to be involved. In this study, parameters were estimated in different rearing environments, and at different 'end-points'. It has

also derived economic values for different hill farm types for selection indexes to be appropriate for a wide range of production levels. This approach allows breeding programmes for UK hill sheep to be adapted to a wide range of hill-farming situations and breeding goals. Newman and Ponzoni (1994) advocate that a flexible approach to genetic evaluation services, by defining breeding objectives in different ways and according to the traits' suitability and breeders' preferences, is the most appropriate course for implementing breed improvement programmes.

Economic values

Modelling three typical hill farm types to account for the wide range in production systems has facilitated the flexible approach to the derivation of economic values and, ultimately, the derivation of selection indexes tailored to suit different farm types. For the first time, estimates of available energy supply and uptake for sheep from hill and mountain pastures, together with that from reseeded (or improved) grassland have been used to provide a base to derive economic values.

The model also shows that genetic improvement in harsh environments is likely to be of greater benefit to farms with fewer constraints to improvements in production, e.g. those with better quality pasture or a higher ratio of improved grassland to hill pasture.

This study has shown that the same economic values are not valid for all levels of production, i.e. they change as productivity changes. Positive economic values may become negative for production levels which are beyond the capacity of the farm. The economic value of increasing the number of lambs reared in the extensive farm situation is positive up to an increase of $+0.25\sigma_g$ (the equivalent of increasing the number of lambs reared, per 100 ewes mated, from 89.3 to 92.5). After this point, marginal profit (defined by the difference in gross margin from an increase in the number of lambs reared) declines until it becomes negative (just before $+1.0\sigma_g$).

The economic value in this study is the tangent (or first derivative) of the slope, and it becomes negative after $+0.25\sigma_g$. These defined limits would not necessarily be the same for *all* extensive store lamb production farms, but this result demonstrates that economic values themselves depend on the levels of production at a given time and that the balance between positive and negative weights on some farms for some traits can be delicate. Amer *et al.*, (1999) also showed that one of the key factors affecting economic values for prolificacy, was the average level of flock prolificacy.

Normally, economic values for goal traits are derived only for changes in the desired direction. By using the *rate of change* in economic values, the non-linearity (i.e. the financial benefits of increasing the trait differ in magnitude from the financial penalties of decreasing it) in the economic weights produced by the farm models for some traits is accounted for. Theoretically, this approach widens the limits of the levels of production to which the economic values derived apply.

Detailed sensitivity analyses of theoretical 'optimum' performance levels could be done for each goal trait, and for each farm type. Such analyses would provide further insight to determine 'suggested production limits' for individual farm systems, thereby facilitating the tailoring of economic indexes for hill breeds to suit different farming systems operating in different environments. This may be particularly relevant for breeds of sheep which have very different genotypes within it. Such detailed sensitivities for economic values are interesting, but unless the methods to implement flexible breeding programmes are in place, they are unlikely to be useful in practice. Using data typical for their own production systems, economic values for other major hill breeds could be produced with some modifications to the model, and provide a useful tool for breeders and genetic evaluation agencies.

Index calculations

The results from the index calculations show that the use of multi-trait production indexes in selection programmes can improve both flock productivity and economic returns for UK hill sheep for a range of different production levels and production systems.

Using the three sets of economic values to derive three separate indexes compares the relative benefits of genetic improvement for a) different production levels, b) different farm types and c) different farm systems for purebred Blackface hill farms. Improvement in maternal characteristics including reduced lamb losses is achieved along with more modest improvements in lamb carcass traits. Selecting simultaneously for traits that are either antagonistic, or weakly correlated, results in lower responses in the individual traits (but higher economic gain) than if they were selected for separately (Hazel *et al.*, 1994, Mohammed *et al.*, 1998). However, Sales and Hill (1976) showed that including too many traits in the index makes it vulnerable to imprecise estimates of the genetic correlations, and in the worst situation, responses might even decrease, compared to an index with fewer traits included.

These indexes apply to breeders where lambs are either kept for breeding or else sold for meat, and have not been applied to farm systems which sell surplus ewe lambs for breeding. Further work is needed in this area to either incorporate new traits, or re-evaluate economic values applicable to producers of female breeding stock. Unless type traits were to be included, such an exercise would be difficult, because breeding females are sold at auction, and prices closely adhere to physical appearance (and farm reputation).

Including new 'sustainability' traits such as lamb losses and ewe longevity into the breeding goal, in addition to more established goals for productivity, will ensure that high production will not necessarily be achieved at the expense of

shorter ewe lifespan or higher lamb losses, thereby improving or maintaining a high standard of animal welfare. This is important, because experiences from breeding programmes with other species have shown that high producing animals may have more health problems than their lower-productive contemporaries. For example, Pryce *et al.* (1997) reported that selection for milk yield in dairy cattle may have caused a deterioration in health and fertility.

These indexes pose a dilemma for the hill farmer, as they are expected to lead to an increase in the mature size of the sheep. For some farms, the increase may at first sight appear unacceptable, but the improvements in lamb weaning and carcass weights, as well as the predicted economic returns would be smaller (or even negative) if the increase in mature size were to be further constrained. Including mature size in the breeding goal with a negative economic value already constrains its correlated increase as a result of selecting heavier lambs, but to ensure it does not increase at all, results show that the economic value has to be almost nine times that of the original value.

The small responses in lamb carcass traits and, for the semi-intensive farm, the small predicted decrease in lamb carcass weight is of some concern. The reasons for this are a combination of low heritabilities and weak correlations among the index and goal traits as well as low economic values. The antagonistic REVs for lamb weaning weight and mature weight also might explain the low responses. Although carcass traits are high on the perceived list of priorities for genetic improvement, this study has shown that the real costs of improving carcass traits are frequently overlooked. As the model to derive the economic values has included these costs, the economic value for carcass weight is much lower than is generally perceived. Sometimes, there is no clear association between the direction of changes generally perceived and accepted as desirable and the system of payment to the producer. The results for the response in carcass weight and quality traits are an example of this, also seen in the Australian meat industry.

Newman and Ponzoni (1994) advocated that using the 'target' level (or 'desired gains') approach to breeding objectives may be more readily understood and accepted by breeders. This approach defines breeding objectives by setting target production levels for the population in question, sometimes with a time frame (Atkins and Mortimer, 1990). Inflating the economic value above the value derived from the model increases the responses in carcass weight and would overcome this problem. This can be done if it is anticipated that the price of lamb carcasses to the producer are to significantly increase in the future, due to either changes in policy, or to changes in market forces. With the new regulations governed by the European Union 'Agenda 2000' imminent in the farming industry, and a decline in the home consumption of lamb, it is unlikely that the value of lambs to the producer will go much beyond those used in the model to derive the economic value for carcass weight. Inflating the economic value of carcass weight is also applicable, if higher premiums are paid for 'niche market' lambs, such as 'organic' or 'naturally reared' lambs.

The difficulties of measuring live weight and fat and muscle depths at weaning to predict fat class and conformation at slaughter so far in advance are reflected by the index results. In practice, lambs which are heavier at weaning (measured at a constant time, and adjusted for age) are likely to reach the point of slaughter (at a constant condition score, an indication of fatness) sooner than lambs which are lighter at weaning. As the average carcass weight increases with age, lambs which are older at slaughter have heavier carcasses than their contemporaries who grew faster and were slaughtered sooner. It is often difficult to interpret the effects of weaning and post-weaning forage availability on the rate of growth and maturity of hill lambs. The individual variation in the ability of lambs to cope with the stress of weaning and different nutritional finishing regimes (frequently involving a 'store' period), may offer some explanation for the inconsistencies in predicted responses. The indexes predict that lambs will get leaner and

conformation score will decline by a small amount. This result has been seen in practice with Suffolk sheep (Lewis *et al.*, 1996). It is anticipated that farmers will overcome this by keeping lambs longer to reach the desired level of finish (fatness) and so no decline in conformation score will be apparent.

The differences between the three farm systems in the results of the index calculations show that monetary returns and, in general, the economic values for all traits are smaller for the extensive than the other two farm systems, but the predicted responses in goal traits are not. The intensive index predicts greater progress in lamb production traits overall compared to the other two farming systems. These results imply that the more extensive, lower production level farms will gain less from the incorporation of carcass traits in the breeding goal, compared to more productive farms.

The results from the sensitivity analyses show that, in general, the index is robust to individual changes in economic values by proportionally 0.5 above and below the original value. However, there are a few key traits in the index, which, when their economic values were altered, caused a disproportionate change in response for some traits. These results highlight the need to re-evaluate economic values at regular intervals and to alter them if necessary. This will ensure that appropriate, long term selection is implemented, which is relevant to the current and expected future marketplace.

The predicted responses from the alternative selection indexes for the intensive hill farm situation show the effects of incorporating different breeding goals and using a different strategy to meet the same goals. They show, as expected, that using fewer goal traits and 'sub-optimal' indexes result in reduced economic return. For example, this is the case when fleece weight is not recorded as an index measurement but remains in the breeding goal, or when it is left out of the goal altogether. It is also seen when fat and muscle depths are measured on the

ewe rather than on the lamb. Selection indexes help apportion selection emphasis among traits in a rational way, but do not answer the question of whether performance recording is economically justified. Using the index based on measuring fat and muscle on the ewe may well be the most cost-effective strategy. At £2.50 per scan, the difference in cost between using the original index than that using measurements of fat and muscle on the ewe, is £227.50. This is based on measuring 120 lambs reared for the intensive farm type compared to 29 replacement ewes. The predicted economic benefit of this index is only £40.11 less than that measuring fat and muscle on all lambs, and is therefore a cheaper index to implement.

The results from these index calculations generally agree with expectations as to what would be desirable changes in the different environments, e.g. more output in the intensive system. In general, the index results highlight the need for a flexible approach to breeding objectives and breed improvement in hill flocks, to suit the farm production system and physical limitations to genetic improvement. Such flexibility may well pave the way for a greater involvement by the hill sector in genetic improvement programmes.

Future work

The intensive and extensive selection indexes described in Chapter 5 are to be offered to hill sheep breeders in the UK by Signet in the near future. This thesis has focused on studies using the Scottish Blackface, the predominant hill breed. Undoubtedly, the UK hill sheep industry would benefit from parameter estimates for growth and body composition for other major hill breeds. Apart from other parameters for the same breed estimated by Atkins (1984), some estimates for lamb growth have been published only for Welsh Mountain sheep (Pollot *et al.*, 1994; Aslaminejad *et al.*, 1998).

The hill and mountain regions of Wales and England differ from those of

Scotland in both climate, topography and botanical composition. The mean levels of performance of the sheep breeds in the different hill environments also differ. The model to derive economic weights for Scottish Blackface could be adapted to suit other regions and breeds, and relative economic values can be compared between them. Such studies would reveal whether there are wide differences between them, and whether using separate economic values for the same traits for different breeds, or for different regions, are justified.

The results from all four chapters make a strong argument for tailoring indexes further, by using different parameter estimates and different economic values according to the farm production system, as well as perhaps for different grazing locations within each farm system. However, it is obvious that such an approach may be difficult to implement for industry-wide breeding programmes, in particular for co-operative breeding schemes such as Sire Referencing.

X-Ray Computerised Tomography (CT) is currently being used at SAC to assess carcass composition in Terminal Sire breeds, and internal fat depletion/repletion at four stages in the reproductive cycle of Blackface sheep. Using information from this technology, together with conventional measurements of physical performance and pedigree information, will provide us with information on which fat depots are important in key physiological states (e.g. lactation), whether they are under genetic control, and their correlations with other fat depots. If results indicate that it is feasible to manipulate internal fat through genetic selection, then it may be possible to select hill sheep for higher levels of internal fat, but reduced carcass fat. X-Ray CT could also be used to help the understanding of how animals are being altered physically through selection, for example, through changes in internal organ size.

Further work is required on including new traits into breeding goals for hill sheep: for example, traits which are important for disease resistance, lambing difficulty,

type traits, pelt characteristics, maternal behaviour, grazing and other behaviours such as docility. The presence of genetic variation for resistance to internal parasites such as *Ostertagia circumcincta*, coupled with increased consumer pressure against the use of drugs, would make the inclusion of resistance to internal parasites a valuable contribution to the breeding goals for all sectors of the UK sheep industry. Incorporating such traits alongside conventional ones alters the emphasis of livestock production towards greater sustainability of the sheep farming system. This study demonstrates clearly that productivity and sustainability can be improved simultaneously to improve the economic viability of hill farms. Implementation of the indexes described here should help to maintain the image of a natural product, and maintain the acceptability of lamb to increasingly discerning consumers.

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Appendix I

Abbreviations used in Appendix I tables are as follows:

Abbreviation	Description
WWT	= weaning weight
AVFD	= average ultrasonic fat depth
MD	= ultrasonic muscle depth
SLWT	= pre-slaughter live weight
CS	= pre-slaughter condition score
MLCfat	= MLC fat score
CONF	= MLC conformation score
CCWT	= cold carcass weight
r ²	= squared correlation coefficient
rsd	= residual standard deviation
μ	= mean
Subfat	= subcutaneous fat
Ifat	= intermuscular fat
AF	= total fat (subcutaneous fat + intermuscular fat)
L	= lean
B	= bone
WT	= shoulder pre- dissection weight
CWT	= half carcass (side) weight

Prediction equations for carcass composition

Lean weight

$$\mu L + 4.282(L - \mu L) + 1.0 (B - \mu B)$$

Lean %

$$\mu L\% + 0.776(L\% - \mu L\%) - 0.129 (\text{subfat}\% - \mu \text{subfat}\%) + 0.1 (\text{Ifat}\% - \mu \text{Ifat}\%) + 0.361(B\% - \mu B\%)$$

Subcutaneous fat weight

$$\mu \text{Subfat} + 3.409 (\text{Subfat} - \mu \text{Subfat}) + 0.374 (\text{Ifat} - \mu \text{Ifat}) - 0.089 (L - \mu L) + 0.407 (\text{WT} - \mu \text{WT}) + 1.707 (B - \mu B)$$

Subcutaneous fat %

$$\mu\text{Subfat}\% + 0.5358 (\text{Subfat}\% - \mu\text{Subfat}\%) - 0.1521 (\text{L}\% - \mu\text{L}\%) - 0.4409 (\text{B}\% - \mu\text{B}\%)$$

Intermuscular fat weight

$$\mu\text{IF} + 1.029 (\text{Ifat} - \mu\text{Ifat}) + 0.143(\text{Subfat} - \mu\text{Subfat}) + 1.800(\text{WT} - \mu\text{WT})$$

Intermuscular fat %

$$\mu\text{Ifat}\% + 0.3619 (\text{Ifat}\% - \mu\text{Ifat}\%) + 0.1531(\text{Subfat}\% - \mu\text{Subfat}\%) - 0.0524(\text{L}\% - \mu\text{L}\%) + 0.00000463(\text{WT} - \mu\text{WT})$$

Bone weight

$$\mu\text{B} + 3.249(\text{B} - \mu\text{B}) + 0.433(\text{L} - \mu\text{L}) + -0.166(\text{Subfat} - \mu\text{Subfat})$$

Bone %

$$\mu\text{B}\% + 0.7439(\text{B}\% - \mu\text{B}\%) + 0.0019(\text{L}\% - \mu\text{L}\%) - 0.1086 (\text{Subfat}\% - \mu\text{Subfat}\%)$$

Total fat weight

$$\mu\text{AF} - 1.234(\text{AF} - \mu\text{AF}) + 5.186(\text{WT} - \mu\text{WT}) + 1.651(\text{L} - \mu\text{L})$$

Total fat %

$$\mu\text{AF}\% + 0.9546(\text{AF}\% - \mu\text{AF}\%) + 0.1952(\text{L}\% - \mu\text{L}\%) + 0.00000619(\text{WT} - \mu\text{WT})$$

Carcass weight

$$2 \times (\mu\text{WT} + 2.960(\text{WT} - \mu\text{WT}) + 2.656(\text{Subfat} - \mu\text{Subfat}) + 2.198(\text{L} - \mu\text{L}))$$

Supplementary Tables for Chapter 3

Table A1 *R-squared values and residual standard deviations for predicted traits*

Trait	R ²	rsd
Lean weight	0.93	174.14
Lean %	0.78	0.015
Subcutaneous fat weight	0.86	92.03
Subcutaneous fat %	0.83	0.01
Intermuscular fat weight	0.80	76.35
Intermuscular fat %	0.66	0.008
Bone weight	0.71	113.12
Bone %	0.60	0.01
Total fat weight	0.88	14.76
Total fat %	0.83	0.004
CCWT	0.93	294.88

Table A2 *Univariate heritability estimates (s.e.) at a constant cold carcass weight (ccwt) and constant age at slaughter.*

	CCWT	AGE
Shoulder weight	-	0.16 (.08)
Subfat	0.20 (.09)	0.21 (.10)
Ifat	0.10 (.07)	0.03 (.05)
Lean	n/c†	0.23 (.10)
Bone	0.24 (.10)	0.35 (.13)
Total fat (2+3)	0.18 (.09)	0.14 (.08)
SLWT	0.31 (.12)	0.23 (.10)
Conformation	0.08 (.06)	0.07 (.06)
MLCfat	0.13 (.08)	0.13 (.08)
CCWT	-	0.18 (.09)
Age	0.19 (.10)	-

† No convergence/calculation

Table A3 *Univariate heritability estimates for actual and predicted traits compared:(a) at a constant cold carcass weight and (b) at a constant age*

Trait	Actual	Predicted
<i>(a) At a constant cold carcass weight</i>		
Subcutaneous fat	0.20 (0.09)	0.20 (0.09)
Intermuscular fat	0.10 (0.07)	0.16 (0.08)
Total fat	0.18 (0.09)	0.18 (0.09)
Lean	n/c†	n/c†
bone	0.24 (0.10)	0.16 (0.08)
<i>(b) At a constant age</i>		
Shoulder weight	0.16 (0.08)	0.16 (0.08)
Subcutaneous fat	0.21 (0.10)	0.19 (0.09)
Intermuscular fat	0.03 (0.05)	0.10 (0.07)
Total fat	0.14 (0.08)	0.13 (0.08)
Lean	0.23 (0.10)	0.24 (0.10)
Bone	0.35 (0.13)	0.35 (0.13)

† No convergence/calculation

Table A4 *Estimates of heritabilities, genetic and phenotypic correlations† between lamb growth, live measures of body composition, pre- and post- slaughter characteristics at a constant age at slaughter*

Shoulder weight	0.16	0.65	0.69	0.89	0.76	0.77	0.82	0.25	0.31	0.89	0.64	0.07	0.58	0.20	0.25
Subfat	.06	0.21	0.49	0.33	0.33	0.90	0.52	0.24	0.38	0.63	0.39	0.10	0.31	0.30	0.10
Intermusc. fat	.34	.10	.03	.03	.03	.01	.03	.03	.03	.02	.03	.04	.03	.03	.04
Lean	0.67	0.41	0.03	0.46	0.39	0.82	0.54	0.19	0.33	0.62	0.42	0.08	0.41	0.25	0.17
Bone	.30	.62	.05	.03	.03	.01	.03	.03	.03	.02	.03	.04	.03	.03	.04
All fat	0.90	-0.17	0.40	0.23	0.73	0.44	0.74	0.21	0.18	0.79	0.59	0.02	0.52	0.08	.26
SLWT	.07	.37	.62	.10	.02	.03	.02	.03	.03	.01	.02	.04	.03	.04	.03
CONF	0.86	-0.05	0.19	0.84	0.35	0.41	0.75	0.12	0.10	0.72	0.54	0.00	0.59	0.03	0.21
MLCfat	.11	.32	.62	0.10	.13	.03	.01	.03	.03	.02	.03	.04	.03	.03	.03
CCWT	0.40	0.94	0.63	-0.02	0.04	0.14	0.61	0.25	0.42	0.74	0.46	0.11	0.40	0.33	0.15
Price	.31	.05	.34	.40	.34	.08	.02	.03	.03	.02	.03	.03	.08	.05	.10
CS	0.81	-0.04	-0.09	0.88	0.86	-0.04	0.23	0.24	0.27	0.91	0.65	0.06	0.61	0.14	0.23
WWT	.12	.35	.55	.09	.09	.37	.10	.03	.03	0.01	.02	.04	.02	.04	.03
AVFD	0.04	-0.17	-0.84	0.24	0.22	-0.38	0.32	0.07	0.23	0.31	0.33	0.07	0.13	0.10	0.21
MD	.44	.44	.37	.41	.37	.44	.38	.06	.03	.03	.03	.04	.04	0.04	.03
	0.59	0.41	0.59	0.42	0.25	0.56	0.13	-0.09	0.13	0.35	0.09	0.16	0.15	0.22	0.14
	.27	.30	.46	.32	0.30	.29	.33	.42	.08	.03	.04	.04	.04	.04	.04
	.99	0.09	0.63	0.98	0.83	0.18	0.81	0.05	0.41	0.18	0.71	0.09	0.61	0.22	0.29
	.02	.37	.54	.05	.12	.38	.11	.50	.30	.09	.02	.04	.02	.04	.03
	0.79	-0.09	0.05	0.90	0.65	-0.19	0.89	0.37	-0.30	0.81	0.23	0.02	0.46	0.14	0.26
	.15	.36	.47	.10	.19	.43	.11	.45	.32	.13	.10	.04	.03	.04	.03
	-0.85	-0.74	-0.95	-0.61	-0.41	-0.75	-0.86	-0.52	-0.43	-0.70	-0.51	0.00	0.00	0.02	-0.04
	.32	.41	.20	.63	.49	.32	.37	NC	.70	.43	.54	.03	.04	.04	.04
	0.38	-0.21	-0.23	0.51	0.40	-0.06	0.57	0.01	0.30	0.38	0.36	-0.73	0.17	0.34	0.48
	.33	.42	.88	.26	.27	.36	.25	.56	.32	.31	.30	.40	.09	.03	.03
	-0.49	-0.00	-0.25	-0.40	-0.39	0.20	-0.38	-0.54	0.44	-0.52	-0.46	-0.60	0.34	0.23	0.28
	.36	.38	.90	.31	.25	.30	.34	.42	.28	.34	.25	.36	.33	.08	.03
	-0.26	-0.86	-0.82	0.28	0.20	-0.66	0.21	-0.40	-0.75	-0.11	0.50	0.05	0.54	-0.53	0.12
	.41	.28	.32	.40	.32	.23	.47	.74	.23	.50	.32	.61	.29	.30	.05

† Estimates of heritabilities on the diagonal, genetic correlation estimates (and standard errors) below the diagonal and phenotypic correlation estimates (and standard errors) above the diagonal. NC no convergence.

