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Genotype, environment and disease resistance in hill sheep

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Genotype, Environment and Disease Resistance in Hill Sheep

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Summary

This thesis attempted to provide estimates of (co)variance components, heritabilities and genetic and phenotypic correlations between traits of economic importance in two breeds of hill sheep, the Welsh Mountain and the Beulah Speckled Face. Maternal effects were important in univariate models for weight and ultrasonically-scanned traits, and generally a model that included direct additive effect, additive maternal genetic effect, maternal permanent environmental effect and maternal temporary environmental effect was found to be the most appropriate. Direct heritabilities (h^2) for eight-week weight (EWW), scan weight (SW), ultrasonically-scanned muscle (MD), ultrasonically-scanned fat depth (FD), litter size born (LSB), litter size reared (LSR) and total litter weight at eight-weeks (LW) were 0.18, 0.25, 0.24, 0.21, 0.13, 0.09, and 0.11 respectively in the Welsh Mountain, and 0.09, 0.18, 0.19, 0.20, 0.13, 0.08, and 0.10 respectively in the Beulah Speckled Face. Direct heritability for mature weight (MW) was 0.52 in the Welsh Mountain. All genetic correlations between weight and ultrasonically-scanned traits were positive. Genetic correlations among weight traits were high in both breeds. Genetic correlations between litter traits and other (weight and ultrasonic) traits were positive in all but one case. LSB was strongly correlated with LSR but both were negatively or weakly correlated with LW. Cytoplasmic factors as a source of inheritance in weight and ultrasonically-scanned traits was investigated in the Welsh Mountain breed. No effect of cytoplasmic inheritance was apparent for EWW and MD, and the effect was generally non-significant for SW and FD. Scrapie genotype data from one Welsh Mountain flock were examined. Ten genotypes, four alleles (ARH, ARQ, ARR, and VRQ) covering all five NSP risk categories were present. There was little evidence of association between PrP genotypes and EWW, SW, MD and FD, and the selection of ARR homozygous did not appear detrimental to breeding progress in these traits.

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A General Introduction to the Thesis

The advantage of sheep in agricultural systems is their ability to utilise pasture to produce meat and wool products. They are particularly important in situations such as in hill and upland areas, where vast tracts of land have little value for other agricultural purposes.

Plate 1.1 Two yearling Welsh Mountain ewes on Y Garn

Hill breeds (Plate 1.1) are adapted to survive the most extreme climatic conditions and the poorest-quality grazing land of the UK. Despite the unfavourable conditions in which they live, these breeds of the hill sector represent an important component of the UK sheep industry, as the largest producers of breeding ewes and the second most important contributors to lamb carcass production.

Sheep production in the UK has been largely influenced by policies of both the UK government and European Union (EU). Financial support in the form of subsidies can account for a large proportion of a sheep farmer's income. Early subsidies were introduced to address the strategic need for food security. For instance, the 1946 Hill Farming Act was introduced with the purpose of promoting rehabilitation of farming land. Grants were provided for capital improvements of hill, mountain and heath together with payments for hill sheep and cattle were made. The EU Common Agricultural Policy (CAP) was

introduced in 1962 and applied to the UK after it entered the EU in 1973. Initially, subsidies were paid solely for hardy hill breeds, but from 1980 all breeding ewes of all sectors received the Sheep Annual Premium (SAP). Farms in locations classified as Less Favoured Areas (LFA) also received the Hill Livestock Compulsory Allowance (HLCA) or Tir Mynydd in Wales. However, in more recent CAP reforms, such as Agenda 2000, policy has shifted from production support to environmental and rural economy measures. The 2003 CAP Reform agreed that a single farm payment (instead of various production-related subsidies) would be paid from 2005. In Wales, the single farm payment is calculated based upon previous subsidy claims, and farmers receive Tir Mynydd payments (HLCA) based upon the stock they keep. Cross-compliance standards need to be met by farmers to receive the subsidies; these include Statutory Management Requirements (SMR) and maintenance of their land in Good Agricultural and Environmental Condition (GAEC). Payments for Tir Gofal (whole farm scheme), Organic Farming Scheme, ESA (Environmentally Sensitive Area) and other agri-environmental schemes are to continue and a new farm scheme, Tir Cynnal introduced in January 2006.