Table A5 *Estimates of heritabilities, genetic and phenotypic correlations† between lamb growth, live measures of body composition, pre- and post- slaughter characteristics at a constant cold carcass weight*

Shoulder weight	0.05	0.30	0.42	0.60	0.24	0.42	-0.07	-0.09	0.02	-0.06	0.00	0.07	-0.01	-0.02	-0.02
Subfat	.05	.02	.02	.02	.02	.03	.04	.03	.03	.04	.04	.02	.04	.04	.04
Ifat	0.78	0.20	0.34	-0.43	-0.37	0.88	-0.22	0.06	0.31	-0.38	0.15	0.14	0.26	0.07	-0.37
Lean	.15	.09	.03	.03	.03	.01	.04	.03	.03	.03	.04	.04	.03	.04	.03
Bone	0.55	0.52	0.10	-0.16	-0.32	0.75	-0.31	0.02	0.25	-0.24	0.14	0.10	0.10	0.02	-0.12
All Fat	.31	.37	.07	.03	.03	.02	.03	.03	.03	.03	.04	.04	.04	.04	.04
SLWT	NC	NC	NC	NC	0.43	-0.40	0.12	-0.09	-0.24	0.25	-0.14	-0.08	-0.20	-0.06	0.25
CONF	.03	.03	.04	.04	.03	.03	.04	.04	.03	.03	.04	.04	.03	.04	.03
MLC fat	0.38	-0.17	-0.36	1.00	0.24	-0.42	0.41	0.19	-0.33	0.22	0.17	0.14	-0.15	-0.04	0.12
Price	.30	.31	.39	.00	.10	.03	.03	.03	.03	.04	.04	.04	.04	.04	.04
CS	0.83	0.94	0.74	-0.61	-0.21	0.18	-0.31	0.04	0.32	-0.39	0.18	0.14	0.23	0.06	-0.32
WWT	.17	.05	.20	.25	.32	.09	.03	.04	.03	.03	0.03	.04	.04	.04	.03
AVFD	0.13	0.02	-0.66	0.03	0.56	-0.37	0.31	-0.18	-0.21	0.15	-0.18	0.19	0.00	0.01	-0.08
MD	.37	.32	0.28	.37	.21	.29	.12	.04	.04	.04	.04	.04	.04	.04	.04
Age	-0.13	0.14	-0.48	-0.07	-0.01	0.22	0.28	0.08	0.15	0.08	0.08	-0.06	0.01	0.11	0.00
	.48	.43	.50	.48	.41	.43	.44	.06	.04	.04	.04	.04	.04	.04	.04
	0.71	0.33	0.33	0.46	0.08	-0.43	-0.46	0.02	0.13	-0.32	0.20	0.02	0.16	0.11	-0.16
	.26	.35	.43	.32	.36	.28	.27	.48	.08	.03	.03	.04	.04	.04	.04
	-0.80	-0.10	-0.38	-0.35	-0.23	-0.20	0.63	0.53	-0.78	0.14	-0.27	-0.35	-0.17	-0.24	0.63
	.35	.39	.46	.59	.39	.39	.25	.47	.22	.08	.03	.03	.04	.03	.02
	0.50	0.22	-0.05	0.43	0.06	0.17	-0.19	-0.03	0.15	-0.71	0.07	0.07	0.02	0.02	-0.20
	.57	.46	.67	NC	.51	.50	.45	.67	.52	.33	.05	.04	.04	.04	.03
	0.94	-0.11	-0.06	0.70	0.23	-0.11	0.29	-0.09	0.12	-0.33	0.28	0.20	0.41	0.57	-0.62
	.28	.36	.48	.43	0.34	.38	.30	.46	.36	.35	.46	.10	.03	.02	0.02
	0.61	0.34	0.26	-0.29	-0.24	0.35	0.04	-0.25	0.44	-0.14	-0.38	0.47	0.20	0.36	0.33
	.47	.32	.43	.56	.33	.33	.32	.41	.31	.39	.47	.28	.10	.03	.03
	0.62	-0.35	-0.22	0.75	0.21	-0.33	0.07	-0.06	-0.56	-0.29	0.99	0.77	-0.27	0.18	-0.48
	.49	.35	.46	.55	.35	.37	.33	.44	.24	.39	.08	.17	.40	.08	.03
	-0.97	0.15	0.18	-0.35	-0.36	0.18	0.17	0.18	-0.06	0.63	-0.95	-0.52	0.07	-0.92	0.19
	.14	.37	.47	.59	.34	.39	.32	.47	.36	.24	.13	.26	.38	.22	.10

† Estimates of heritabilities on the diagonal, genetic correlation estimates (and standard errors) below the diagonal and phenotypic correlation estimates (and standard errors) above the diagonal. NC no convergence

Appendix II

Table A6 *Main Assumptions and Input Variables for Intensive Hill Farm used for HGMM*

Vegetation Community	Area	Heather Cover(%)	Fescue Agrostis in heather(%)
Newly burnt heather	5	-	30
Pioneer heather	5	55	45
Building heather	5	85	15
Mature heather	5	95	0
Fescue Agrostis	2	0	-
Reseeded pasture (not included in model run)	5		

Table A7 *Main Assumptions and Input Variables for Semi-Intensive Hill Farm used for HGMM*

Vegetation Community	Area	Heather Cover(%)	Fescue Agrostis in Heather/Nardus(%)
Newly burnt heather	7.5	-	20
Pioneer heather	7.5	55	30
Building heather	7.5	85	10
Mature heather	7.5	95	0
Nardus dom.	10	-	15
Reseeded pasture (not included in model run)	3		

Table A8 *Main Assumptions and Input Variables for Extensive Hill Farm used for HGMM*

Vegetation Community	Area	Heather Cover(%)	Fescue Agrostis in Heather/Nardus(%)
Newly burnt heather	15	-	20
Pioneer heather	15	55	30
Building heather	15	85	10
Mature	15	95	0
Nardus dom.	20	-	15
Reseeded pasture (not included in model run)	1		

Appendix III

Feed requirements for ewes and lambs.

The following equations have been used to derive feed requirements for ewes and lambs in the hill sheep model. Some of these have are used in the SAC Advisory Nutrition Software, which in turn is based on AFRC (1993) recommendations .

Energy requirements of Ewes (MJ Net Energy)

1. Ewe Maintenance + activity allowance

$$EM=(W/1.08)^{0.75}*0.226+0.0106*W + 0.024*W$$

Where W = ewe weight

2. Pregnancy

Energy for conceptus

$$EC=\exp((3.322-(4.979*(\exp(-0.00643*PD)))))*2.30258)$$

adjustment for lamb birth weight

$$EC=EC*(0.07372*(\exp(-0.00643*PD)))*(LW/4)$$

where PD = no. days pregnant

LW= lamb birth weight

Liveweight change (LG) during pregnancy

$$LG = 26 \text{ MJ/kg/ liveweight gain}$$

3. Lactation

Energy for milk supply (EL)

$$E L = \text{yield} * 4.51$$

Table A9 *Milk yield - assumptions used in the three models (ARC 1993).*

		Days of lactation			
		15	45	75	105
twin	(milk/l)	3	2.25	1.5	1.5
inbye					
single		1.25	1.05	0.7	0.7
hill					

Liveweight change during lactation (EG)

Liveweight gain during lactation = 23.85 MJ/kg

Energy supplied from liveweight loss = 20.0 MJ ME /kg

(Assumptions for liveweight change used in the model for all classes of livestock across the year are shown below)

Total energy requirements for maintenance and production (EMP)

EMP=EM+EC+EG+EL

4. Efficiencies of utilisation of Metabolisable Energy (ME).

The net energy requirements of animals were converted to ME values using adjustments for the efficiency of utilisation of ME. This is because the efficiency of utilisation of ME differs for maintenance (Km), pregnancy (Kp), lactation (Kl), and growth (Kg), and depend on the ratio of ME to GE (gross energy).

$K_m = 0.019 \times M/D + 0.503$

$K_p = 0.029 \times M/D - 0.1595$

$K_l = 0.019 \times M/D + 0.42$

$K_g = 0.024 \times M/D + 0.006$

Where M/D is the energy concentration of the diet (ME).

5. Energy Requirements for lambs and other sheep

Maintenance

$EM = (\text{bodyweight}/1.08)^{0.75} \times 0.226$ (if over 12 months) and $(\text{bodyweight}/1.08)^{0.75} \times 0.25$ (if less than 12 months). Entire males multiplied by factor of 1.15.

Growth

$EG = (\text{Weight Gain}) \times (2.5 + (\text{Live weight} \times 0.35))$ - Entires

$EG = (\text{Weight Gain}) \times (2.1 + (\text{Live weight} \times 0.45))$ - Females

6. Energy Value of Ewe Milk

Energy Value of milk (MJ/litre) = $(0.0328 \times 70) + (\text{Days of lactation} \times 0.0025) + (2.2033)$

Assumptions for liveweight changes of stock classes: extensive farm example.

Table A10 *Weight gain and loss of gimmers and ewes (kg):*

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
Gim	-2.5	-2	-2	-1	-3	-0.5	3	3.5	3	2.1	1.9	0	2.5
Ewe	-2	-2	-1	-1	-3	-1	1	2	3	3	1	0	0

Table A11 *Lambs: proportion of growth obtained (all farms)*

	Days of lactation			
	15	45	75	105
twin	25	30	25	20
single	20	30	30	20

Ewe lambs (hoggs)

Assumptions:

- Hoggs away wintered from November to April inclusive
- Gimmer weight is reached at 95% of mature weight. Weight changes are proportional to target growth.

Table A12 *Ewe lamb weight gain*

Month	Weight gain (kg)
January	0
February	0
March	0
April	0
May	2.28
June	3.43
July	3.43
August	3.43
September	2.28
October	2.28
November	0
December	0
TOTAL	17.12

Grass Production from Reseeded Pasture

1. Inbye Production and response to fertiliser nitrogen

$$\text{Grass Production (kg DM/ha)} = 42.8\text{SoilN} + 18.3\text{FertN} - 0.025(\text{FertN}*\text{FertN}) - 0.061\text{FertN} * \text{SoilN} + 0.049\text{FertN} * \text{SoilW} + 0.031\text{FertN} * \text{SummerRainfall}$$

(Doyle and Lazenby, 1984).

2. Adjustment to altitude for Climatic Zone

Adjusted Altitude (masl)=(1.08*(altitude+(249.97))) (for climatic zone 6 in HGMM). Lance 1985 did not estimate winter grass growth; Winter grass production is as estimated by Armstrong et al.(1997a).

Table A13 *Adjustment to altitude for climatic zone*

	Unadjusted proportions of annual prodn (from Lance,1985)	Further adjustment for adjusted altitude over 300m asl - Doyle and Edwards (1986)
January	0.013	0.5
February	0.015	0.5
March	0.037	0.5
April	0.138	0.5
May	0.161	1
June	0.159	1
July	0.153	0.7
August	0.127	0.7
September	0.083	0.7
October	0.06	0.5
November	0.034	0.5
December	0.02	0.5

Appendix IV

Background to costs of changing fat

Assumptions:

1. Time from weaning - slaughter is constant.
2. Differences in carcass composition are expressed post weaning only.
3. Small changes in carcass composition do not affect energy requirements for maintenance.
4. As Lean increases by 1%, fat decreases by 0.814%.
5. Protein content in Lean = 0.256
6. Energy costs

Fat Energy density = $39.3 \text{ kJ/g kf} = 0.745 \Rightarrow 53 \text{ MJ/kg}$

Protein Energy density = $23.6 \text{ kJ/g kp} = 0.45 \Rightarrow 53 \text{ MJ/kg}$

7. Carcass composition of Blackface lambs:

Lean proportion = 0.538

Fat proportion = 0.292

Method

1. Lean mass = 0.538 weight \Rightarrow protein mass = 0.138 weight \Rightarrow Energy cost = $(0.138 \times 53\text{MJ}) = 7.3 \text{ weight}$

Fat mass = 15.476 weight

Total Energy cost = 22.776 W

2. Increase Lean by 1%, energy cost for lean mass increases by 0.135W to 7.435W, and energy cost for fat mass decreases by 0.424W to 15.052W.

Total new energy cost = 22.487W

\Rightarrow 1.3% decrease in energy costs. Assuming .60 of this is for maintenance, and .40 for growth, the decrease in energy costs is **0.52%**.

Appendix V

Table A14 *HGMM data for extensive farm model*

	JAN	FEB	MAR	APR	MAY	JUN	JLY	AUG	SEP	OCT	NOV	DEC
Total Production	341.89	396.69	952.58	1740.7	6918.0	17299	29418	6702.8	1946.5	1571.1	892.55	514.13
Total Offtake Kg Dm (whole hill)	2597.4	1140.4	1438.8	911.66	1618.4	2970.0	4263.7	3546.7	4031.3	3853.8	2772.6	0
Digestibility of Organic matter in DM (0.85 ave)	0.475	0.484	0.536	0.639	0.681	0.670	0.661	0.657	0.653	0.636	0.555	0
ME = OMD * 0.157	7.46	7.59	8.42	10.0	10.7	10.5	10.48	10.3	10.2	9.99	8.72	8.09
Total ME offtake / month (GJ/month)	19.39	8.667	12.11	9.151	17.29	31.25	44.51	36.61	41.34	38.49	24.17	0

Table A15 *HGMM data for the semi- intensive farm model*

	JAN	FEB	MAR	APR	MAY	JUN	JLY	AUG	SEPT	OCT	NOV	DEC
Total production	394.49	457.72	1099.1	2008.5	9099.4	24442	41280	8589.0	2245.9	1812.8	1029.9	593.22
Total offtake kg DM	2262.3	1369.2	1762.8	1271.7	1881.7	3652.3	5436.2	4574.9	4410.0	3974.3	3146.6	1988.2
Digestibility of Organic Matter in DM	0.464	0.474	0.521	0.621	0.678	0.663	0.663	0.654	0.651	0.628	0.542	0.505
ME = OMD * 0.157	7.28	7.45	8.18	9.75	10.6	10.4	10.4	10.37	10.2	9.85	8.52	7.93
Total ME offtake per month (GJ/month)	16.47	10.19	14.43	12.40	20.02	38.00	56.56	46.99	45.08	39.16	26.80	15.77

Appendix VI

Extensive farm gross margin (base)

Financial information per 100 ewe flock				Farm model ?			
				3			
GROSS OUTPUT				No.	Prices	Per head	total £
Lamb sale	siter	males		0.00	2.2	0.00	0.00
		females		0.00	2.2	0.00	0.00
	store	males		42.67	0.9	23.57	1022.2725
		females		13.73	0.9	22.35	306.91772
Valuation finishing lambs				0.00	0.9	#DIV/0!	0.00
				Total lamb sales		1329.19	
				Per ewe			
Ewe sales:	draft		5.0344186		47		236.61767
	cast		13.089488		0.5	25	327.23721
				Total ewe sales		563.85488	
				P/kg wool			
Wool sales	ewes		94.425485		0.96		167.69966
	hoggs		29.710905		0.96		58.481186
				Total wool sales		226.18085	
Compensatory Allowances				100	5.75		575
Annual premium				100	11.5		1150
LFA suppl't				100	5.35		535
				Total subsidies		2260	
LESS replacements(rams)			1	240			-240
TOTAL OUTPUT						4139.23	
Variable costs:							
FEED							
Bought in (ewes + tups)					2.5378296	253.78296	
lambs (siter)			0.00	5.005	0	0	
Forage							
Net cost					0.2379136	23.791363	
Vet,med and dip					3.173	317.277	
Haulage (draft ewes)			5.0344186	1	0.0503442	5.0344186	
Haulage (cast ewes)			13.089488	1	0.1308949	13.089488	
Haulage (hoggs)			30.935969	3	0.9280791	92.807907	
Hogg wintering			30.935969	12	3.7123163	371.23163	
Shearing hoggs			30.935969	0.6	0.1856158	18.561581	
Shearing ewes			94.425485	0.45	0.4249147	42.491468	
Shearing tups			2	0.6	0.012	1.2	
Miscellaneous (ewes)			94.425485	0.25	0.2360637	23.606371	
Miscellaneous (lambs)			89.33	0.5	0.4466575	44.665753	
TOTAL V. COSTS						12.075404	1207.5404
GROSS MARGIN				Per ewe		29.316856 2931.69	
GM + slaughter GM						0 0.00	

Semi intensive farm gross margin (base)

Financial information per 100 ewe flock

Farm model ?

GROSS OUTPUT			No.	Prices	Per head	total £		
Lamb sale	siter	males	25.27	2.2	36.85	931.10		
		females	11.11	2.2	35.31	392.40		
	store	males	25.27	0.9	24.68	636.67151		
		females	11.11	0.9	23.49	261.01657		
Valuation finishing lambs			36.38	0.9	24.67571	897.69		
Total lamb sales						1795.38		
Per ewe								
Ewe sales:	draft		5.167647	47		242.87941		
	cast		13.435882	0.5	26.75	359.40985		
Total ewe sales						602.28925		
P/kg wool								
Wool sales	ewes		95.009918	0.96		168.73761		
	hoggs		29.151977	0.96		57.381027		
Total wool sales						226.11864		
Compensatory Allowances								
			100	5.75		575		
Annual premium								
			100	11.5		1150		
LFA suppl't								
			100	5.35		535		
Total subsidies						2260		
LESS replacements(rams)								
			1	240		-240		
TOTAL OUTPUT						4643.78		
Variable costs:								
FEED								
Bought in (ewes + tups)					4.3257879	432.57879		
lambs (siter)					36.38	5.005	1.8207901	182.07901
Forage								
Net cost					0.6012334	60.123337		
Vet,med and dip								
					3.529	352.929		
Haulage (draft ewes)								
			5.167647	1	0.0516765	5.167647		
Haulage (cast ewes)								
			13.435882	1	0.1343588	13.435882		
Haulage (hoggs)								
			30.307589	3	0.9092277	90.922766		
Hogg wintering								
			30.307589	12	3.6369107	363.69107		
Shearing hoggs								
			30.307589	0.6	0.1818455	18.184553		
Shearing ewes								
			95.009918	0.45	0.4275446	42.754463		
Shearing tups								
			2	0.6	0.012	1.2		
Miscellaneous (ewes)								
			95.009918	0.25	0.2375248	23.75248		
Miscellaneous (lambs)								
			105.07	0.5	0.5253322	52.533217		
TOTAL V. COSTS					14.57273	1457.273		
GROSS MARGIN								
					Per ewe	31.865111	3186.51 per 100 ewe flock	
GM + slaughter GM								
					34.30249	3430.25		

Finishing lamb gross margin

	no	prices	perhead	total £
Lamb purchase	36.38	0.9	24.67571	897.69
Lamb feed	36.38	0.055	5.005	182.07901
Lamb sales	36.38	2.2		1323.5049

243.73786

Intensive farm gross margin (base)

Financial information per 100 ewe flock

Farm model ?

1

GROSS OUTPUT		No.	Prices	Per head	total £	
Lamb sale	siter	males	58.32	2.2	38.00	2216.18
		females	30.90	2.2	36.50	1128.04
	store	males	0.00	0.9	26.23	0
		females	0.00	0.9	25.18	0
Valuation finishing lambs		89.23	0.9	26.234532	2340.83	
Total lamb sales					2340.83	
Per ewe						
Ewe sales:	draft	5.3322779		47	250.61706	
	cast	13.863922		0.5	395.12179	
Total ewe sales					645.73885	
P/kg wool						
Wool sales	ewes	95.800351		0.96	170.14142	
	hoggs	28.454479		0.96	56.008112	
Total wool sales					226.14954	
Compensatory Allowances						
		100		5.75	575	
Annual premium						
		100		11.5	1150	
LFA suppl't						
		100		5.35	535	
Total subsidies					2260	
LESS replacements(rams)						
		1		240	-240	
TOTAL OUTPUT					5232.72	
Variable costs:						
FEED						
Bought in (ewes + tups)				4.7181059	471.81059	
lambs (siter)		89.23	5.005	4.4658123	446.58123	
Forage						
Net cost				0.946083	94.608298	
Vet,med and dip						
				3.994	399.368	
Haulage (draft ewes)						
		5.3322779	1	0.0533228	5.3322779	
Haulage (cast ewes)						
		13.863922	1	0.1386392	13.863922	
Haulage (hoggs)						
		29.417239	3	0.8825172	88.251718	
Hogg wintering						
		29.417239	12	3.5300687	353.00687	
Shearing hoggs						
		29.417239	0.6	0.1765034	17.650344	
Shearing ewes						
		95.800351	0.45	0.4311016	43.110158	
Shearing tups						
		2	0.6	0.012	1.2	
Miscellaneous (ewes)						
		95.800351	0.25	0.2395009	23.950088	
Miscellaneous (lambs)						
		120.64	0.5	0.6032213	60.322129	
TOTAL V. COSTS					15.724742 1572.4742	
GROSS MARGIN					Per ewe 36.602432 3660.24 per 100 ewe flock	
GM + slaughter GM					42.170491 4217.05	

Finishing lamb gross margin

	no	prices	perhead	total £
Lamb purchase	89.23	0.9	26.234532	2340.83
Lamb feed	89.23	0.055	5.005	446.58123
Lamb sales	89.23	2.2		3344.2161
				556.80583

Publications

Refereed (appended to this thesis)

Bishop, S.C., Conington, J., Waterhouse, A., Simm, G. (1996) Genotype X environment interactions for sheep early growth and ultrasonic measurements in hill sheep. *Animal Science* **62**: 271-277.

Conington, J., Bishop, S.C., Waterhouse, A., Simm, G. (1995). A genetic analysis of early growth and ultrasonic measurements in hill sheep. *Animal Science* **61**:85-93.

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Review

Simm, G., Conington, J., Bishop, S.C., Dwyer, C.M., Pattinson, S. (1996). Genetic selection for extensive conditions. *Applied Animal Behaviour Science* **49**: 47-59.

In preparation

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Conington, J., Bishop, S.C., Waterhouse, A., Grundy, B. and Simm, G. (1999) Sustainable selection indexes for UK hill Sheep.

Submitted

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- 3 **J Conington, S C Bishop, A Waterhouse & G Simm**, *A comparison of growth and carcass traits in Scottish Blackface lambs sired by genetically lean or fat rams*, Animal Science, Volume 67 Part 2, 299-309

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A genetic analysis of early growth and ultrasonic measurements in hill sheep

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Abstract

Genetic parameters were estimated for early lamb growth and ultrasonic measurements taken on Scottish Blackface lambs reared under extensive conditions on two Scottish hill farms. Measurements were taken on approximately 2000 lambs born to unselected ewes, and sired by 32 rams previously selected for divergent predicted carcass lean content. Heritabilities for birth weight, marking weight (at approx. 6 weeks of age) and weaning weight (at 17 weeks) were 0.07 (s.e. 0.04), 0.02 (s.e. 0.03), and 0.14 (s.e. 0.05), respectively. Heritabilities for ultrasonic muscle and fat depths at weaning were 0.27 (s.e. 0.09) and 0.16 (s.e. 0.06), respectively. There was a strong maternal effect on weight which declined from birth with lamb age and was relatively unimportant for the ultrasonic measurements. The rearing environment of the lambs (hill pasture v. 'improved' (or 'inbye') pasture) was an important environmental effect on the heritability estimate for backfat thickness, with that for lambs reared on improved pasture being twice that of hill-reared lambs. The implications of the results from this work on genetic improvement of sheep in hill environments are discussed.

Keywords: environmental factors, genetic parameters, sheep, ultrasonic measurements.

Introduction

Proportionately, 0.41 of the breeding ewes in the United Kingdom are hill sheep. They are adapted to survive in extreme climatic conditions, frequently living on the poorest quality grazing, unsuitable for any other farming activity. Despite the unfavourable conditions in which they live, they are by far the most important sector for producing ewes for breeding, contributing proportionately 0.56 of the genes of all breeding ewes in the UK. The predominant hill breeds are the Scottish Blackface, Welsh Mountain and Swaledale which comprise an estimated 3.1, 1.8 and 1.4 million ewes, respectively (Meat and Livestock Commission (MLC), 1988).

As well as being important producers of pure and crossbred breeding stock, hill sheep are the second most important contributors to lamb carcass production (after terminal sire breeds), with proportionately 0.34 of the genes of all slaughtered lambs in Britain originating from hill ewes (MLC,

1988). It is widely recognized that lamb carcass quality from some hill breeds does not meet target, home-market specifications.

The main problem is that many lambs from the hill breeds tend to reach the desired fatness (MLC fat class 2 to 3L) at light weights, which leads to a financial penalty unless specialist markets for light lambs can be identified. A certain amount of reticence exists amongst the farming community towards improving carcass characteristics in hill breeds, not only due to the difficulties of recording in such conditions, but also due to the effects which selection might have on the overall performance and survival of ewes. In particular, the expected increase in ewe live weight, as a correlated response to selecting for lean growth, is undesirable for many hill sheep breeders.

In response to consumer preferences for leaner meat, considerable research effort has been expended in recent years on approaches to identify genetically

leaner animals (Bennett, 1990; Simm, Dingwall, Murphy and FitzSimons, 1990; Cameron and Bracken, 1992; Fennessy, Bain, Greer and Johnstone, 1992; Waldron, Clarke, Rae, Kirton and Bennett, 1992; Bishop, 1993). However, the majority of selection experiments and genetic parameter estimates for growth, fat and muscle come from either terminal sire breeds or other sheep managed with less limiting nutritional inputs than those in hill flocks. With the exception of one well documented flock (Atkins, 1984 and 1986; Atkins and Thompson, 1986), a dearth of genetic information exists on animals extensively managed on poor-quality grass in hill environments. There appears to be no genetic information on body composition characteristics of sheep reared in such environments.

In an attempt to address the problem of lack of knowledge in this area, a joint Scottish Agricultural College (SAC), and Roslin Institute (RI) experimental programme was instigated in 1990/91: (i) to investigate the consequences of selection for reduced carcass fatness on the performance and survival of hill sheep; (ii) to estimate phenotypic and genetic parameters for growth, carcass attributes, maternal ability, wool characteristics and maternal behaviour; and (iii) to determine whether selection for divergent carcass fatness of rams under *ad libitum* feeding conditions has been effective in altering carcass composition of their progeny reared under extensive (hill) situations. As part of the above experiment, this paper describes animal performance, phenotypic and genetic parameters for early lamb growth and ultrasonic carcass measurements at weaning, for two lines of Scottish Blackface lambs in four contrasting hill environments.

Material and methods

Management of animals

The lambs described in this study were born on two SAC hill farms over a period of 2 years. They were sired by 32 rams from the two divergent selection lines (FAT and LEAN) of Scottish Blackface sheep described by Bishop (1993). These rams had been selected for four generations based on an index used by Cameron and Bracken (1992), i.e. $0.204 \times W20_s - 0.996 \times FAT_s$, where $W20$ is 20-week body weight, and FAT is the average of ultrasonic backfat thickness measurements taken over the 13th rib and the 3rd lumbar vertebra at 20 and 21 weeks of age, and the subscripts indicate that both traits were corrected for known fixed effects and standardized to have a residual standard deviation of 1.0. The above index did not change live weight of the two lines, so that differences between lines were a function of carcass composition rather than a function of body weight or maturity. Rams from

these two lines were used for this experiment. Nine rams from each selection line were used in the 1st year, and 10 LEAN, and nine FAT line sires were used in the 2nd year. Five of these sires were used in both years to provide genetic links between years. A total of 2303 matings were made by laparoscopic artificial insemination (AI) to unselected Scottish Blackface ewes on two SAC hill farms during 1990 and 1991. AI was used to enable all sires to be represented on both farms, and to concentrate the lambing period. A total of 1660 ewes lambed to AI in the following 2 years.

The two SAC farms represent two contrasting hill environments typical of those found in Scotland. Farm 1 is located in the Pentland National Park, Midlothian and rises from 305 to 488 m above sea level, with an average rainfall of 800 mm. Farm 2 is located near Crianlarich, West Perthshire and is a much harsher, wetter farm rising from 180 to 1034 m with 2900 mm average rainfall. Ewes in this trial were managed according to normal farm policy alongside the remaining ewes in each flock. Management policy was similar on the two farms except in two matters. Firstly, preferential feeding and housing was given to multiple bearing ewes from about week 10 of pregnancy until lambing, at farm 2, but not on farm 1. Secondly, all ewes from farm 1, but only single-bearing ewes from farm 2, lambed outside in hill paddocks. Multiple bearing ewes on farm 2 were housed and lambed indoors, being transferred to pasture between 12 and 36 h post lambing. Recording took place within 24 h of ewes giving birth. Ewes either reared one or two lambs; single lambs were reared on the hill, and twin lambs were reared on enclosed and improved pasture (inbye). This grazing distinction between rearing types is common practice on hill farms, and hence was followed here, although it does lead to confounding of some effects in subsequent analyses. Within hill grazings, distinct groups of ewes graze on specific areas of the open hill, with no fencing between them. This is known as 'hefting', and generally a ewe born into a heft will 'home' to that area during its life within the flock. It was therefore important to distinguish between ewes from different hefts, as hefting can have an extremely important environmental influence on their performance.

Three key weights were recorded; birth weight (BWT), marking weight (MWT) at an average age of 6 to 7 weeks (when lambs are ear marked for their ownership and male lambs castrated), and weaning weight (WWT) at an average age of 17 weeks. At weaning all lambs were ultrasonically scanned at the level of the 3rd lumbar vertebra using a Vetscan ultrasonic machine with a 5 MHz 56 mm probe.

Table 1 Two-year lambing performance summary

	1991		1992	
	Farm 1	Farm 2	Farm 1	Farm 2
No. of ewes inseminated	586	588	558	571
No. of ewes lambing to AI (and %)	376 (64.2)	428 (72.8)	438 (78.5)	418 (73.2)
No. of lambs born alive per ewe lambing (and %)	560 (148.9)	628 (146.7)	675 (155.0)	523 (125.1)

Photographed scan images were subsequently interpreted using computer-based semi-automatic image analysis software. Four individual fat depth measurements (FD1 to FD4) were taken laterally from the boundary of the vertical process of the vertebra and the *m. longissimus* muscle. Average fat depth (AVFD) was calculated between the 1st and 4th depth site (not as the average of the four individual measurements). One muscle depth measurement was also taken at the deepest point on the muscle.

Statistical analysis

The data were analysed initially using the GENSTAT package (Lawes Agricultural Trust, 1983) to identify significant sources of variation, using regression. GENSTAT residual maximum likelihood (REML) was then used to calculate fixed effect means. The main effects fitted were sire selection line (LEAN or FAT), dam age (2, 3 + 4 or 5+ years), sex and grazing code, where grazing code accounted for farm, heft, birth type, rearing type and year. The covariable day of birth was fitted for post-birth traits, and a covariable for day of marking was fitted for marking weight. Weaning took place over 2 days in each year and at each farm, whereas marking was spread over a 2-week period for farm 2 in the 2nd year as weather conditions prevented the sheep from being gathered. The interactions of dam age by farm, dam age by year and birth type by farm were used in the model for all traits. The first two interactions take into account different performance levels between ewes of the same age on the two farms, and in the 2 years respectively. The interaction between birth type and farm accounted for preferential feeding of twin-rearing ewes on farm 2. Finally, sire was fitted as a random effect, nested within line.

Within line univariate genetic parameters were calculated for all traits using a derivative free REML algorithm (DFREML) (Meyer, 1985), fitting an animal model and the fixed effects described above. The fitted pedigree included all genetic relationships between the sires, however all ewes were assumed to be unrelated as their pedigrees were not known. The

observed variation for each trait was partitioned into additive genetic and maternal common environmental (c^2) components, which were assumed to be uncorrelated. The c^2 effect potentially includes maternal genetic as well as maternal environmental effects. However, given the structure of the dataset it was not possible at this stage to disentangle these two components. A total of 736 ewes had two or more lambs and hence contributed to the c^2 estimate. The DFREML algorithm was assumed to have converged when the difference in the variances of the log likelihoods of successive iterations was less than 10^{-6} .

Within line genetic and phenotypic correlations between traits were calculated using multivariate REML techniques (REMLPK; Meyer, 1985) fitting a sire model for all traits, and fitting the fixed effects described above. The sire model (see **Results** section) gave almost identical heritability estimates to the animal model including maternal effects, as well as allowing standard errors for all variance components and correlations to be estimated readily. The analysis continued therefore with the sire model for computational ease. The REML algorithm was assumed to have converged when the maximum proportional difference in genetic variance components on the canonical scale was less than 10^{-5} between iterations.

Due to the strong environmental influences on the performance of the lambs, genetic parameters were also estimated separately for hill reared and inbye reared lambs, again using REMLPK and fitting a sire model.

Results

Phenotypic performance

The number of ewes artificially inseminated, the number lambing and the resulting number of lambs born alive are shown in Table 1, for each farm and for each year.

The mean number of lambs per sire group used for this analysis was 56.3, which ranged from 41 to 91 for rams used in 1 year only. For the five rams with 2

Table 2 Least-squares mean (LSM) values and phenotypic standard deviation (s.d.) for lamb live weights and ultrasonic measurements

	No. of observations	LSM	s.d.
Live weight (in kg):			
at birth	2085	3.97	0.63
at marking	2067	13.76	1.98
at weaning	1922	28.54	3.36
Scan measurements (in cm)			
Fat depth 1	1896	0.19	0.065
Fat depth 2	1896	0.19	0.071
Fat depth 3	1896	0.22	0.087
Fat depth 4	1896	0.24	0.094
Average fat depth	1896	0.21	0.074
Muscle depth	1896	1.77	0.192

years of data, the mean was 125.8, ranging from 95 to 148 lambs per sire. There were similar numbers of lambs born in each sire line each year.

The number of lambs used in this analysis, their mean body weights from birth to weaning and ultrasonic measurements are shown in Table 2, together with the phenotypic standard deviation of each trait. Despite the small absolute depths of fat (less than 2.5 mm at all measurement sites), fat depth measurements were much more variable than muscle depths, and particularly so towards the lateral edge of the muscle. The average live weight, fat and muscle depths were similar for both years.

Table 3 Least-squares means of growth and ultrasonic measurements according to sire line

	Sire line		s.e.d.	Significance	
	Lean	Fat			
	No.	Mean	No.	Mean	
Live weight (in kg):					
at birth	1037	3.99	1048	3.95	0.039
at marking	1033	13.85	1034	13.66	0.112
at weaning	961	28.70	961	28.38	0.266
Scan measurements (in cm)					
Fat depth 1	945	0.18	967	0.21	0.005 ***
Fat depth 2	945	0.18	967	0.21	0.005 ***
Fat depth 3	945	0.20	967	0.24	0.006 ***
Fat depth 4	945	0.22	967	0.26	0.007 ***
Average fat depth					
depth	945	0.19	967	0.22	0.006 ***
Muscle depth	945	1.76	967	1.78	0.019

Table 4 Least-squares means of live weight and ultrasonic measurements according to dam age†

	Dam age			Average s.e.d.
	2	3 + 4	5+	
Live weights (in kg):				
at birth	3.71 (558)†	4.04 (1085)	4.16 (442)	0.037
at marking	13.14 (552)	14.19 (1075)	13.95 (440)	0.121
at weaning	27.47 (494)	29.29 (1010)	28.87 (418)	0.210
Scan measurements (in cm):				
Fat depth 1	0.18 (493)	0.20 (1005)	0.19 (414)	0.004
Fat depth 2	0.18 (493)	0.21 (1005)	0.20 (414)	0.004
Fat depth 3	0.20 (493)	0.23 (1005)	0.22 (414)	0.005
Fat depth 4	0.22 (493)	0.25 (1005)	0.25 (414)	0.005
Average fat depth				
depth	0.19 (493)	0.22 (1005)	0.21 (414)	0.004
Muscle depth	1.75 (493)	1.79 (1005)	1.76 (414)	0.011

† Figure in brackets represent number of lambs observed.

Table 3 shows the least squares means of each line and the standard error of differences between them, for all traits. As expected, no differences were seen in live weights between the two lines (the aim of the selection index used to create the two RI selection lines was to produce divergent lines for carcass fat content without a correlated response in live weight). Lambs born from FAT line sires had significantly greater fat depths at all measurement sites than lambs from LEAN line sires. The average difference in backfat depth between the two lines was proportionately 0.15 overall, although this difference was not uniform between the 2 years (differences were proportionately 0.11 and 0.18 in 1991 and 1992 respectively). No difference between the two lines in the depth of muscle was apparent. Again, this is in line with results obtained in the RI flock (Bishop, 1993).

The dam age was an important component in the analysis, the effects of which can be seen in Table 4. Lambs from gimmers (2-year-old ewes) and older ewes (5+ years) were lighter, had less fat and had less muscle than lambs from ewes of intermediate age. All values were significantly different from each other with the exception of fat depths 2, 4 and AVFD between 3+4 and 5-year-old ewes.

Differences between farms for most traits reflect the difference in mature live weight of ewes of about 10 kg, and the severity of the environment in which lambs were reared. Table 5 shows how preferential treatment of multiple-born lambs on farm 2, by being reared inbye, has benefited their performance. This is

Table 5 Least-squares means of live weights and ultrasonic measurements according to farm and rearing type[†]

	Farm 1		Farm 2	
	Inbye	Hill	Inbye	Hill
Live weights (in kg):				
at birth	3.76	4.63	3.32	4.17
at marking	12.82	14.41	14.98	12.97
at weaning	28.04	31.14	27.67	25.57
Scan measurements (in cm):				
Fat depth 1	0.18	0.22	0.19	0.16
Fat depth 2	0.19	0.24	0.19	0.16
Fat depth 3	0.21	0.26	0.21	0.19
Fat depth 4	0.23	0.28	0.24	0.21
Average fat depth	0.19	0.25	0.21	0.17
Muscle depth	1.73	1.83	1.82	1.67

† Rearing location is confounded with rearing type.

because there is a greater contrast between the quality of inbye and hill grazings on farm 2 compared with farm 1. This has resulted in their post-birth live weights being heavier than those of single-born lambs reared on the hill. Performance of the multiple-born lambs reared inbye on farm 1 was poorer than their single-born counterparts. They were 1.59 kg and 3.1 kg lighter at marking and weaning respectively.

Male lambs were heavier than females at each weighing session, and they had less fat at all scan measurements sites, although they had similar muscle depths to female lambs.

Genetic parameters

Table 6 summarizes univariate heritability estimates and maternal common environmental effects

Table 6 Univariate heritabilities (h^2) and maternal common environmental (c^2) effects

	h^2	c^2
Live weights		
at birth	0.08	0.41
at marking	0.02	0.23
at weaning	0.12	0.18
Scan measurements		
Fat depth 1	0.13	0.10
Fat depth 2	0.17	0.11
Fat depth 3	0.14	0.08
Fat depth 4	0.12	0.10
Average fat depth	0.14	0.12
Muscle depth	0.23	0.10

calculated for all traits. Heritability estimates for pre-weaning weights were both below 0.1, although that for live weight at weaning was slightly higher (0.12). Heritability estimates for ultrasonic fat measurements ranged between 0.13 and 0.17 with an average of 0.14. The heritability for muscle depth was higher at 0.23. The effect of selection of rams on the heritability estimates for fat depth will be discussed in another paper in this series. Maternal common environmental effects were greater for the live weight measurements than for the ultrasonic measurements, with the effects being larger at younger lamb ages. At birth, for example, almost half of the observed phenotypic variation in live weight is due to maternal effects.

Table 7 shows correlations and heritability estimates for all traits measured on all lambs, calculated using a sire model. The heritabilities for live weights were estimated using a univariate model, because of

Table 7 Heritability estimates[†], genetic[‡] and phenotypic[§] correlations for live weights and ultrasonic measurements for all lambs

	Live weights (WT)			Fat depths				Muscle depth (MD)	
	At birth (B)	At marking (M)	At weaning (W)	FD1	FD2	FD3	FD4		Average (AVFD)
BWT	0.07 (0.04)	0.50	0.36	0.03	0.02	0.02	0.04	0.03	0.08
MWT	0.42	0.02 (0.03)	0.63	0.21	0.20	0.19	0.19	0.22	0.34
WWT	0.48	0.85	0.14 (0.05)	0.40	0.40	0.36	0.35	0.40	0.55
FD1	-0.10	-0.29	-0.20	0.15 (0.06)	0.81	0.73	0.71	0.83	0.31
FD2	-0.10	0.08	-0.11	0.91	0.18 (0.07)	0.86	0.81	0.94	0.31
FD3	-0.09	-0.19	-0.23	0.86	0.92	0.16 (0.06)	0.90	0.96	0.33
FD4	-0.01	-0.18	-0.25	0.77	0.84	0.98	0.15 (0.06)	0.93	0.35
AVFD	-0.09	-0.08	-0.21	0.92	0.97	0.99	0.94	0.16 (0.06)	0.35
MD	-0.41	0.17	0.30	-0.39	-0.20	-0.17	-0.14	-0.21	0.27 (0.09)

† On the diagonal. Standard error of heritability is given in brackets.

‡ Below the diagonal.

§ Above the diagonal.

Table 8 Heritabilities† and phenotypic correlations‡ for growth and ultrasonic measurements for hill-reared lambs§

	BWT	MWT	WWT	AVFD	MD
BWT	0.14 (0.07)	0.48	0.34	-0.05	0.04
MWT		0.06 (0.05)	0.64	0.28	0.36
WWT			0.15 (0.09)	0.17	0.32
AVFD				0.12 (0.08)	0.34
MD					0.26 (0.11)

† On the diagonal. Standard deviation of heritability estimates shown in brackets.

‡ Above the diagonal. Standard errors of phenotypic correlations ranged from 0.02 to 0.03.

§ Number of lambs = 759. A key to abbreviations is given in Table 7.

different numbers of records for each weight and slightly different fixed effects and covariates, whereas the heritabilities for, and correlations between ultrasonic measurements were estimated simultaneously using a multivariate model.

The heritability estimates were almost identical to those in Table 6, with pre-weaning weights both below 0.1 and live weight at weaning slightly higher at 0.14. Heritability estimates for ultrasonic fat measurements ranged between 0.15 and 0.18 with an average of 0.16. The heritability of ultrasonic muscle depth was 0.27. By comparing the heritability estimates in Tables 6 and 7, it can be seen that the two computational procedures used produced similar results.

The fat depth measurements were very strongly positively correlated with each other, both genetically and phenotypically. There were moderate positive correlations between successive live weight measurements. There were small negative genetic correlations between the live weight and ultrasonic backfat measurements, but small to moderate positive phenotypic correlations. There was a fairly strong negative genetic relationship between birth weight and muscle depth, although subsequent

marking and weaning weights were positively genetically correlated with muscle depth (0.17 and 0.30 respectively). Finally, the fat and muscle depth measurements were positively phenotypically correlated, but the genetic correlations were small and negative. The standard errors of the phenotypic correlations ranged between 0.002 and 0.02, and for the genetic correlations they ranged between 0.01 and 0.28.

Tables 8 and 9 show heritability estimates and phenotypic correlations for the two different rearing environments, inbye and hill. There were no significant differences in heritability estimates between rearing types for live weights and muscle depth, but there was an important difference for estimates of heritabilities for average backfat thickness, (0.24 and 0.12 for inbye and hill reared lambs respectively). The estimates for the individual fat depth measurements for inbye-reared lambs ranged from 0.15 to 0.28, and those for hill-reared lambs ranged from 0.09 to 0.12. The phenotypic variance of average fat depth for hill-reared lambs was higher than that of inbye-reared lambs, being 0.0065 cm² and 0.0047 cm², respectively. The correlation between weaning weight and fat depth was also reduced in the hill environment. These two

Table 9 Heritabilities† and phenotypic correlations‡ for growth and ultrasonic measurements for inbye-reared lambs§

	BWT	MWT	WWT	AVFD	MD
BWT	0.08 (0.05)	0.51	0.39	0.09	0.13
MWT		0.04 (0.03)	0.64	0.26	0.37
WWT			0.14 (0.07)	0.32	0.41
AVFD				0.24 (0.09)	0.36
MD					0.26 (0.09)

† On the diagonal. Standard deviation of heritability estimates shown in brackets.

‡ Above the diagonal. Standard errors of phenotypic correlations ranged from 0.01 to 0.03.

§ Number of lambs = 1143. A key to abbreviations is given in Table 7.

subsets of data were too small to allow reliable genetic correlations to be estimated.

Discussion

There is a dearth of genetic information on body weight and *in vivo* body composition in sheep under UK hill farming conditions. It is important that relationships between carcass and other traits are estimated and fully understood, in order that meaningful breeding programmes incorporating carcass attributes can be designed. The results reported here are from an experiment designed for these purposes.

In the present study, the decreasing importance of the maternal component with lamb age to around 0.1 for all measurements at weaning, is in line with expectations. This pattern corresponds to the findings of Atkins (1986), also working with Scottish Blackface sheep.

The low heritability estimates (less than 0.1) for pre-weaning weights are also in line with those of Atkins (1984 and 1986), although the estimate for live weight at weaning was higher in this study (0.14) compared with his estimate of 0.05 and that of Atkins and Thompson (1986), of 0.08. Atkins' estimates were obtained with the same breed, at similar ages, reared under similar environmental conditions and with no nutritional supplementation. In New Zealand, with grass reared Romney and Romney cross lambs, Waldron *et al.* (1992), reported a higher heritability estimate for live weight of 0.27, (although at an average age of 205 days). This is more in line with heritability estimates for live weight, which ranged from 0.23 to 0.38, for sheep offered nutritional supplementation at some stage in their growth phase (Mavrogensis, Louca and Robinson, 1980; Barillet, Bibé and Bouix, 1982; Simm, Young and Beatson, 1987 (review); Young, 1989; Bishop, 1993; María, Boldman and Van Vleck, 1993). The higher heritability estimates for the New Zealand studies may in part be due to better quality grazing than that in the present study.

The heritability estimates for ultrasonic backfat measurements of between 0.15 and 0.18 for all lambs were lower than that of 0.23 estimated by Waldron *et al.* (1992) and also that of 0.25 from Fennessy *et al.* (1992), (with Coopworth lambs reared on grass and clover swards also in New Zealand). The heritability estimates were also lower than published heritability estimates for ultrasonic backfat measurements, from animals given nutritional supplementation (see the review of Simm *et al.* (1987)).

When backfat heritability estimates were calculated according to rearing location, those for inbye-reared

lambs were on average twice those of hill-reared lambs. The former were well within the range of estimates cited by Simm (1992) at a constant age, however the average backfat depth heritability for hill-reared lambs was low (0.12). Lambs reared on the hill had a slightly lower additive genetic variance of 0.00078 cm², compared with 0.00113 cm² for inbye-reared lambs. Conversely, hill reared lambs had a much larger environmental variance of 0.00572 cm² compared with 0.00357 cm² for inbye-reared lambs. This shows that the harsher rearing environment (hill) has inflated the error variance, which partly explains the low ultrasonic backfat heritability estimates. This may have important implications for improvement programmes in harsh environments, with the objective of reducing fat levels. A second explanation for low estimates in this study (and the comparable study by Atkins, 1986) could be that they have been calculated at a relatively early stage of the lambs' maturity, with the latest measurements taken at approximately 0.4 of mature size. In other studies, heritabilities were calculated when animals were proportionately over 0.5 of mature live weight (Young and Simm, 1990; Waldron *et al.*, 1992; Bishop, 1993; Cameron and Bracken, 1992). A third reason for the low heritability estimates for ultrasonic backfat depth in this study will be described in another paper. The selection experiment criterion (described above) was dominated by fat depth. As selection reduces genetic variation, within-line heritability estimates will normally be reduced. As the rams used in this study were from these established selection lines, the heritabilities for fat depth in this study have been under-estimated. However, the pattern between rearing locations remains the same, with higher heritabilities for inbye *v.* hill reared lambs.

The heritability estimate for muscle depth in the present study was within the range of published estimates, although at the lower end of the scale. Unlike the backfat measurements, the heritability estimates for muscle depth were consistent for both rearing types in this study, and appear not to have been influenced by the harsh environment.

The negative genetic correlations between muscle depth and fat depths are not in accordance with estimates at a constant age published by Bioux, Bibé and Lefevre (1982) (with muscle area); Young and Simm (1990); Henningsson and Malmfors (1992) and Bishop (1993). However, the negative genetic correlations were in agreement with findings of Wolf, Smith, King and Nicholson (1981); Cameron and Bracken (1992) and Waldron *et al.* (1992). The latter found negative partial genetic correlations between all lean indicator traits and dissected fat weight, (although at a constant weight). It was not

possible to calculate genetic correlations between traits according to rearing types in this study due to insufficient data. However phenotypic correlations for both rearing types showed positive relationships for all traits, with the exception of birth weight and ultrasonic backfat measurements, where correlations were all small and negative for hill-reared lambs.

Estimates of phenotypic correlations between live weight at weaning, backfat and muscle depth measurements were well within the range of estimates reported by Simm *et al.* (1987); Cameron and Bracken (1992) (from a review of the literature) and Young (1989) (from analysis of a selection experiment).

The results of this study show that selecting animals reared under non-limiting nutritional conditions for divergent subcutaneous backfat levels does result in their offspring reared in extensive conditions also being divergent in backfat thickness. The results clearly show how important the environmental components are in affecting the growth and body composition of hill lambs, in particular for those reared on the hill rather than on improved pasture inbye. However, the heritability estimates for ultrasonic fat depth show that genetic improvement of carcass characteristics is a feasible option, although annual progress would be slower (by approx. 0.4) for hill reared lambs than lambs reared on improved pasture, (based on phenotypic variances of 0.0065 and 0.0047 cm² and heritabilities of 0.12 and 0.24 for hill and inbye-reared lambs respectively). Further work is in progress to investigate the effects of selection for carcass composition on maternal performance and survival characteristics.

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A comparison of growth and carcass traits in Scottish Blackface lambs sired by genetically lean or fat rams

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Abstract

An experimental programme was initiated in 1990 to investigate the consequences of selection for reduced fatness in hill sheep and to estimate genetic parameters for carcass traits in the same class of animal. Thirty-two progeny groups of lambs were born as a result of mating Scottish Blackface rams to ewes of the same breed on two Scottish Agricultural College hill farms in 1991 and 1992. Sires were from two divergent selection lines for subcutaneous back fat depth and were selected under ad libitum feeding conditions on an index combining live weight and ultrasonic fat depth at 20 weeks of age. The index was designed to alter body composition but not body weight. Weaned male progeny (reared extensively) were brought together from both farms in August of each year, reared on grass and finished for slaughter on swedes at a target condition score of 3. Measurements taken at weaning were: live weight, average ultrasonic measurements of average subcutaneous fat depth and muscle depth. At slaughter, traits measured were: pre-slaughter live weight, pre-slaughter condition score, age at slaughter, cold carcass weight, killing-out proportion, Meat and Livestock Commission (MLC) fat class and MLC conformation class. Side and shoulder dissections were made on proportionally 0.2 and 0.8 of lambs respectively and lean tissue, subcutaneous fat, intermuscular fat and bone were measured. Comparisons were made between the two genetic lines and genetic parameters were estimated from data adjusted to three different 'end-points': constant dissected subcutaneous fat weight, constant age at slaughter and constant cold carcass weight. Moderate to low heritability estimates were obtained for most traits: pre-slaughter live weight = 0.36, cold carcass weight = 0.39, fat class = 0.13, conformation class = 0.09, lean weight = 0.27, bone weight = 0.36 (constant subcutaneous fatness), intermuscular fat = 0.10, subcutaneous fat = 0.20 (constant cold carcass weight). Correlations between ultrasonic measurements at weaning, and slaughter and dissected carcass components were moderate to weak. However, there is sufficient genetic variation in the carcass traits to warrant inclusion in breeding goals for hill sheep. The results also show that genetic differences obtained by selection under intensive rearing conditions for divergent fatness are also seen in progeny reared under extensive (hill) conditions.

Keywords: carcass composition, extensive husbandry, genetic parameters, live weight, sheep.

Introduction

Hill sheep in Britain provide pure and crossbred females for lowland breeding flocks, in addition to providing lambs for meat production. They also sustain farming communities in the most remote and difficult areas of the United Kingdom (UK). An improvement in the income of hill flocks would increase their financial viability, make them more competitive and less vulnerable to fluctuations in hill farming subsidies. One method of achieving this would be to improve the carcass traits of hill lambs. Hill sheep such as the Scottish Blackface tend to become fat at light weights, due to their small mature size, (McClelland *et al.*, 1976). Usually, UK abattoirs

penalize over-fat lamb carcasses, reflecting consumer demand. Whilst there is a clear need to improve genetically the carcass characteristics of hill lambs, this is only part of a broader selection goal. Other traits relevant to the multi-purpose rôle of hill sheep, including their ability to survive and produce lambs in harsh environments, must also be addressed.

To date, carcass traits have not been incorporated into selection objectives for hill sheep. First, this is because of an absence of reliable estimates of genetic and phenotypic parameters in the relevant breeds for carcass characteristics and associated traits which may be used as selection criteria e.g. ultrasonic

measurements. Secondly, little is known about the relationships between carcass characteristics and other traits relevant to breeding goals for hill sheep. The consequences of reducing fatness are of particular concern, because of its assumed importance for survival, pregnancy and subsequent lactation.

The aims of the studies reported in this paper were threefold; (i) to investigate whether or not selection for divergent fatness (using ultrasound techniques) in animals reared under *intensive* conditions, results in different fatness in the carcasses of their progeny when reared under *extensive* conditions; (ii) to compare carcasses of lambs sired by rams from two genetic lines selected for divergent carcass fatness, slaughtered according to commercial finishing criteria; (iii) to estimate heritabilities, phenotypic and genetic correlations for carcass and growth traits.

Material and methods

Management of animals

The lambs described in this study were born on two Scottish Agricultural College (SAC) hill farms in 2 years. They were sired by 32 rams from the two divergent selection lines (FAT line and LEAN line) of Scottish Blackface sheep described by Bishop (1993). These rams had been selected for up to 4 years based on an index (Cameron and Bracken, 1992) designed to alter carcass composition:

$$0.204 \times W20_s - 0.996 \times FAT_s$$

where $W20$ is 20-week body weight and FAT is the average of ultrasonic backfat thickness measurements taken over the 13th rib and the third lumbar vertebra at 20 and 21 weeks of age, and the subscript s indicates that both traits were corrected for known fixed effects and standardized to have a residual standard deviation of 1.0. The above index was not expected to change live weight of the two lines, so that differences between lines were a function of carcass composition rather than a function of differences in body weight or degree of maturity. Nine rams from each selection line were used in the 1st year, and 10 LEAN line, and nine FAT line sires were used in the 2nd year. Five of these sires were used in both years to provide genetic links between years. A total of 2303 matings were made by laparoscopic artificial insemination (AI) to unselected Scottish Blackface ewes on two SAC hill farms during 1990 and 1991. AI was used to enable all sires to be represented on both farms and to concentrate the lambing period. A total of 1660 ewes lambed to AI in the 2 years and 2386 live lambs were born. The two SAC farms represent two contrasting hill environments typical of those found in the east and the west of Scotland. Farm 1 is located in the

Pentland National Park, Midlothian, and rises from 305 to 488 m above sea level, with an average rainfall of 800 mm per annum. Farm 2 is located near Crianlarich, West Perthshire and is a much harsher, wetter farm rising from 180 to 1034 m, with 2900 mm average rainfall. A more detailed description of the management of the breeding ewes and their lambs on each farm is given by Conington *et al.* (1995).

Weaning took place on each farm at an average age of 17 weeks, when all lambs were weighed and ultrasonically scanned at the level of the third lumbar vertebra using a Vetscan ultrasonic machine with a 5 MHz 56-mm probe. Photographed scan images were subsequently interpreted using computer-based semi-automatic image analysis software. Four individual fat depth measurements were taken laterally from the boundary of the vertical process of the vertebra and the *m. longissimus* muscle. Average fat depth (AVFD) was calculated between the first and fourth depth site (not as the average of the four individual measurements). A single muscle depth measurement (MD) was also taken at the deepest point on the muscle. Weaned male lambs (which had been reared extensively) were brought together from both farms in August of each year and managed as one flock on improved lowground pastures at SAC Bush Estate. They were grazed on silage aftermath until November of each year and subsequently given access to swedes *ad libitum*, supplemented by an average of 0.4 kg/day of a concentrate ration containing proportionately 0.16 crude protein and 10.8 MJ metabolizable energy per kg dry matter. Lambs were weighed and condition scored fortnightly and selected for slaughter at a target condition score of 3 by the same person on all occasions.

Pre- and post-slaughter measurements

Traits measured at weaning were: weaning weight (WWT), ultrasonic muscle depth (MD) and average fat depth (AVFD). A pre-slaughter weight (SLWT) was taken on average 6 h after removal from grass. The lambs were slaughtered approximately 13 h later. In addition, traits measured at slaughter were: pre-slaughter condition score (CS), cold carcass weight (CCWT) and killing-out proportion (KO). KO was calculated as $CCWT/SLWT$ and cold carcass weight was recorded approximately 24 h post-slaughter with the pelt removed. Age at slaughter (AGE) was calculated for each lamb. In addition, all carcasses were scored by the Meat and Livestock Commission (MLC) classifier on duty at the abattoir for assessments of subcutaneous fat (MLC FAT) and conformation (CONF). Since the interval between MLC fat classes is not equal, data were transformed to their corresponding estimated

subcutaneous fat proportion before analysis: 1 = 0.04, 2 = 0.08, 3L = 0.11, 3H = 0.13, 4L = 0.15, 4H = 0.17 and 5 = 0.20 (Kempster *et al.*, 1986). MLC conformation class was coded as E = 5, U = 4, R = 3, O = 2, and P = 1.

Carcass dissection data were available on 997 lambs slaughtered. Two hundred and twenty-four left side dissections were made, representing proportionally about 0.2 of the carcasses in each sire progeny group. This proportion of lambs chosen was based on a formula of Cook *et al.* (1983). The sides were separated into eight joints (breast, chump, end-neck, leg, loin, mid-neck, scrag and shoulder) as described by Cuthbertson *et al.* (1972). For the remainder, the shoulder joint alone was dissected. Each joint was dissected into lean, fat (subcutaneous and intermuscular), bone and waste components. The shoulder joint was chosen as the sample joint to dissect from all lambs because of the reported high correlation (0.9) between the lean content of the shoulder and the carcass (Cook *et al.*, 1983).

Traits derived

The dissected components of interest are proportions of lean tissue (LEAN), subcutaneous fat (SUBFAT), intermuscular fat (IFAT), total fat (ALLFAT) (= SUBFAT + IFAT) and bone (BONE). Double sampling techniques using regression to predict whole body composition, as suggested by Conniffe and Moran (1972), were used in this analysis. Specifically, shoulder data from the side dissection animals were used to derive prediction equations to best describe total carcass weight, lean, subcutaneous fat, intermuscular fat and bone. The equations derived were then used to estimate predicted carcass weight (PCWT), predicted carcass lean (PLEAN), predicted subcutaneous fat (PSUBFAT), predicted intermuscular fat (PIFAT), predicted total fat (PALLFAT) (=PSUBFAT + PIFAT) and predicted bone (PBONE). *R*-squared values and residual standard deviations for predicted carcass components are shown in Appendix Table A1.

Statistical analysis

The analyses were made on data adjusted to three 'end points': (1) a constant dissected subcutaneous fat weight, (2) a constant age at slaughter and (3) a constant cold carcass weight. Adjustments to constant subcutaneous backfat and cold carcass weight were made by linear regression and adjustment to a constant age was by quadratic regression. As the lambs were selected for slaughter at a constant condition score, an estimate of subcutaneous fat cover in the live animal, results from a constant fat level measured in the carcass are likely to be the most accurate. Results from data adjusted to the other two 'end points' have been

extrapolated from the data and hence must be interpreted with care. In practice, UK farmers select animals for slaughter according to a combination of live weight and fatness, with the emphasis on market signals. The data were analysed initially using the GENSTAT package (Lawes Agricultural Trust, 1983) to identify significant sources of variation, using regression. GENSTAT residual maximum likelihood (REML) was then used to calculate fixed effect means. The main effects fitted were sire selection line (LEAN line or FAT line), dam age (2, 3 + 4 or 5+ years), fully castrated, or cryptorchid males (males with one visible testicle, no. = 52) (MALE) and grazing code (GRAZ), where grazing code accounted for farm, birth type, rearing type and year. For each of the three 'end points', the relevant factor was also fitted as a covariate. Finally, sire was fitted as a random effect, nested within line. Prediction equations were derived using regression techniques using the GENSTAT statistical package.

Price per lamb was compared at a fixed MLC fat class (and hence transformed to an estimated subcutaneous fat proportion), adjusted for MALE, with day of slaughter fitted with a quartic regression coefficient, as linear, quadratic, cubic and quartic terms were all significant but higher order terms were not. Again, sire was fitted as a random effect, nested within line.

Within-line univariate heritability estimates, and multivariate genetic and phenotypic correlations were estimated for all traits using multivariate REML techniques (REMLPK; Meyer, 1985), fitting a sire model and the fixed effects described above. The fitted pedigree included all genetic relationships between the sires, however all ewes were assumed to be unrelated as their pedigrees were not known. The REMLPK algorithm was assumed to have converged when the difference in the variances of the log likelihoods of successive iterations was less than 10^{-6} .

Results

Least-square means and phenotypic standard deviations for live weight at weaning, average fat and muscle depths, slaughter characteristics and dissected shoulder components from all lambs are presented in Table 1. (More details of earlier growth, and individual fat depth measurements taken at weaning are given by Conington *et al.*, 1995).

Figure 1 compares the MLC fat classification scores of lambs from the FAT or LEAN genetic lines. Chi-square tests show a significant difference between the two lines ($\chi^2 = 9.3$, $P < 0.01$) in fat scores. More lambs from the LEAN line fell into category 2 and more lambs from the FAT line fell into category 3H, despite there being no difference between the two

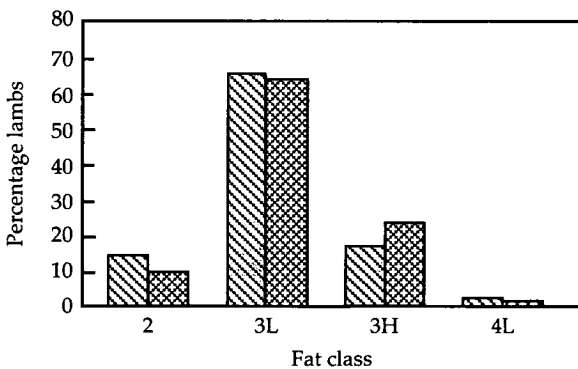
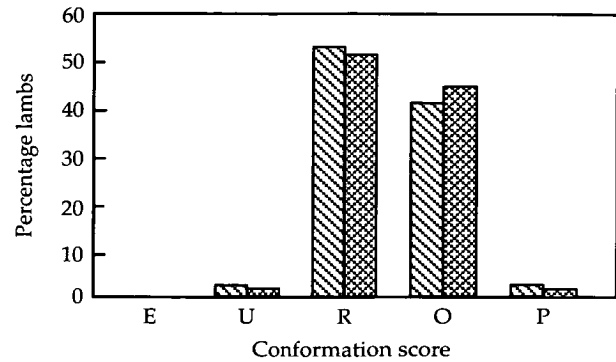
Table 1 Least-square means and phenotypic standard deviation (s.d.) for all measured traits

	Mean	s.d.
Weaning weight (kg)	28.54	3.36
Average fat depth (cm)	0.21	0.074
Muscle depth (cm)	1.77	0.192
Pre-slaughter condition score	2.90	0.40
Pre-slaughter live weight (kg)	38.20	3.65
Age at slaughter (days)	247.00	48.69
Killing-out proportion	0.453	0.019
MLC estimated subcutaneous fat proportion	0.112	0.015
MLC conformation score (E = 5)	2.60	0.50
Price received (£)	31.41	4.76
Dissected proportions		
Subcutaneous fat	0.136	0.028
Intermuscular fat	0.156	0.019
All fat	0.292	0.037
Lean	0.538	0.032
Bone	0.164	0.013

lines in the condition score prior to slaughter. When the MLC fat scores were transformed to the linear fat scale described above, to describe biological differences, the difference between the two lines was not significant. There were no differences between the two lines in conformation score, as shown in Figure 2.

Environmental influences

Important environmental effects on lamb performance are detailed by Conington *et al.* (1995). In general, the influence of dam age on slaughter and dissection traits was less important than in traits measured earlier in life; lambs from 2-year-old ewes were lighter at slaughter than lambs from 3- to 5-year-old ewes (37.68 kg *v.* 38.42 kg); cryptorchid lambs were classified leaner, (MLC FAT 0.1078 *v.* 0.1132), were heavier, (39.82 kg *v.* 36.17 kg), took

**Figure 1** MLC fat class for 1991 and 1992 born male lambs: (▨) Lean line; (▩) Fat line.**Figure 2** MLC conformation class for 1991 and 1992 born male lambs: (▨) Lean line; (▩) Fat line.

longer to finish (259.7 days *v.* 234.5 days) and had a lower killing-out proportion (0.4488 *v.* 0.4552) than fully castrated lambs. Differences between farms for most traits reflect the difference in mature live weight of ewes of about 10 kg and the severity of the environment in which lambs were reared. Farm differences were greater than differences between years, although both were significant for most traits. Figure 3 shows farm differences in the cumulative proportions of lambs drawn for slaughter. It illustrates how lambs from the different farms performed in both finishing seasons, in the time taken to reach slaughter. Despite being managed as one group post weaning, lambs from farm 2 took approximately 1 month longer to finish than lambs from farm 1 in both years.

Comparison between lines

Table 2 shows least-square means for carcass traits from lambs of the two selected lines (LEAN and FAT) corrected to a constant dissected fat level. LEAN line lambs were 850 g heavier pre-slaughter (SLWT) and produced carcasses which were 340 g

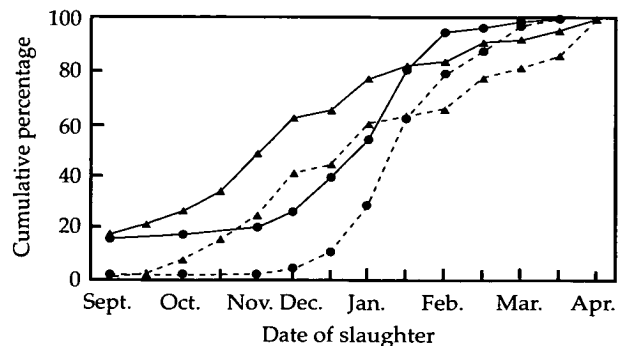
**Figure 3** Slaughter pattern according to farm: —●— 1991 farm 1; - -●- - 1991 farm 2; —▲— 1992 farm 1; - -▲- - 1992 farm 2.

Table 2 Sire line means and differences in carcass characteristics compared at a constant dissected subcutaneous fat level†

Trait	LEAN	FAT	s.e.d.
No. of observations	429	496	
SLWT (kg)	38.38	37.53	0.442
CS	2.893	2.885	0.011
AGE (days)	247.0	245.6	6.203
CCWT (kg)	17.27	16.93	0.200
CONF (E = 5)	2.583	2.494	0.046
KO	0.45	0.45	0.002
Dissected proportions‡			
IFAT (pifat)	0.1560	0.1541	0.0019
LEAN (plean)	0.5411	0.5413	0.0023
BONE (pbone)	0.1660	0.1653	0.0012

† See Appendix Table 1 for all abbreviations.

‡ Dissected shoulder joint only.

heavier post slaughter (CCWT), than lambs from the FAT line. They also tended to have better conformation scores. Lean line lambs had a slightly poorer killing-out proportion and took an average of 1.4 days longer to reach slaughter. The tendency for LEAN line lambs to be heavier than FAT line lambs from *actual* shoulder dissection data were significantly different for predicted half carcass weight, line difference = 0.36 ± 0.17 kg. Predicted line differences are more robust estimates (due to a greater sample size) than those calculated from actual carcass dissections.

Table 3 shows results adjusted to the same cold carcass weight for lambs from LEAN and FAT lines. LEAN line lambs had significantly lower dissected subcutaneous and total fat proportions, more lean and more bone than FAT line lambs. Despite having the same condition score prior to slaughter, they were also classified significantly leaner by MLC.

Table 3 Sire line differences in carcass characteristics compared at a constant cold carcass weight†

Trait	LEAN	FAT	s.e.d.
No. of observations	429	496	
CS	2.890	2.893	0.007
AGE (days)	240.3	238.0	0.007
KO	0.448	0.451	0.002
MLC fat	0.109	0.112**	0.001
CONF (E = 5)	2.509	2.476	0.044
Dissected proportions‡			
SUBFAT	0.1291	0.1413**	0.0029
IFAT	0.1557	0.1554	0.0019
ALLFAT	0.2847	0.2966**	0.0039
LEAN	0.5425	0.5357*	0.0030
BONE	0.1675	0.1640*	0.0014

† See Appendix Table 1 for all abbreviations.

‡ Dissected shoulder joint only.

Table 4 Sire line differences in carcass characteristics compared at a constant age†

Trait	LEAN	FAT	s.e.d.
No. of observations	428	496	
SLWT	38.31	37.96	0.360
CS	2.895	2.897	0.007
CCWT	17.29	17.29	0.162
MLC fat	0.1108	0.1136*	0.0014
CONF	2.585	2.550	0.045
KO	0.452	0.456	0.0022
Dissected proportions‡			
SUBFAT	0.1313	0.1428**	0.0030
IFAT	0.1566	0.1562	0.0019
ALLFAT	0.2878	0.2991**	0.0040
LEAN	0.5409	0.5347	0.0032
BONE	0.1655	0.1620**	0.0013

† See Appendix Table 1 for all abbreviations.

‡ Dissected shoulder joint only.

Table 4 shows results adjusted to a constant age. When lambs were compared at a constant weight, there was little difference in the age at slaughter, so it follows that there would be little difference in the live and dead weights of the lambs when compared at a constant age. Again, the most consistent results were seen in the fat measurement comparisons. These show that the LEAN line lambs had significantly less subcutaneous and total fat than the FAT line lambs. As in the previous analyses, there was no difference between the intermuscular fat levels between the two lines but LEAN line lambs did have greater lean and bone proportions than FAT line lambs.

Price differences

Comparing prices received for the carcasses between the two lines is a complex procedure, due to the seasonal price fluctuations experienced during the finishing period. Lamb prices tend to rise after the summer, reaching a peak in the following spring. Once these seasonal price fluctuations had been accounted for, however £0.57 per lamb extra was received for the LEAN line lambs compared with the FAT line lambs. This is approximately £0.20 lower than the anticipated sum, based purely on a differential carcass weight between the two lines and ignoring the leaner fat class scores of the LEAN line.

From regression analyses, the main traits affecting price received per carcass were cold carcass weight and day of slaughter (fitted as a quartic effect because of seasonal price fluctuations), which together accounted for proportionately more than 0.80 of the variation in price. When fat and conformation class were included in the regression model, the total variance accounted for increased to only 0.83. A further multiple regression analysis was

undertaken on the residual values, after slaughter day had been accounted for. Cold carcass weight explained 0.50 of the residual variation and together with fat and conformation score, accounted for 0.62 of the residual variation. Dissected carcass proportions and condition score prior to slaughter had only a very small influence.

By drawing lambs to a target of commercial fat class 3L, we might expect the difference in fatness between the two sire lines to be very small and the proportion of variation in price explained by differences in fatness also to be very small. Conversely, drawing lambs at a constant live weight would reduce the apparent influence of live weight on price and increase the variation explained by carcass fatness.

Heritability estimates

Heritabilities of the slaughter and carcass traits estimated at a constant dissected subcutaneous fatness are presented in Table 5. A similar table is shown in **Appendix Table A2i** for the other two end-points. All the estimates tend to be low to moderate but in general, bone and slaughter weight have the highest heritabilities and intermuscular fat, conformation and condition score have the lowest. The heritability estimates range from 0.09 for conformation score, to 0.36 for pre-slaughter weight and bone measurements and 0.39 for cold carcass weight. Some fluctuation in values is seen according to the end-point.

Heritability estimates for MLC fat and conformation scores and condition score prior to slaughter, (all 'subjective' measurements) are low, and similar at each 'end' point.

Table 5 Heritability estimates for traits adjusted to a constant fatness

Trait†	h^2	s.e.
WWT‡	0.20	0.10
AVFD‡	0.22	0.10
MD‡	0.20	0.10
SLWT	0.36	0.13
CS	0.10	0.04
AGE	0.34	0.12
CCWT	0.39	0.14
MLC fat	0.13	0.08
CONF	0.09	0.07
Shwt	0.28	0.11
IFAT	0.10	0.07
LEAN	0.27	0.11
BONE	0.36	0.13

† See Appendix Table 1 for all abbreviations.

‡ End-point correction not fitted.

Table 6 Univariate heritability estimates (with s.e.) using data from shoulder and predicted carcass traits, compared at a constant dissected subcutaneous fatness

Trait	Shoulder	Predicted
Weight†	0.28 (0.11)	0.28 (0.11)
Intermuscular fat	0.10 (0.07)	0.15 (0.08)
Lean	0.27 (0.11)	0.27 (0.11)
Bone	0.36 (0.13)	0.34 (0.13)

† Shoulder joint weight compared with predicted carcass weight.

Heritability estimates for predicted carcass traits were almost identical to heritability estimates for actual carcass traits shown in Table 6, compared at a constant subcutaneous fat weight. This was also the case for traits compared at the other two end-points, with the exception of bone estimated at a constant cold carcass weight (0.24 ± 0.10 , *v.* 0.16 ± 0.08) for BONE and PBONE, respectively. These estimates are shown in **Appendix Table A2ii**.

Correlations

Phenotypic and genetic correlations adjusted to a constant dissected subcutaneous fatness are summarized in Table 7. Similar tables for the other two end-points are shown in **Appendix Table A3**. Most phenotypic correlations are robust, with no standard errors greater than 0.04. However, there are large standard errors for several genetic correlations between traits at all three end-points. This is particularly the case where one or both traits have low heritabilities and it limits the interpretation of many correlations.

The correlations between ultrasonic measurements made at weaning and carcass and slaughter characteristics were moderate to low. The phenotypic correlation (r_p) between average fat depth and dissected subcutaneous backfat is 0.26 and 0.30 at a constant cold carcass weight and constant age respectively. The genetic correlations between the same traits, at the same end-points, are unreliable due to the large standard errors.

The relationships between price and several carcass components are interesting. Obviously, the relationship between price and carcass weight is positive and very strong. But this is also exacerbated by the fact that lamb prices per kg live weight increased throughout the lamb finishing period, so older (heavier) lambs made more money. At a constant cold carcass weight, moderate negative phenotypic (-0.32) but strong negative genetic (-0.78) correlations are seen between MLCfat and price. The relationships between CONF and price are less clear.

Table 7 Heritability estimates, genetic and phenotypic correlations† between lamb growth, live body composition, pre- and post-slaughter characteristics at a constant subcutaneous backfat level

Shwt	0.28 (0.11)	0.54 (0.02)	0.96 (0.00)	0.82 (0.01)	0.79 (0.01)	0.20 (0.03)	0.07 (0.04)	0.88 (0.01)	0.73 (0.02)	-0.12 (0.03)	0.20 (0.03)	-0.13 (0.04)	-0.05 (0.04)	0.58 (0.02)
Ifat	0.71 (0.20)	0.10 (0.07)	0.38 (0.03)	0.25 (0.03)	0.30 (0.03)	0.13 (0.03)	0.19 (0.03)	0.45 (0.03)	0.29 (0.03)	0.04 (0.04)	0.14 (0.03)	-0.03 (0.05)	-0.01 (0.04)	0.27 (0.03)
Lean	1.00 (0.00)	0.81 (0.19)	0.27 (0.11)	0.79 (0.01)	0.78 (0.01)	0.21 (0.03)	0.04 (0.04)	0.87 (0.01)	0.73 (0.02)	-0.14 (0.04)	0.17 (0.03)	-0.13 (0.04)	-0.04 (0.04)	0.58 (0.02)
Bone	0.91 (0.06)	0.56 (0.31)	0.88 (0.08)	0.36 (0.13)	0.81 (0.01)	0.12 (0.04)	-0.05 (0.04)	0.80 (0.01)	0.68 (0.02)	-0.17 (0.04)	0.28 (0.04)	-0.11 (0.04)	-0.03 (0.04)	0.48 (0.03)
SLWT	0.93 (0.05)	0.42 (0.31)	0.94 (0.05)	0.90 (0.06)	0.36 (0.13)	0.18 (0.03)	0.04 (0.04)	0.89 (0.01)	0.74 (0.02)	-0.18 (0.02)	0.28 (0.03)	-0.06 (0.04)	-0.02 (0.04)	0.49 (0.03)
Conf	0.37 (0.35)	-0.14 (0.48)	0.48 (0.35)	0.40 (0.36)	0.44 (0.33)	0.09 (0.07)	0.18 (0.04)	0.29 (0.03)	0.29 (0.03)	0.04 (0.02)	0.00 (0.04)	-0.03 (0.04)	0.09 (0.04)	0.19 (0.03)
MLC fat	0.39 (0.33)	0.37 (0.41)	0.40 (0.32)	0.26 (0.34)	0.14 (0.34)	0.19 (0.44)	0.13 (0.08)	0.14 (0.04)	-0.03 (0.04)	0.15 (0.04)	0.01 (0.04)	0.08 (0.04)	0.08 (0.04)	0.04 (0.04)
CCWT	1.00 (0.20)	0.77 (0.20)	0.99 (0.01)	0.85 (0.08)	0.88 (0.06)	0.44 (0.35)	0.29 (0.28)	0.39 (0.14)	0.81 (0.01)	-0.12 (0.04)	0.20 (0.04)	-0.10 (0.04)	-0.03 (0.04)	0.62 (0.02)
Price	0.85 (0.09)	0.59 (0.28)	0.84 (0.09)	0.72 (0.14)	0.92 (0.06)	0.62 (0.32)	-0.06 (0.31)	0.89 (0.06)	0.32 (0.12)	-0.23 (0.03)	-0.03 (0.04)	-0.12 (0.04)	-0.16 (0.04)	0.77 (0.01)
CS	-0.69 (0.15)	-0.60 (0.25)	-0.64 (0.23)	-0.57 (0.21)	-0.69 (0.16)	-0.42 (0.38)	-0.09 (0.38)	-0.73 (0.21)	-0.87 (0.14)	0.10 (0.04)	0.02 (0.04)	-0.01 (0.04)	0.02 (0.02)	-0.19 (0.04)
WWT	0.21 (0.32)	0.02 (0.40)	0.19 (0.30)	0.14 (0.32)	0.18 (0.31)	-0.06 (0.46)	0.17 (0.34)	0.07 (0.31)	-0.11 (0.32)	0.06 (0.39)	0.20 (0.10)	0.36 (0.03)	0.55 (0.03)	-0.35 (0.03)
AVFD	-0.46 (0.27)	-0.25 (0.37)	-0.45 (0.28)	-0.47 (0.26)	-0.38 (0.28)	-0.64 (0.42)	0.24 (0.32)	-0.45 (0.25)	-0.41 (0.27)	-0.08 (0.32)	-0.41 (0.29)	0.22 (0.10)	0.35 (0.03)	-0.27 (0.04)
MD	-0.31 (0.31)	-0.28 (0.39)	-0.26 (0.32)	-0.28 (0.31)	-0.35 (0.30)	-0.37 (0.48)	-0.58 (0.27)	-0.41 (0.29)	-0.54 (0.26)	-0.97 (0.02)	0.67 (0.20)	-0.06 (0.36)	0.20 (0.10)	-0.40 (0.03)
AGE	0.56 (0.20)	0.57 (0.28)	0.54 (0.20)	0.50 (0.22)	0.67 (0.17)	0.43 (0.37)	0.15 (0.31)	0.67 (0.15)	0.84 (0.09)	0.95 (0.09)	-0.37 (0.27)	-0.22 (0.29)	-0.94 (0.08)	0.34 (0.12)

† Heritability estimates on the diagonal. Genetic correlations (and standard errors) below the diagonal. Phenotypic correlations (and standard errors) above the diagonal.

Discussion

This study has demonstrated that selection for divergent subcutaneous fatness under intensive feeding conditions results in progeny which are also divergent in subcutaneous backfat, when reared under extensive conditions. This observation was first seen at weaning (Conington *et al.*, 1995), when lambs born from LEAN line sires had significantly less subcutaneous fat measured ultrasonically, compared with lambs born from FAT line sires. After slaughter, LEAN line lambs were classified leaner than FAT line lambs by MLC, even though they were selected for slaughter at a condition score of 3. This difference in fatness was verified by results from carcass dissection, which showed that LEAN line lambs had less subcutaneous fat than FAT line lambs. These results indicate that body composition in lambs reared in hill situations can be manipulated through genetic selection. The design of this experiment follows what actually happens, to a certain extent, in the hill sheep breeding community. Hill farms in more favourable locations produce rams for selling to other hill farms, often in harsher environments. Frequently, these rams receive supplementary feeding and are reared on good

quality pasture. Once sold, they are normally managed on hill pastures of poorer quality than those on which they were reared. The results from this trial are therefore particularly relevant for the UK hill sheep breeding industry.

Comparing lambs from LEAN and FAT sires at three end-points at slaughter enables the effects of such divergent selection to be assessed on a large number of traits, although results at a constant cold carcass weight and constant age must be interpreted cautiously, since slaughter was actually at a target constant fatness. It is also appropriate to compare animals at three different end-points, because objective selection decisions are based on parameter estimates estimated at a given end-point. It may appear inappropriate for the end-point in this trial to be constant fatness when differences between genetic lines in fatness are under investigation. However, under commercial conditions, lambs are selected for slaughter normally at an acceptable level of fatness and therefore commercial carcass grades are available for each lamb slaughtered. Other carcass characteristics, such as carcass weight and age at slaughter, are then the indicators of performance.

These are important for hill lamb producers, as payment is based on a combination of weight and fatness and to a lesser extent, age of lamb.

Australia or New Zealand and therefore use sheep genotypes adapted to extensive management systems.

The information on the traits affecting price received per lamb from the regression analyses is informative. The timing of slaughter and weight of lamb at slaughter appear to have overriding influence on the ultimate price obtained for the lambs. The 'quality' traits seemingly had a minor influence in comparison. However, it must be recognized that by selecting animals to a constant body condition score, in order to ensure the majority of lambs would fall into the 'normal' grades, would limit the variation seen in fatness and hence minimize the price differentials per kg received per lamb. If lambs had been selected for slaughter at a constant weight, undoubtedly a greater proportion of variation in price would be explained by differences in fatness.

Most estimates of heritability for live weight at slaughter and cold carcass weight in this study, are within the range of published estimates for these traits for lambs reared on pasture, although estimates for carcass weight are based on hot carcass weight and none of the estimates has been calculated at a constant fat level. The slight differences amongst estimates according to the end-point of the analysis can be partly explained by the different interpretation of what are superficially the same traits at differing end-points. For example, fatness adjusted for live weight is roughly equivalent to fat percentage, and live weight adjusted for age is essentially lamb growth rate. It is interesting to note that heritability estimates for pre- and post-slaughter weights are considerably higher when measured at a constant fatness. Heritability estimates for carcass composition are comparable with those cited in the literature, with the exception of bone, which is higher than several estimates quoted in the literature for pasture-based rearing systems.

Table 8 summarizes heritability estimates from previously published papers, mainly from grass-based finishing systems. None of the estimates reviewed is specifically from hill or mountain breeds, although most references are for work done in

Table 8 Summary of published heritability estimates

Referencet	Trait	h^2 (s.e.)	End point	No. of sires and breed
	Fat depth			
1	5-9 months	0.01 (0.03)	Fixed age	161/Poll Dorset
	10-13 months	0.18 (0.07)	Fixed age	161/Poll Dorset
	14-18 months	0.28 (0.15)	Fixed age	161/Poll Dorset
2	205 days	0.23	Fixed age	60/Romney 40/Romney X
1	5-9 months	0.11 (0.05)	Fixed live weight	161/Poll Dorset
	10-13 months	0.33 (0.09)	Fixed live weight	161/Poll Dorset
	14-18 months	0.29 (0.16)	Fixed live weight	161/Poll Dorset
5		0.25	Fixed age	10/Coopworth
4		0.33	Fixed live weight	20/Southdown
6		0.28 (0.08)	Fixed live weight	130/Hyfer
6		0.22 (0.08)	Fixed age	130/Hyfer
7	7 months	0.38 (0.03)	Fixed live weight	125/Coopworth
	Muscle depth			
	5-9 months	0.15 (0.05)	Fixed live weight	161/Poll Dorset
1	10-13 months	0.15 (0.06)	Fixed live weight	161/Poll Dorset
	14-18 months	0.19 (0.12)	Fixed live weight	161/Poll Dorset
2		0.38	Fixed age	60 Romney 40 Romney X
	Muscle width	0.63	Fixed age	60 Romney 40 Romney X
3	Pre-slaughter liveweight	0.31 (0.12)	Fixed age	79/Swedish Pelt sheep
	Carcass weight	0.17 (0.10)	Fixed age	79/Swedish Pelt sheep
	Dressing proportion	0.05 (0.09)	Fixed age	79/Swedish Pelt sheep
	Fat score	0.21 (0.11)	Fixed age	79/Swedish Pelt sheep
	Subcutaneous fat (mm)	0.20 (0.11)	Fixed age	79/Swedish Pelt sheep
	Dissected lean	0.08 (0.09)	Fixed age	79/Swedish Pelt sheep
	Dissected fat	0.15 (0.10)	Fixed age	79/Swedish Pelt sheep
	Dissected bone	0.26 (0.11)	Fixed age	79/Swedish Pelt sheep

† (1) Gilmour *et al.* (1994). (2) Waldron *et al.* (1992). (3) Henniřsson and Malmfors (1995). (4) Solis-Ramirez *et al.* (1993). (5) Fennessy *et al.* (1992). (6) Fogarty *et al.* (1994). (7) Morris *et al.* (1997).

Some of the information provided in this paper will be used to incorporate carcass characteristics into an index of overall merit for hill sheep. The relationships between these traits and maternal performance are yet to be determined but the results from these analyses demonstrate that components of body composition are under significant genetic control in hill sheep and that it is possible to alter them under extensive rearing conditions.

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Appendix

Abbreviations used in the Appendix tables are as follows: shwt = shoulder weight; subfat = subcutaneous fat; ifat = intermuscular fat; SLWT = slaughter weight; conf = conformation; MLCfat = MLC fat score; CS = pre-slaughter condition score; CCWT = cold carcass weight; WWT = weaning weight; AVFD = average fat depth; MD = ultrasonic muscle depth.

Table A1 R-squared values and residual standard deviations for predicted traits

Trait	R ²	Residual s.d.
Lean	0.93	174.14
Subfat	0.86	92.03
Ifat	0.80	76.35
Bone	0.71	113.12
Total fat	0.88	14.76
CCWT	0.93	294.88

Table A2i Univariate heritability estimates (with s.e.) at a constant cold carcass weight (CCWT) and constant age at slaughter

	CCWT	Age
Shwt		0.16 (0.08)
Subfat	0.20 (0.09)	0.21 (0.10)
Ifat	0.10 (0.07)	0.03 (0.05)
Lean	n/c†	0.23 (0.10)
Bone	0.24 (0.10)	0.35 (0.13)
All fat (2 + 3)	0.18 (0.09)	0.14 (0.08)
SLWT	0.31 (0.12)	0.23 (0.10)
Conf	0.08 (0.06)	0.07 (0.06)
MLCfat	0.13 (0.08)	0.13 (0.08)
CCWT		0.18 (0.09)
Age	0.19 (0.10)	

† No convergence/calculation.

Table A2ii Univariate heritability estimates (with s.e.) for actual and predicted traits compared: (a) at a constant cold carcass weight and (b) at a constant age

Trait	Actual	Predicted
(a) At a constant cold carcass weight		
Subfat	0.20 (0.09)	0.20 (0.09)
Ifat	0.10 (0.07)	0.16 (0.08)
Total fat	0.18 (0.09)	0.18 (0.09)
Lean	n/c†	n/c†
Bone	0.24 (0.10)	0.16 (0.08)
(b) At a constant age		
Shwt	0.16 (0.08)	0.16 (0.08)
Subfat	0.21 (0.10)	0.19 (0.09)
Ifat	0.03 (0.05)	0.10 (0.07)
Total fat	0.14 (0.08)	0.13 (0.08)
Lean	0.23 (0.10)	0.24 (0.10)
Bone	0.35 (0.13)	0.35 (0.13)

† No convergence/calculation.

Table A3i Heritability estimates, genetic and phenotypic correlations† between lamb growth, live body composition, pre- and post-slaughter characteristics at a constant age at slaughter

Shwt	0.16	0.65	0.69	0.89	0.76	0.77	0.82	0.25	0.31	0.89	0.64	0.07	0.58	0.20	0.25
	(0.06)	(0.02)	(0.02)	(0.01)	(0.01)	(0.01)	(0.01)	(0.03)	(0.03)	(0.01)	(0.02)	(0.04)	(0.02)	(0.04)	(0.03)
Subfat	0.27	0.21	0.49	0.33	0.33	0.90	0.52	0.24	0.38	0.63	0.39	0.10	0.31	0.30	0.10
	(0.34)	(0.10)	(0.03)	(0.03)	(0.03)	(0.01)	(0.03)	(0.03)	(0.03)	(0.02)	(0.03)	(0.04)	(0.03)	(0.03)	(0.04)
Ifat	0.67	0.41	0.03	0.46	0.39	0.82	0.54	0.19	0.33	0.62	0.42	0.08	0.41	0.25	0.17
	(0.30)	(0.62)	(0.05)	(0.03)	(0.03)	(0.01)	(0.03)	(0.03)	(0.03)	(0.02)	(0.03)	(0.04)	(0.03)	(0.03)	(0.04)
Lean	0.90	-0.17	0.40	0.23	0.73	0.44	0.74	0.21	0.18	0.79	0.59	0.02	0.52	0.08	0.26
	(0.07)	(0.37)	(0.62)	(0.10)	(0.02)	(0.03)	(0.02)	(0.03)	(0.03)	(0.01)	(0.02)	(0.04)	(0.03)	(0.04)	(0.03)
Bone	0.86	-0.05	0.19	0.84	0.35	0.41	0.75	0.12	0.10	0.72	0.54	0.00	0.59	0.03	0.21
	(0.11)	(0.32)	(0.62)	(0.10)	(0.13)	(0.03)	(0.01)	(0.03)	(0.03)	(0.02)	(0.03)	(0.04)	(0.03)	(0.03)	(0.03)
Allfat	0.40	0.94	0.63	-0.02	0.04	0.14	0.61	0.25	0.42	0.74	0.46	0.11	0.40	0.33	0.15
	(0.31)	(0.05)	(0.34)	(0.40)	(0.34)	(0.08)	(0.02)	(0.03)	(0.03)	(0.02)	(0.03)	(0.03)	(0.08)	(0.05)	(0.10)
SLWT	0.81	-0.04	-0.09	0.88	0.86	-0.04	0.23	0.24	0.27	0.91	0.65	0.06	0.61	0.14	0.23
	(0.12)	(0.35)	(0.55)	(0.09)	(0.09)	(0.37)	(0.10)	(0.03)	(0.03)	(0.01)	(0.02)	(0.04)	(0.02)	(0.04)	(0.03)
Conf	0.04	-0.17	-0.84	0.24	0.22	-0.38	0.32	0.07	0.23	0.31	0.33	0.07	0.13	0.10	0.21
	(0.44)	(0.44)	(0.37)	(0.41)	(0.37)	(0.44)	(0.38)	(0.06)	(0.03)	(0.03)	(0.03)	(0.04)	(0.04)	(0.04)	(0.03)
MLC fat	0.59	0.41	0.59	0.42	0.25	0.56	0.13	-0.09	0.13	0.35	0.09	0.16	0.15	0.22	0.14
	(0.27)	(0.30)	(0.46)	(0.32)	(0.30)	(0.29)	(0.33)	(0.42)	(0.08)	(0.03)	(0.04)	(0.04)	(0.04)	(0.04)	(0.04)
CCWT	0.99	0.09	0.63	0.98	0.83	0.18	0.81	0.05	0.41	0.18	0.71	0.09	0.61	0.22	0.29
	(0.02)	(0.37)	(0.54)	(0.05)	(0.12)	(0.38)	(0.11)	(0.50)	(0.30)	(0.09)	(0.02)	(0.04)	(0.02)	(0.04)	(0.03)
Price	0.79	-0.09	0.05	0.90	0.65	-0.19	0.89	0.37	-0.30	0.81	0.23	0.02	0.46	0.14	0.26
	(0.15)	(0.36)	(0.47)	(0.10)	(0.19)	(0.43)	(0.11)	(0.45)	(0.32)	(0.13)	(0.10)	(0.04)	(0.03)	(0.04)	(0.03)
CS	-0.85	-0.74	-0.95	-0.61	-0.41	-0.75	-0.86	-0.52	-0.43	-0.70	-0.51	0.00	0.00	0.02	-0.04
	(0.32)	(0.41)	(0.20)	(0.63)	(0.49)	(0.32)	(0.37)	‡	(0.70)	(0.43)	(0.54)	(0.03)	(0.04)	(0.04)	(0.04)
WWT	0.38	-0.21	-0.23	0.51	0.40	-0.06	0.57	0.01	0.30	0.38	0.36	-0.73	0.17	0.34	0.48
	(0.33)	(0.42)	(0.88)	(0.26)	(0.27)	(0.36)	(0.25)	(0.56)	(0.32)	(0.31)	(0.30)	(0.40)	(0.09)	(0.03)	(0.03)
AVFD	-0.49	-0.00	-0.25	-0.40	-0.39	0.20	-0.38	-0.54	0.44	-0.52	-0.46	-0.60	0.34	0.23	0.28
	(0.36)	(0.38)	(0.90)	(0.31)	(0.25)	(0.30)	(0.34)	(0.42)	(0.28)	(0.34)	(0.25)	(0.36)	(0.33)	(0.08)	(0.03)
MD	-0.26	-0.86	-0.82	0.28	0.20	-0.66	0.21	-0.40	-0.75	-0.11	0.50	0.05	0.54	-0.53	0.12
	(0.41)	(0.28)	(0.32)	(0.40)	(0.32)	(0.23)	(0.47)	(0.74)	(0.23)	(0.50)	(0.32)	(0.61)	(0.29)	(0.30)	(0.05)

† Heritability estimates on the diagonal, genetic correlations (and standard errors) below the diagonal and phenotypic correlations (and standard errors) above the diagonal.

‡ No convergence/calculation.

Table A3ii Heritability estimates, genetic and phenotypic correlations† between lamb growth, live body composition, pre- and post-slaughter characteristics at a constant cold carcass weight

Shwt	0.05 (0.05)	0.30 (0.02)	0.42 (0.02)	0.60 (0.02)	0.24 (0.02)	0.42 (0.03)	-0.07 (0.04)	-0.09 (0.03)	0.02 (0.03)	-0.06 (0.04)	0.00 (0.04)	0.07 (0.02)	-0.01 (0.04)	-0.02 (0.04)	-0.02 (0.04)
Subfat	0.78 (0.15)	0.20 (0.09)	0.34 (0.03)	-0.43 (0.03)	-0.37 (0.03)	0.88 (0.01)	-0.22 (0.04)	0.06 (0.03)	0.31 (0.03)	-0.38 (0.03)	0.15 (0.04)	0.14 (0.04)	0.26 (0.03)	0.07 (0.04)	-0.37 (0.03)
Ifat	0.55 (0.31)	0.52 (0.37)	0.10 (0.07)	-0.16 (0.03)	-0.32 (0.03)	0.75 (0.02)	-0.31 (0.03)	0.02 (0.03)	0.25 (0.03)	-0.24 (0.03)	0.14 (0.04)	0.10 (0.04)	0.10 (0.04)	0.02 (0.04)	-0.12 (0.04)
Lean	NC	NC	NC	NC	0.43 (0.03)	-0.40 (0.03)	0.12 (0.04)	-0.09 (0.04)	-0.24 (0.03)	0.25 (0.03)	-0.14 (0.04)	-0.08 (0.04)	-0.20 (0.03)	-0.06 (0.04)	0.25 (0.03)
Bone	0.38 (0.30)	-0.17 (0.31)	-0.36 (0.39)	1.00 (0.00)	0.24 (0.10)	-0.42 (0.03)	0.41 (0.03)	0.19 (0.03)	-0.33 (0.03)	0.22 (0.04)	0.17 (0.04)	0.14 (0.04)	-0.15 (0.04)	-0.04 (0.04)	0.12 (0.04)
All fat	0.83 (0.17)	0.94 (0.05)	0.74 (0.20)	-0.61 (0.25)	-0.21 (0.32)	0.18 (0.09)	-0.31 (0.03)	0.04 (0.04)	0.32 (0.03)	-0.39 (0.03)	0.18 (0.03)	0.14 (0.04)	0.23 (0.04)	0.06 (0.04)	-0.32 (0.03)
SLWT	0.13 (0.37)	0.02 (0.32)	-0.66 (0.28)	0.03 (0.37)	0.56 (0.21)	-0.37 (0.29)	0.31 (0.12)	-0.18 (0.04)	-0.21 (0.04)	0.15 (0.04)	-0.18 (0.04)	0.19 (0.04)	0.00 (0.04)	0.01 (0.04)	-0.08 (0.04)
Conf	-0.13 (0.48)	0.14 (0.43)	-0.48 (0.50)	-0.07 (0.48)	-0.01 (0.41)	0.22 (0.43)	0.28 (0.44)	0.08 (0.06)	0.15 (0.04)	0.08 (0.04)	0.08 (0.04)	-0.06 (0.04)	0.01 (0.04)	0.11 (0.04)	0.00 (0.04)
MLC fat	0.71 (0.26)	0.33 (0.35)	0.33 (0.43)	0.46 (0.32)	0.08 (0.36)	-0.43 (0.28)	-0.46 (0.27)	0.02 (0.48)	0.13 (0.08)	-0.32 (0.03)	0.20 (0.03)	0.02 (0.04)	0.16 (0.04)	0.11 (0.04)	-0.16 (0.04)
Price	-0.80 (0.35)	-0.10 (0.39)	-0.38 (0.46)	-0.35 (0.59)	-0.23 (0.39)	-0.20 (0.39)	0.63 (0.25)	0.53 (0.47)	-0.78 (0.22)	0.14 (0.08)	-0.27 (0.03)	-0.35 (0.03)	-0.17 (0.04)	-0.24 (0.03)	0.63 (0.02)
CS	0.50 (0.57)	0.22 (0.46)	-0.05 (0.67)	0.43 NC	0.06 (0.51)	0.17 (0.50)	-0.19 (0.45)	-0.03 (0.67)	0.15 (0.52)	-0.71 (0.33)	0.07 (0.05)	0.07 (0.04)	0.02 (0.04)	0.02 (0.04)	-0.20 (0.03)
WWT	0.94 (0.28)	-0.11 (0.36)	-0.06 (0.48)	0.70 (0.43)	0.23 (0.34)	-0.11 (0.38)	0.29 (0.30)	-0.09 (0.46)	0.12 (0.36)	-0.33 (0.35)	0.28 (0.46)	0.20 (0.10)	0.41 (0.03)	0.57 (0.02)	-0.62 (0.02)
AVFD	0.61 (0.47)	0.34 (0.32)	0.26 (0.43)	-0.29 (0.56)	-0.24 (0.33)	0.35 (0.33)	0.04 (0.32)	-0.25 (0.41)	0.44 (0.31)	-0.14 (0.39)	-0.38 (0.47)	0.47 (0.28)	0.20 (0.10)	0.36 (0.03)	0.33 (0.03)
MD	0.62 (0.49)	-0.35 (0.35)	-0.22 (0.46)	0.75 (0.55)	0.21 (0.35)	-0.33 (0.37)	0.07 (0.33)	-0.06 (0.44)	-0.56 (0.24)	-0.29 (0.39)	0.99 (0.08)	0.77 (0.17)	-0.27 (0.40)	0.18 (0.08)	-0.48 (0.03)
Age	-0.97 (0.14)	0.15 (0.37)	0.18 (0.47)	-0.35 (0.59)	-0.36 (0.34)	0.18 (0.39)	0.17 (0.32)	0.18 (0.47)	-0.06 (0.36)	0.63 (0.24)	-0.95 (0.13)	-0.52 (0.26)	0.07 (0.38)	-0.92 (0.22)	0.19 (0.10)

† Heritability estimates on the diagonal, genetic correlations (and standard errors) below the diagonal and phenotypic correlations (and standard errors) above the diagonal.
NC no convergence.

Genotype \times environment interactions for early growth and ultrasonic measurements in hill sheep

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Abstract

Genotype \times environment and genotype \times sex interactions were investigated using lines of Scottish Blackface sheep that had been divergently selected under intensive husbandry conditions for predicted carcass lean proportion, and offspring of rams from these selection lines which were reared under extensive hill conditions. Traits considered were live weight and ultrasonic fat and muscle depth. These were measured at 20 weeks of age on the intensively reared lambs and at 17 weeks of age on the extensively reared animals. Heritabilities for the two environments were 0.39 and 0.20 for fat depth, 0.36 and 0.25 for muscle depth and 0.23 and 0.12 for live weight. Genetic correlations between the environments were 0.54 (s.e. 0.17), 0.90 (s.e. 0.14) and 0.11 (s.e. 0.43) for fat depth, muscle depth and live weight, respectively. The extensive environment may be subdivided according to whether the lambs are reared on improved pasture or on the hill side. The genetic correlations (with s.e.s where estimable) between performance in these two environments were 0.70 (s.e. 0.33), 0.71 (s.e. 0.23) and 1.00 for fat depth, muscle depth and live weight. Genetic correlations between male and female performance under extensive conditions were 0.84 (s.e. 0.28), 0.99 (s.e. 0.14) and 1.00 for fat depth, muscle depth and live weight. For fat depth, the genetic correlations of the intensively reared lambs (males only) with extensively reared females and males were 0.37 (s.e. 0.22) and 0.67 (s.e. 0.17), respectively.

Keywords: *genotype environment interaction, genotype sex interaction, live weight, sheep, ultrasonic measurements.*

Introduction

The genetic improvement of hill sheep in the United Kingdom poses several problems. First, there is a lack of clearly defined breeding objectives, which are a prerequisite before embarking on any genetic improvement programme. Secondly, there is a paucity of relevant genetic parameters for traits which are thought to be important for hill sheep breeds, e.g. growth, carcass composition and maternal performance characteristics. Thirdly, the environments under which the hill sheep have to perform vary greatly, and the applicability of genetic parameters measured in one environment to performance in another environment is not known, especially when the different environments pose different constraints on the animals. Finally, there is a practical difficulty in recording and measuring animals in some harsh hill environments.

A trial designed to provide information necessary for the genetic improvement of hill sheep is described by Conington, Bishop, Waterhouse and Simm (1995). By using animals which had been performance tested under intensive conditions as sires, this trial also allowed a comparison of performance between intensive husbandry conditions and different harsh extensive (hill) environments and hence allowed possible genotype \times environment interactions to be estimated. These results will also indicate whether or not it is necessary to record and select animals under the harshest environmental conditions, or whether environments more favourable to both the animals and the recorders can be used.

The main aim of the work described in this paper was to quantify possible genotype \times environment interactions for early growth and ultrasonic

measurements for hill lambs, using the Scottish Blackface breed as a model for hill sheep. Comparisons were made between intensive and extensive rearing conditions, and also between extensive environments differing in their severity. A secondary aim was to investigate possible genotype \times sex interactions which are of interest if traits important in the (predominantly male) slaughter lamb are different from those determining subsequent maternal performance in the female.

Material and methods

Source of data

The data analysed in this paper were collected from two sources. First, on Blackface lambs in a selection experiment (Bishop, 1993b) and, secondly, on progeny of selected ram lambs from this experiment which were reared under extensive hill conditions (Conington *et al.*, 1995). In the selection experiment, lambs were born outside on improved pasture but housed from 4 weeks of age. From 10 to 20 weeks of age, male lambs were group penned and offered a concentrate diet *ad libitum*. Divergent selection was practised using a selection index designed to alter carcass composition but not live weight at 20 weeks of age. This index was $0.204 \times W20_s - 0.996 \times \text{SUBFAT}_s$, where $W20$ and SUBFAT are live weight and ultrasonic subcutaneous fat depth at 20 weeks of age, and the subscript s denotes that these two measurements were corrected for known fixed effects and scaled to have a mean of zero and a residual standard deviation of 1.0. Thirty-two rams from these divergent lines (FAT and LEAN), 16 per line, were then mated by artificial insemination to unselected Blackface ewes on two Scottish Agricultural College (SAC) hill farms, in two successive years (1990 and 1991), giving a total of 2476 lambs born alive. The sires used were among the most extreme males in the FAT and LEAN lines, in years 2, 3 and 4 of the selection experiment.

The ewes and lambs born on the hill farms were managed according to normal policy on Scottish hill farms. Ewes identified as carrying single lambs at pregnancy scanning were kept on unimproved hill areas whilst ewes identified as carrying two or more lambs were grazed on improved pastures, with those on farm 2 (the harsher of the two farms) receiving supplementary food and housing from pregnancy scanning until after parturition. Hence, multiple and single reared lambs experienced large differences in both their nutritional and climatic environments. Live weight was recorded at various ages but this paper will concentrate on weaning weight, at about 17 weeks of age, and ultrasonic fat and muscle depth, also measured at weaning.

Interactions investigated

The data collected in the two trials were used to investigate the following genotype \times environment interactions: (i) performance under intensive conditions in the selection experiment compared with performance of all animals under the extensive hill farm conditions; (ii) performance in the selection experiment compared with performance of lambs reared on improved pasture, on the hill farms; (iii) performance in the selection experiment compared with performance of lambs reared on the hill; and (iv) performance of the hill farm lambs reared on improved pasture *v.* hill reared lambs.

Additionally, the following genotype \times sex interactions were investigated: (i) selection experiment (male) lambs compared with male lambs on the hill farms; (ii) selection experiment (male) lambs compared with female lambs on the hill farms; and (iii) the genetic relationship between male and female lambs on the hill farms.

All these interactions were quantified by calculating genetic correlations between the appropriate subsets of data, as described below. These correlations can be estimated using genetic links created by both the 32 sires and the dams rearing lambs in both the hill and improved pasture environments, in subsequent years, or rearing both male and female lambs. No genetic links existed between the dams used on the two hill farms and as a result the dataset was too small to allow meaningful correlations to be calculated between the two farms.

Statistical analyses

Genetic parameters were calculated using bivariate derivative-free residual maximum likelihood techniques (DFREML; Meyer, 1989), using the technique outlined by Thompson, Crump, Juga and Visscher (1995) in their model 1. In this application of bivariate DFREML techniques, the two traits in each analysis are measured on separate, but genetically related, groups of animals. Therefore, genetic covariances exist between the two traits in each analysis, but there are no environmental covariances.

The selection experiment traits analysed were live weight, ultrasonic fat and muscle depths, all measured at 20 weeks of age, and the selection index designed to alter carcass composition. The fixed effects of year, and interactions between dam age and litter size were fitted, along with the covariate of actual age at measurement. The traits measured on the hill farm lambs analysed in this paper were weaning weight (at approx. 17 weeks), and ultrasonic muscle depth and fat depth. When comparing the selection experiment data with the hill farm data, 'weight corrected fat depth' (fat depth

$-\beta$ (weight - mean weight), where β is the regression of fat depth on weight) was also calculated for the hill farm data. Fixed effects fitted, where appropriate, included grazing code (accounting for farm, year, birth type and rearing environment), sex and the interactions of farm with birth type and farm with dam age, along with a covariable of day of birth. Additionally, when data from the hill farms alone was used in the analyses, line (LEAN or FAT) was also fitted.

An animal model was used in all analyses and each bivariate analysis yielded heritabilities for the two traits and genetic correlations between these traits. For the bivariate analyses comparing the intensive environment (selection experiment) with lambs on the hill farms, the entire selection experiment dataset up to year 4, the year when the youngest sires were born, was included in the analyses. Therefore, when the selection index was the selection experiment trait considered in the bivariate analyses, all selection of sires used on the hill farms is accounted for and the genetic parameters will be unbiased. For analyses which utilized the hill farms' data only, the effect of selection line was fitted, with sires nested within line.

In the analyses comparing the entire selection experiment with the entire dataset from the hill farms the observed variation for hill farm lambs was partitioned into additive genetic and maternal common environmental components. Exclusion of this common environment component was found to have a negligible effect on the genetic correlations, and for subsequent analyses it was not fitted. The structure of the selection experiment data was inadequate to calculate meaningful maternal components but the rearing environment was designed to minimize such effects.

Table 1 Comparative performance of lambs under intensive and extensive rearing conditions†

Environment category	Sex	No.	Live weight (kg)	Fat depth (cm)	Muscle depth (cm)
Intensive:‡	Male	428	43.6	0.224	2.35
Extensive:§	Male	508	26.8	0.171	1.74
	Female	517	25.6	0.195	1.77
Hill	Male	495	30.4	0.212	1.77
	Female	464	29.1	0.241	1.79

† Measurements taken at 20 weeks of age for intensively reared lambs and 17 weeks of age (on average) for extensively reared lambs.

‡ 17-week weight was 37.0 kg.

§ All hill reared lambs are singles, improved pasture reared lambs are predominantly twins.

Standard errors for each genetic parameter of interest were calculated from the second derivative of the log likelihood, evaluated at the parameter estimate. To enable this derivative to be evaluated, a likelihood profile was obtained by fixing the parameter at points at, and on either side of, the REML parameter estimate and then remaximizing the likelihood for all other variance components.

Genotype \times environment and genotype by sex interactions were additionally tested on the hill farm data by fitting sire by rearing environment and sire by sex interactions respectively in least squares analyses of the data, using the GENSTAT package (Lawes Agricultural Trust, 1983).

Results

Comparative performances in the different environments considered in this paper are shown in Table 1. Several points need to be made when interpreting these values. First, the results for the improved pasture and hill reared lambs were, to a large extent, confounded with birth type, as ewes grazing improved pasture tended to be those raising twin lambs whereas only single-bearing ewes were grazed in the hill environments. This helps to explain the relatively poor performance of the improved-pasture lambs compared with the hill-reared lambs. Secondly, considerable variation existed between the hill environments, with the performance of hill-reared lambs on farm 2 being much poorer than those in the equivalent environment on farm 1. These environments were pooled however, because there were insufficient data to calculate meaningful genetic parameters for each subenvironment. Finally, the ultrasonic measurements were made using a different machine and interpreted by a different person for the intensive and the extensive environments.

Genetic parameters describing the relationships between performance in the intensive (selection experiment) and extensive environments are presented in Table 2. The heritabilities for each measured trait are shown, along with the genetic correlations between each pair of traits. The heritabilities for the extensive environment differ slightly from those presented by Conington *et al.* (1995), i.e. 0.12, 0.23 and 0.14 for weaning weight, muscle and fat depth, which were calculated on a within-line basis. The values were estimated including the information on which the sires of the extensive environment lambs were selected and while this has only a small effect on the heritabilities for weaning weight and muscle depth, it has a larger effect on the fat depth value, as the sires were selected on an index dominated by fat depth. The

Table 2 Genetic parameters describing relationships between traits measured on intensively and extensively reared lambs†

	Intensive environment					
	h^2 §	c^2	Fat depth $h^2 = 0.39$	Muscle depth $h^2 = 0.36$	20-week weight $h^2 = 0.23$	INDEX‡ $h^2 = 0.45$
Extensive environment						
Fat depth	0.20	0.12	0.54	-0.02	-0.53	-0.54
s.e.			0.17	0.29	0.39	0.17
Muscle depth	0.25	0.10	0.04	0.90	0.19	-0.07
s.e.			0.19	0.14	0.43	0.18
Weaning weight	0.12	0.18	-0.29	-0.08	0.11	0.27
s.e.			0.19	0.33	0.43	0.18

† Heritabilities in first row and column, genetic correlations (and s.e.s) in main part of Table.

‡ INDEX is the selection index, designed to alter carcass composition but not live weight.

§ Genetic parameters obtained from bivariate analyses with INDEX as trait 1.

genetic correlations of greatest interest are those between equivalent, or similar, traits measured in the two environments. Muscle depth can be seen to be very strongly correlated between the two environments, compared with the moderate positive correlation for fat depth and the weak correlation for live weight. The live weight correlation has a very large standard error, however, and should be interpreted with caution until further data are available. Correlations involving the selection index used in the selection experiment are similar in magnitude but opposite in sign to those including fat depth measured in the selection experiment. Finally, the correlations of weight corrected fat depth with fat depth and the selection index under intensive

conditions were 0.59 (s.e. 0.15) and -0.59 (s.e. 0.15), respectively. The genetic correlation of the selection index in both environments, constructed for the extensive environment using the genetic parameters in Table 2 and those presented by Conington *et al.* (1995), was 0.56.

Genetic correlations between the selection experiment traits and the two categories of extensively reared lambs are shown in Table 3, along with heritabilities and variance components for the improved pasture and hill-reared lambs. These variance components were taken from bivariate analyses fitting the selection index on which the sires were selected, as the first trait. The heritability for fat

Table 3 Comparison of genetic correlations (and s.e.s) between intensively reared lambs and extensively reared lambs, either improved pasture or hill reared, and variance components for improved pasture or hill reared lambs†

	Extensive environment					
	Fat depth		Muscle depth		Weaning weight	
	Inbye	Hill	Inbye	Hill	Inbye	Hill
Intensive environment						
Fat depth	0.54	0.56	0.09	0.13	-0.35	-0.20
s.e.	0.18	0.22	0.20	0.21	0.21	0.25
Muscle depth	0.09	-0.20	0.76	1.00	-0.01	-0.02
s.e.	0.31	0.35	0.20	‡	0.36	0.40
20-week weight	-0.54	-0.62	0.05	0.21	0.15	-0.07
s.e.	0.35	0.42	0.47	0.49	0.46	0.57
INDEX	-0.54	-0.57	-0.07	-0.10	0.33	0.19
s.e.	0.17	0.20	0.19	0.19	0.19	0.22
h^2	0.27	0.16	0.25	0.27	0.12	0.10
σ_a^2	0.00131	0.00104	0.0093	0.0102	1.32	1.12
σ_e^2	0.00350	0.00551	0.0273	0.0273	10.11	9.83

† Variance components obtained from bivariate analyses with INDEX as trait 1.

‡ Standard error not estimable.

Table 4 Genetic correlations (and s.e.s) between traits measured on improved pasture or hill reared lambs

	Fat depth	Muscle depth	Weaning weight
Genetic correlation	0.70	0.71	1.00
s.e.	0.33	0.23	†

† Standard error not estimable.

depth was greater for improved pasture than for hill-reared lambs, this difference being largely a result of the inflated error variance for the hill-reared lambs. However the genetic parameters for muscle depth and weaning weight are little affected by rearing environment. Despite the effect of environment on heritability for fat depth, there was almost no effect of environment type on the genetic correlations involving fat depth, i.e. the correlations between selection experiment and improved pasture-reared lambs were similar to those between selection experiment and hill-reared lambs.

Genetic correlations between traits measured on improved pasture and hill-reared lambs are shown in Table 4. The correlations were strongly positive for all three traits considered and for weaning weight the correlation converged to 1.0. Sire \times rearing environment interactions were not significant for weaning weight and of marginal significance ($P < 0.10$) for fat and muscle depth.

Genetic correlations between selection experiment lambs and either males or females reared extensively are shown in Table 5. Only fat depth is considered, as this is the only trait which gave indications of a genotype \times sex interaction. It can be seen that both fat depth and the selection index, measured under intensive conditions, were more strongly correlated with fat depth measured on male lambs than on female lambs. This is in agreement with the observation that the selection line divergence in

Table 5 Genetic correlations (and s.e.s) describing relationships between intensively reared males and either male or female lambs, reared extensively

	h^2	Extensive environment	
		Fat depth (females)	Fat depth (males)
Intensive environment		0.25	0.25
Fat depth		0.37	0.67
s.e.		0.22	0.17
INDEX		-0.39	-0.68
s.e.		0.19	0.16

Table 6 Genetic correlations (and s.e.s) between male and female performance

	Fat depth	Muscle depth	Weaning weight
Genetic correlation	0.84	0.99	1.00
s.e.	0.28	0.14	†

† Standard error not estimable.

females was about 0.6 times the divergence in male lambs. Also tabulated are the heritabilities for fat for male and female lambs, separately. Interestingly, both values are slightly higher than the overall heritability for fat depth, 0.20, and the phenotypic variances for males and females for this trait were 0.00484 and 0.00633, respectively.

The correlations between male and female performance under extensive conditions are shown in Table 6. Although all values were very high, the value for fat depth is somewhat less than for muscle depth or body weight. None of the sire by sex interactions was significant, however the line \times sex interaction was significant for fat depth ($P < 0.05$).

Discussion

The concept of genotype \times environment interaction is not new and the implications for animal breeding have been recognized for many years (Dickerson, 1962). Such interactions have been investigated and documented for pigs (e.g. Merks, 1989) and cattle (see below) but few studies have investigated performance of genetically related sheep (of the same breed) in different environments. We are not aware of any studies utilizing environments differing as widely as the intensive (selection experiment) and extensive environments of this study. It should be stressed that the intensive environment utilized in the selection experiment is not typical of production environments used for British hill sheep breeds, although many breeders do provide supplementary feeding and rear their animals in environments which are more favourable than those used for commercial sheep. The selection environment was designed to facilitate the expression of genetic differences in production traits and hence enable rapid responses to selection. However regimes allowing rapid early growth should not be ruled out as possible selection environments for the genetic improvement of hill sheep.

As may be expected from the better control of environmental factors, all traits were more highly heritable under the intensive than the extensive regime. The genetic correlations between individual traits ranged from low for live weight, albeit with a

large standard error, to moderate for fat depth and very strong for muscle depth. In contrast to these results, there were strong and consistent correlations between the performance of lambs in the improved pasture and hill subenvironments within the extensive environment. Although these subenvironments differed substantially, they are representative of the environments in which hill sheep breeds are found. As well as environmental factors, the average age difference of 3 weeks between the intensively and extensively reared lambs is another factor which might affect the relative magnitude of the genetic correlations.

With regard to other studies, the performance on improved pasture of the crossbred offspring of Texel-Oxford sires selected for the same criterion as the Blackface sires, i.e. predicted carcass lean content at 20 weeks of age under intensive feeding conditions, has been reported by Cameron (1992). Line differences in carcass lean and fat weight were similar to those predicted from the sire line differences indicating that, for the environments considered, genotype \times environment interactions are probably of little consequence. Likewise the growth of crossbred offspring of Suffolk sires selected on a lean growth index comprising measurements of live weight and ultrasonic muscle and fat depth, was similar to that expected from differences in the purebred lines (Simm and Murphy, 1996). However, differences in fatness, measured either by dissection (Lewis, Simm, Dingwall and Murphy, 1996) or by trimming during commercial preparation of carcasses (Simm and Murphy, 1996) were apparently lower than expected from *in vivo* measurements on sires. This may represent either a genotype \times environment interaction, or a lower response than expected in the purebred lines — a question currently under investigation.

More detailed investigations of genotype \times environment interactions have been undertaken in beef cattle, with the general pattern emerging that large interactions are only apparent where there are marked climatic and nutritional differences between environments. For example, (Frisch, 1981) observed large interactions for beef cattle selected under Australian tropical conditions. When investigated under less stressful conditions, the superiority of the selected animals disappeared. However, under controlled experimental conditions where only the nutritional regimen differs, a number of studies have failed to find any evidence of genotype \times environment interactions (Bailey, Gilbert and Lawson, 1990; Baker, Neville and Utley, 1991; Hough and Benyshek, 1988). Finally, some evidence of genotype \times environments interactions was observed for Hereford cattle selected on an intensive feeding

regimen and tested on pasture (Bishop, 1993a), although the coheritabilities (i.e. $r_{gh_1h_2}$) were sufficiently high for the interactions to be of little practical consequence.

The heritabilities and genetic correlations in Tables 2, 3 and 4 can be used to determine the environment in which selection should take place to maximize genetic gain. Consider, first, the comparison of intensive *v.* extensive environments. If the objective is to improve individual traits in the extensive environment, then the intensive environment may be inappropriate for improving live weight, slightly inferior for altering fat depth, and possibly marginally superior for improving muscle depth. Secondly, consider the comparison of improved pasture *v.* hill subenvironments. If the objective is to improve performance on improved pasture, then selection should take place on improved pasture for all of the traits considered. If the objective is to improve hill performance, however, then the optimal solution is less obvious. For muscle depth, it would appear to be better to select amongst hill-reared lambs. However both environments would be equally effective for either fat depth or weaning weight. From a practical viewpoint, it is a much easier husbandry task to record accurately animals reared on improved pasture, and if all other things are equal then this would be the subenvironment of choice in which to record and select animals. Most hill farms disseminating breeding stock would have both improved pasture and hill subenvironments, so altering the testing environment of choice, if necessary, should not pose large logistical problems.

The results presented in this paper also give some indication of a genotype \times sex interaction for fat depth, operating at the selection line level rather than for sires within line. This was especially apparent when making the contrast between the intensive and extensive rearing environments, as the correlation between males in the two environments was almost double the correlation between males and females. A similar result was observed for beef cattle by Bishop (1993a), where the genetic correlation between intensive (males only) and grassland performance (both sexes) for lean growth rate was 0.56 to 0.57. However if the dataset was restricted to males only, this correlation rose to 0.70 to 0.80.

It can be speculated that a genotype \times sex interaction for fat depth may be advantageous when overall breed improvement is considered for hill sheep. For the improvement of the male slaughter lamb, a reduction in carcass fatness is an obvious selection criterion. Reducing the fatness of the female lamb, and hence the adult ewe, may not be a desirable consequence, however, if carcass fat reserves are

required by the ewe to survive and produce under harsh environmental conditions. A genotype \times sex interaction for carcass fatness may assist in finding a compromise between these two conflicting objectives if it enables differential selection responses in the two sexes. These questions will be addressed both theoretically and experimentally as part of the ongoing research programme with these selected lines of sheep.

In summary, comparison of the performance of lambs in a variety of contrasting environments has revealed evidence of genotype \times environment interactions for live weight and ultrasonic measurements. For genetic improvement of lambs under extensive environments, an intensive rearing environment would be inefficient for selecting for either weight gain or fat depth. When considering extensively reared lambs, for both genetic and practical reasons it may be preferable to rear and select lambs on improved pasture, to improve the performance of both improved pasture and hill-reared lambs. There is also some evidence for a genotype \times sex interaction for fat depth, which may be beneficial when deriving selection objectives to improve the performance of both slaughter lambs and the hill ewe.

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Genetic selection for extensive conditions

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Genetic selection for extensive conditions

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Abstract

Humans have selected animals which are more suited for food production or other purposes, since the process of domestication of livestock began, whether this selection was done knowingly or unknowingly. The deliberate selection of improved breeds and strains has been a particularly important feature of agriculture in the last couple of centuries, especially in the industrialised countries. For most of this period, selection has been based on subjective assessment of the merits of animals, but objective tools for selection (e.g. performance recording and statistical methods for evaluation of genetic merit) have become widely used in the last few decades. These tools have been used to a large extent in pig, poultry and dairy cattle breeding, but to a much lesser extent in the beef cattle and sheep breeds common in extensive production systems. However, these extensive systems themselves have changed to a much lesser extent than those in which pigs and poultry are kept. Hence there have been opportunities for natural selection for traits conferring better adaptation to these environments. Additionally there has been some subjective selection for traits thought to confer better adaptation. There is considerable scope for wider uptake of existing objective methods of genetic improvement in the harsher areas of the UK, and elsewhere. However, these methods are likely to be more effective if the genetics of traits conferring adaptation to harsh environments are better understood, and if the most important of these traits are included in the breeding goal. Traits conferring better adaptation may include physical attributes such as litter size, fleece type and the ability to store body fat, some aspects of behaviour, especially maternal and grazing behaviour, and disease resistance. A better understanding of the relationships between production traits and these adaptation traits will also be critical for the development of appropriate, sustainable breeding programmes. This approach should

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reduce the risk of there being detrimental correlated effects of selection, and may provide opportunities to improve animal welfare.

Keywords: Adaptation; Breeding; Disease resistance; Extensive systems; Genetic selection; Grazing; Maternal behaviour; Behaviour

1. Introduction

Since the process of domestication of livestock began, about 9000 years ago, humans have selected animals which are more suited for food production or other purposes, whether this selection was done knowingly or unknowingly (see for example Clutton-Brock, 1987). The deliberate selection of improved breeds and strains has been a particularly important feature of agriculture in the last couple of centuries, especially in the industrialised countries. For most of this period, selection has been based on subjective assessment of the merits of animals, but objective tools for selection (e.g. performance recording and statistical methods for evaluation of genetic merit) have become widely used in the last few decades. These tools have been used to a large extent in pig, poultry and dairy cattle breeding. There is no doubt that the selection methods applied have been very effective in altering animal performance, though in some cases there are concerns that these changes in performance have been associated with deleterious genetic changes in 'functional fitness' and welfare. Although objective selection is practised less widely in extensive animal production, economic pressures and a better understanding of the potential benefits are likely to increase the use of this method of improving productivity in these systems.

In the past most public concern over farm animal welfare, and most scientific research effort in farm animal behaviour and welfare has been directed at intensively farmed livestock, particularly pigs and poultry. Usually the focus has been on the effects of intensive management practices (e.g. lack of space and bedding, restricted feeding) on animal welfare. Many of the issues are a result of relatively recent and major man-made changes in the environment (in its widest sense) in which the animals are kept. (Though, as indicated above, there are also cases where genetic selection has been implicated in the welfare problem itself e.g. leg weakness in chickens).

Conversely, many of the perceived welfare problems in extensively farmed livestock (e.g. high lamb mortality in hill sheep flocks, gastrointestinal parasitism) are very long-standing, and more akin to the natural challenges facing wild animals. Hence, it is likely that through a combination of natural selection and some subjective artificial selection over a long period of time, some breeds or strains of animals have become better adapted to particular extensive production systems. Although welfare is notoriously difficult to define, it seems reasonable to assume that animals which are better adapted to a particular environment will have better welfare than those that are not. A better scientific understanding of adaptation to extensive systems is needed, and particularly of the genetic variation in components of that adaptation. This may allow some more objective measures of adaptation to be included in future breeding programmes for livestock in extensive systems. This should reduce the risk of detrimental effects of selection, and may provide opportunities to improve animal welfare.

In this paper we aim to review briefly the strategies currently employed in genetic improvement of livestock, and then to discuss in more detail how these might be modified in future, particularly to incorporate some more objective measures of adaptation to extensive production systems. For the purpose of illustration we will concentrate on hill sheep production in the type of environment for which Scotland is famous—cold and wet! However, the principles should apply to many other species and extensive systems.

2. Strategies for Genetic Improvement

Traditionally three main strategies have been used for the genetic improvement of livestock: selection between breeds or strains, selection within breeds or strains and crossbreeding. These strategies are discussed briefly below, but for more detail on the theory see Falconer (1990) and for practical examples in extensive systems see Simm et al. (1994). In future a fourth option, gene transfer, may become available but we do not intend to address this here.

For any of these strategies to be effective it is important to have a clear view of what the economically important animal characteristics (traits) are. It is then logical to first choose the most appropriate breed or cross, and then to consider whether this breed, or the 'parent' breeds in the case of crossbred animals, can be improved further by within-breed selection.

2.1. *Selection between breeds*

In theory, choices between breeds (or crosses) ought to be made on the basis of objective comparisons of performance in the relevant environment. There are some dramatic examples of the cost of ignoring this rule — in some instances high performing temperate breeds of livestock have been introduced to the tropics without this sort of trial, and have then succumbed to diseases or to nutritional deprivation, to which local breeds were tolerant.

Selection between breeds or strains can achieve dramatic and rapid genetic change when there are large genetic differences between populations in characteristics of economic importance. However, it is obviously costly to replace whole flocks or herds of animals at once. In practice changes are often effected more gradually by 'grading-up' or repeated crossing to the new breed.

2.2. *Crossbreeding*

Crossbreeding is usually used (i) to produce animals of high merit in two or more traits for which different parent breeds are superior, (ii) as an intermediate step in either 'grading up' to a new breed (as mentioned above) or in the creation of a new 'synthetic' breed, or (iii) to exploit 'heterosis' or hybrid vigour. Heterosis is the advantage above

the mid-parent mean which is often seen when two breeds are crossed. To be useful heterosis needs to lift the average level of performance of the crossbred animals above that of the best parent breed. It is usually greatest when the breeds being crossed are very different or inbred, and it is especially important for 'fitness' characteristics like reproductive success and survival.

In many livestock species there is a pyramidal breeding structure with elite pedigree herds or flocks at the top; in theory these are making most of the genetic progress, they sell breeding stock to multiplier herds or flocks which in turn produce larger numbers of breeding stock to sell to the most numerous commercial tier. In many of the livestock species crossbred females are used in this final commercial tier to exploit the benefits of heterosis. However, despite evidence of the benefits of crossbreeding in hill sheep (e.g. Barker et al., 1985) there are relatively few examples of its systematic use in the UK. The wider use of crossbreeding in hill sheep could well have benefits for productivity, survival and other traits related to adaptation.

When objective comparisons of breeds or crosses for extensive systems have been made in the past, these have usually included only indirect or rather crude measures of adaptation. For example, reproductive success may be recorded because of its economic importance, but it also provides a crude measure of adaptation and perhaps an even more crude indication of the absence of severe welfare problems. Occasionally the incidence of economically important diseases may be recorded. Changes in body condition may provide a measure of the adaptation of different breeds or crosses to a harsh environment. Also, survival rates of different breeds and crosses may be measured and these too may provide a crude, but absolute, measure of adaptation.

For those people who believe that there is a place for (humane) animal production in modern society, there may be some intuitive appeal in the 'cost:benefit' approach discussed by Mepham (1993) and Webster (1994). This involves an attempt to assess any welfare costs to the animal, and the economic or other benefits to society. In their case the approach was discussed in the context of new biotechnologies in animal production, but it might apply equally to the ethics of keeping particular breeds, strains or crosses of animal in a particular production system. Although this approach has intuitive appeal, it still requires some means of measuring welfare. Even if this problem can be surmounted, the costs to the animal and the benefits to society are unlikely to be measured in the same currency, and so they will still be difficult to compare.

2.3. Selection within breeds

Objective methods of within-breed selection (i.e. those which rely on recording performance, rather than making subjective judgements about the merit of animals) have become widely used in pig, poultry and dairy cattle breeding over the last few decades. They have been used to a much lesser extent in sheep and beef cattle breeding, but this situation is changing. In many cases the breeds currently used in extensive production systems are already well adapted to them. Hence, there is probably most opportunity to improve further the adaptation and welfare of extensively farmed livestock through within breed selection.

Objective selection within breeds or strains is intended to increase the average level of genetic merit of the population. Ideally, the steps involved are: (i) deciding what to improve (the ‘breeding goal’)—obviously there needs to be genetic variation in this trait or combination of traits if any improvement is to be made; (ii) deciding what to measure and select on (the ‘selection criterion’) in order to make improvements in the breeding goal (in some cases the selection criterion may be the same as the goal; in others some indirect measurement is needed, for example when the goal trait can only be measured in one sex or after slaughter); (iii) designing the breeding programme (e.g. numbers of males and females selected annually, ages at mating); (iv) implementing the programme; (v) monitoring progress and redesigning the programme if necessary.

Many traits of economic importance in farm livestock show continuous variation and are thought to be under the control of a large number of genes. For these traits, rates of genetic improvement depend on four main factors.

1. The selection intensity achieved. This is related to the proportion of animals selected to become parents—the lower the proportion of animals selected, the higher the selection intensity and hence the better they will be.
2. The accuracy with which genetic merit in the trait of interest is predicted. This depends on the extent to which the trait is under genetic control—traits such as growth and wool production tend to be more strongly influenced by the animals’ genetic makeup (have a higher ‘heritability’) than traits associated with reproduction and survival—and also the extent to which performance information on relatives is used. The more information available on relatives, the more accurately an individual’s genetic merit or breeding value can be predicted.
3. The amount of genetic variation in the trait of interest. Again this depends largely on the trait concerned. For example, there is more genetic variation in lamb growth rate than in carcass lean content.
4. The generation interval, which is the average age of parents when their offspring are born.

Generally speaking, the higher the selection intensity, accuracy and genetic variation, and the lower the generation interval, the higher the annual rate of genetic improvement. The main opportunities for breeders to accelerate rates of improvement are through choice of the most accurate methods of predicting breeding values, and by maintaining high selection intensities and low generation intervals. However, there are biological limits on the extent to which selection intensity and generation interval can be altered. It is possible to achieve much higher selection intensities in species (or breeds) with a high reproductive rate. Similarly, shorter generation intervals can be achieved in those species (or breeds) which reach sexual maturity at a younger age. Largely because of biological advantages in these reproductive characteristics, higher rates of genetic change are possible in pigs and poultry than in ruminants.

In most livestock production systems profitability depends on an array of animal characteristics rather than on any single trait. It is important to reflect this in genetic improvement programmes, and animals are usually selected whether objectively or subjectively on a combination of traits. This can be achieved in a number of ways. One approach is to set minimum qualifying standards, or thresholds, in several traits of interest. To qualify for selection animals must then surpass the qualifying standard in

each trait. An informal version of this approach is used by most breeders when they check candidates for selection for any 'functional' defects before breeding from them. Similarly, most shepherds mentally note ewes that are particularly good or bad mothers, and either breed from them or cull them respectively. This approach is probably an efficient way of dealing with functional defects which occur irregularly and are suspected to have a genetic component. However, there are usually several traits of major economic or functional importance. In theory, the optimal method of selection then is to calculate an index of overall genetic merit for each of the animals available for selection. (A good analogy is the entrance system for universities in the UK, where candidates often need to accumulate a minimum points score to be accepted, where this score is calculated from the examination grades they have achieved in several subjects.) Such a selection index for farm animals requires weighting factors to apply to the measurements which have been taken on each animal. To derive these weighting factors it is necessary to know (i) how much genetic variation there is in the traits of interest, (ii) to what extent these traits are associated with each other, and (iii) their relative economic importance. Obtaining reliable estimates of the genetic variation in traits and covariation amongst them requires comprehensive recording of hundreds or thousands of animals and this is a major limitation to the formulation of selection indices for a wider range of breeding goals and production systems.

Where objective within-breed selection has been practised in extensive animal production (e.g. in some hill sheep flocks in the UK) this has usually involved measuring and selecting on productivity (e.g. litter size, lamb growth and ewe mature size). This has been accompanied by a dependence on natural selection to remove animals unsuited to the environment, often together with subjective selection for traits thought to confer better adaptation (e.g. fleece type).

The 'Marshall easy care' Romney from New Zealand is an example of a breed which has been selected 'naturally' for many years (Kilgour and de Langen, 1980). Development of the breed began in the mid 1930s and, at least initially, the ewes were not shepherded at all in the hope that sheep would be selected which could look after themselves in difficult terrain. The result is a strain with a reputedly high survival rate, excellent growth rate, good mobility, good wool production and the ability to thrive in harsh conditions. In a study of maternal ability, this 'easy care' strain had a significantly higher maternal behaviour score than control Romneys, and required less intervention by the shepherd. In a 5 year study, lamb survival in the Marshall Romney averaged 92%, compared with 88%, 86% and 73% in the Dorset-Romney, Perendale and Romney respectively, a result which may be partly due to the smaller litter size of Marshall Romney ewes (Kilgour and de Langen, 1980).

Relying entirely on natural selection is probably not the most effective method of improving adaptation in the short term. For instance, there may be wide fluctuations in exposure to disease agents, temperature and rainfall from one year to the next, and animals which are not particularly well adapted to the environment may get selected in a 'favourable' year. If there is genetic variation in these, it would probably be more efficient to include a limited number of objective measures of adaptation or disease resistance in a formal definition of the breeding objective. This approach is discussed in more detail in the following section.

3. Developing more comprehensive breeding goals for extensively farmed livestock: opportunities and obstacles

As discussed above, most comparisons between breeds and crosses, and most selection schemes within breeds have considered a rather narrow range of traits in the past. It is fairly easy to expand the range of traits considered in comparisons of breeds or strains because these are usually undertaken infrequently. It is much more difficult to do so in within-breed selection where a sustained recording effort is needed, and estimates of genetic (co)variation are needed for traits of interest to make the most effective use of them in selection. However, there is an increasing need to address more comprehensive breeding goals, perhaps particularly for livestock in extensive production systems. Some of the opportunities and obstacles are discussed below for production traits, traits which may confer better adaptation and for disease resistance. Much of this section is based on Conington et al. (1994).

3.1. Production traits

As food production has approached or exceeded requirements in the EU and in other western countries, more attention has been given to product quality. This in turn leads to a need for more comprehensive breeding goals to address quality as well as output. One of the major obstacles to deriving these is the scarcity of relevant genetic parameters (estimates of heritabilities for 'new' traits, and associations amongst these and the existing traits). Similar obstacles apply to the inclusion of adaptation and disease traits in more comprehensive breeding goals.

In meat animals, fatness is a particular issue which has potential implications for extensive animal production. The ability of animals to store body fat is usually seen as an important adaptation to the periods of nutritional deprivation which are common in extensive systems. However, consumers in many countries would like leaner meat than that often produced. It is therefore important to know whether it is possible to breed leaner animals without compromising their ability to survive and reproduce in a harsh environment. This issue is being addressed in a joint SAC/Roslin Institute (RI) research project with hill sheep selected for divergent levels of fatness. Although the experiment is at an early stage, there are no apparent deleterious effects of reducing fatness on survival or reproduction so far, but as discussed earlier, there is a lack of any other more direct measures of welfare. There is evidence from this experiment of quite wide genetic variation in growth and carcass traits, indicating considerable scope for further selection (Conington et al., 1994). The project will produce estimates of genetic parameters for these and other traits including survival, various measures of reproduction, lambing difficulty and wool characteristics. These will allow more comprehensive breeding goals to be developed which should reduce the risk of there being deleterious correlated effects of selection for leanness.

3.2. Traits which may confer better adaptation

3.2.1. Physical adaptation

The coat or fleece of the animal is a primary adaptation to harsh environments and therefore an important characteristic in selection. Breeds such as the Scottish Blackface

have characteristically long outer hairy fibres which provide protection for finer insulating underlying fibres of the fleece. Evidence from the SAC/RI study of Scottish Blackface sheep shows considerable genetic variation in length and other fleece characteristics, indicating the potential for genetic change in these traits. Welsh Mountain lambs with dense hairy birthcoats have been shown to have significant advantages in survival rate compared to lambs with fine curly birthcoats, in particular when the weather was bad (Purser and Karam, 1967).

Differences between and within breeds in their ability to withstand acute cold have been demonstrated in adult and newborn Blackface and Welsh Mountain sheep by Slee (1986). He also showed that hill breeds were more cold tolerant than lowland breeds, and in the same study found the realised heritability for this trait to be 0.36 (Slee and Stott, 1986). Correlated responses included an increase in skinfold thickness and some aspects of metabolic rate (Slee, 1986).

As mentioned earlier, it is often suggested that hill sheep must have the ability to metabolise stored body fat during periods of nutritional deprivation (i.e. especially during winter), as they frequently lose up to 20% of their body weight during this period (Russel et al., 1968). However, hardy primitive breeds such as the Soay are relatively lean (McClelland et al., 1976), so depending on large stores of body fat is obviously not the only strategy for surviving these periods of deprivation. The SAC/RI experiment described above should help to assess the importance of body fat in conferring better adaptation to UK hill conditions.

Webster (1993) suggests that selection should include traits which increase tolerance to long term consequences of prolonged food shortage; not just shortage of energy, but also of N, phosphorus, copper and selenium. Woolliams et al. (1986) showed that lambs from two genetic lines selected for low or high copper status differed substantially in mortality and resistance to infection.

The opportunity for supervision of animals is much lower in extensive than in intensive systems. Hence it is particularly important that ewes have the ability to lamb with minimal difficulty. The genetics of dystocia have been studied less widely in sheep than cattle, but it is likely that there is a small but important genetic component. It is probably particularly important that this is investigated when selection is for increased body size or muscularity.

Litter size will have important direct and indirect effects on the adaptation of ewes to harsh environments. Generally, multiple-bearing ewes (and their lambs) will be at greater risk from nutritional deprivation than their single-bearing counterparts, both pre- and post-partum, unless management is tailored to the litter size of individual ewes. Also, mortality amongst single-born lambs is usually lower than that amongst multiples, for reasons including a higher body weight (although there is an intermediate optimum for birthweight — see for example the review of Haughey, 1993), and a reduced risk of poor maternal behaviour.

3.2.2. *Behavioural adaptation*

Whilst some aspects of behaviour are probably most important from a production viewpoint, others might be considered to confer better adaptation to extensive systems. Most studies of genetic differences in behaviour examine breed differences, rather than

examining genetic variation within breeds. As explained later, more work on within breed variation is needed if behavioural characteristics are to be more widely used in breeding programmes. However, differences between breeds may be useful to highlight potential areas for within-breed investigations

3.2.2.1. Maternal behaviour. What may be considered as adequate maternal behaviour is species-specific, dependent on the developmental stage of the young at birth, and the environment into which they are born. In a synchronised, seasonally-breeding animal such as the sheep, there is a requirement for the rapid formation of an exclusive bond between the ewe and her lambs. Different breeds rely to a varying extent on visual and auditory cues, and differ in their ability to reliably discriminate their young at a distance (Shillito-Walser et al., 1982). All, however, require olfactory cues to form the initial bond with the lamb (Levy and Poindron, 1987). The grooming behaviour, by which the ewe learns to recognise her lambs, also performs a dual function of drying and stimulating the lamb to stand and seek the udder. Genetic differences appear to exist within and between breeds in the degree of grooming behaviour (in both intensity and duration) and in the exclusivity of the bond once formed.

Hill sheep tend to show a narrower range of maternal behaviours, being clustered around the 'good' end of the spectrum, whereas the more intensively reared sheep breeds, such as the Suffolk, show a range of maternal abilities, and an increased propensity to abandon or reject their young. These breeds tend to be slower to begin grooming their lambs, are more easily distracted, show a reduced grooming duration and may also be less exclusive in their bond formation — allowing other lambs to suckle to the detriment of their own lambs. In a range of other maternal behaviours: use of shelters, cooperative behaviour to lamb suckling attempts, lamb proximity to ewe and incidence of lamb stealing, there are distinct breed differences with Suffolk and Merino ewes generally performing poorly (Whateley et al., 1974; Alexander et al., 1983). O'Connor et al. (1985) showed that strong perinatal maternal behaviour in sheep is a crucial factor in decreasing lamb mortality, and an important component of ewe productivity. Anecdotal evidence suggests that nutritionally deprived hill sheep abandon their own lambs—perhaps to increase the chance that they themselves survive. This complex behavioural adaptation is likely to be associated with poor milk supply (hence poor lamb nutrition), and poor expression of maternal and lamb behaviour.

Lamb behaviour also appears to differ within and between breeds, and probably shows a reciprocal relationship with maternal behaviour because, with twins, the more vigorous and vocal lamb tends to elicit the greater degree of maternal attention. Lambs of the hill breeds tend to show a greater behavioural development at birth, are more vigorous, quicker to stand and seek the udder and so enhance their survival chances by early suckling. A new research project is underway at SAC/RI to investigate maternal and lamb behaviour both between and within breeds, and the results may help to address the problem of high lamb mortality in hill flocks.

3.2.2.2. Grazing behaviour. Differences in grazing behaviour between and within breeds may indicate that breeds or individuals within breeds are better adapted to extensive conditions. There are reports of differences between sheep breeds in the time spent

grazing. For example, of six breeds studied by Dudzinski and Arnold (1979) Suffolks had the longest grazing times, followed by Border Leicester, Dorset Horn and Romney sheep, whilst Cheviot and Southdown sheep had the shortest grazing times. In a study of Merino ewes, the individuals with the longer grazing times ended the morning bout later and started the afternoon bout earlier than those individuals with the shorter grazing times (Arnold and Dudzinski, 1978). Similarly, Cheviot and Suffolk sheep commenced grazing earlier in both the morning and the afternoon than Dorset Horn, Southdown and Border Leicester sheep. Romney sheep started grazing later in both the morning and afternoon, but also finished both bouts later (Arnold and Dudzinski, 1978). It is thought that the differences in grazing times are mainly accounted for by increased grazing activity during the grazing bouts.

Certain breeds of sheep which live on hill land, such as the Scottish Blackface and Cheviot sheep, form home ranges, where the daily patterns of movement, at least initially, are learned from the preceding generation (Lawrence and Wood-Gush, 1988; Lynch et al., 1992). Other breeds, such as the Merino, do not establish home ranges, possibly because the same area of land is not used by successive generations.

The distance walked by sheep in a day also varies with breed. Cheviot sheep have been shown to walk further than Romney sheep on both flat and hill land, although the difference between the two breeds was greater on the hill pasture. Distances walked by individual sheep were similar in successive weeks (Cresswell, 1960). The topography of the land, type of vegetation and frequency of drinking will all have effects on the distance travelled.

The distance between grazing animals can vary from 4 m for Merinos to 19 m for the British hill breeds (Arnold and Dudzinski, 1978). Kilgour et al. (1975) found that some sheep, Dorset-Romneys in particular, did not disperse even when herbage availability was very low, whilst Merino sheep have been reported to disperse only under such conditions (Fraser and Broom, 1990). It is thought that breeds which remain close together may not be suited to areas where favoured herbage patches are some distance apart (Hunter, 1960), such as in extensive grazing systems.

Provided that sheep are given sufficient area and choice, they will be selective in their diet (Hafez, 1975; Fraser and Broom, 1990). Sheep may select between different plant species, individual plants, and parts of the plants available (Lynch et al., 1992). Although there are reports that different breeds of sheep prefer different plant species, there is also considerable variation between individuals of the same breed (Arnold, 1981; Lynch et al., 1992). Arnold (1981) showed that sheep from the Australian rangelands preferred different pasture plants to sheep kept on sown pastures, and that differences are strongly influenced by the previous nutritional history of the animal. Similarly, Key and MacIver (1980) found that when Clun Forest lambs were cross-fostered on to Welsh Mountain ewes they preferred the tussock and heather vegetation eaten by the ewes, whilst Welsh Mountain lambs fostered on to Clun Forest ewes preferred the improved pastures grazed by their foster mothers.

In future, more emphasis on research on within breed genetic variation in grazing behaviour, and associations with production and animal welfare would be valuable in helping to formulate breeding goals for extensive systems.

3.2.3. Disease resistance

There is a fairly obvious link between the incidence of some diseases and animal welfare. Prevention of diseases will usually be preferable to curing them, and in cases where there is genetic variation in resistance to a disease, selection may be a useful preventative measure. This approach may be particularly useful in extensive systems where the animals cannot be inspected as regularly as those in more intensive systems.

Variation in disease resistance (or susceptibility) has been found between species, between breeds and also between individuals within breeds. For example, Scottish Blackface sheep are more resistant to *Haemonchus contortus* infection than Finn Dorset sheep (Altaif and Dargie, 1978). Much research into genetic resistance to disease is focused on gastrointestinal parasites, because they impose severe economic constraints on sheep grazing systems. In addition, the increasing resistance of parasites to commercially available anthelmintics, and public concern over chemical residues in meat brings into question the long term effectiveness of parasite control through chemotherapy.

A number of experimental breeding programmes for parasite resistance are currently underway in Australia and New Zealand (Windon et al., 1993). These are providing valuable information on the mechanisms of disease resistance, and their incorporation into multi-trait breeding programmes. Results from this research show that selection for parasite resistance can be successfully based on faecal egg counts (FECs), and that heritabilities for FECs are between 0.2 and 0.4 (i.e. moderately high). The cost effectiveness of including parasite resistance into the breeding goal depends on identification of a reliable and repeatable measure of resistance, the relationships between resistance and other production traits, and the specificity of selection to resistance in terms of other parasite species and non-parasite pathogens. The weighting attributed to parasite resistance in the breeding goal will be dependent on the degree of parasitism in the production environment and the cost-effectiveness of breeding for resistance relative to other control measures.

It could be argued that this economic approach is inappropriate for direct or indirect measures of adaptation or welfare, but apart from arbitrarily inflating these direct economic values, it is difficult to come up with a more appropriate way of incorporating this sort of trait into the breeding goal.

4. Conclusions

In the past, there has been little use of 'objective' selection methods in the cattle and sheep breeds common in extensive production systems. However, the systems themselves have changed to a much lesser extent than those in which pigs and poultry are kept. Hence there have been opportunities for natural selection for traits conferring better adaptation to these environments. Additionally there has been some subjective selection for traits thought to confer better adaptation. There is considerable scope for wider uptake of existing objective methods of genetic improvement in the harsher areas of the UK, and elsewhere. However, these methods are likely to be more effective if the genetics of traits conferring adaptation to harsh environments are better understood, and if the most important of these traits are included in the breeding goal. Traits conferring

better adaptation may include physical attributes such as litter size, fleece type and the ability to store body fat, some aspects of behaviour, especially maternal and grazing behaviour, and disease resistance. A better understanding of the relationships between production traits and these adaptation traits will also be critical for the development of appropriate, sustainable breeding programmes.

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