Genetic improvement within animal breeds is achieved mainly through detailed recording of pedigrees and objectively-measured traits, allowing breeders to select superior animals for breeding. In dairy cattle and pig production this is very much a routine procedure in management to select for breeding replacements. In the UK, the Meat Livestock Commission (MLC) first initiated performance recording schemes in the 1970s, which are now operated by Signet. A range of traits are measured in lambs, including eight-week weight, 20-21 week weight, and ultrasonically-scanned muscle and fat depths. Traits of interest with their relative economic values are combined into a selection index and animals are ranked by index, so that animals with the higher indexes can be identified for breeding. Breeding objectives differ between sectors, breeds and systems; therefore, selection indices ideally need to be developed specifically for each. In the UK, there have been selection indices developed for hill, longwool and terminal sire sheep breeds.

Group breeding schemes and Sire Referencing Schemes (SRS) benefit more from recording than flocks of individual farmers. Until recently, lowland flocks of terminal sire breeds were most likely to take advantage of recording and the use of indices. However, uptake has substantially increased in sectors where there has been additional EU funding, for subsidising the cost of sheep recording and the introduction of selective breeding programmes. For instance, the Welsh Sheep Strategy (WSS), started in 1995 by the MLC and the Development Board of Rural Wales (DBRW), was initiated with the aim of improving the financial viability of hill sheep producers by improving the quality of their lambs in line with specifications of the market. The Welsh Sheep Strategy encouraged the use of advanced recording and reproductive technologies amongst sheep farmers, who were generally reluctant to adopt formalised recording schemes. The schemes used by the Welsh Sheep Strategy were based on those available through Signet and utilised available technologies, such as the ultrasonic scanning now used by the majority of top hill ram breeders, to place emphasis on the improvement of carcass quality.

Maternal effects on commercially-important traits are well documented, particularly in the case of sheep where lambs are dependent on their mother's milk supply until very close to marketing, or at least until they have achieved a high proportion of their slaughter weight (Bradford, 1972). Maternal influences have been examined in detail for twelve-week weight of Welsh Mountain lambs (Saatci *et al*, 1999), but, the implications of these effects have not been examined in the context of selection indices.

Presently there is considerable interest, fuelled by UK/EU eradication policies, in selecting for resistance to scrapie. Whilst there has been extensive genotyping for this disease, through various iniatives of the Welsh Sheep Strategy under the direction of the National Scrapie Plan (NSP), little emphasis has been placed on incorporating scrapie resistance into selection indices. Since the start of this study a Defra-funded project has also commenced to assess the implications of breeding for scrapie resistance for economically-important production and health traits, as well as developing models to determine breeding strategies for the NSP to help minimise the loss of genetic variability (DEFRA, 2003b).

If breeding programmes are to be successful, then they require well-researched indices that farmers can use with confidence and that reflect changes in knowledge about maternal effects, as well as developments in software to evaluate maternal effects and changes in the economic circumstances that affect flock profitability. These include changes in support mechanisms, eradication of diseases and agri-environment schemes.

Selection indices developed for hill breeds include Hill Index 2 and the Welsh Index. The Welsh Index constructed specifically for Welsh hill flocks (Roden, 1999) is also used for other hill breeds, however, development of which relied on literature estimates of genetic parameters, some of which, particularly for carcass traits, were based on comparatively small datasets (Saatci, 1998). The primary aim of the research work is to yield estimates of genetic parameters for economically important traits, which can then be employed in the contruction of a selection index.

1.1 Objectives of the Research

The main research aims are as follows.

1. To assess the importance of random effects, in addition to additive direct effect of the animal, in univariate models for analysing data on economically important traits. These effects include maternal additive effect, maternal permanent environmental effect, maternal temporary environmental effect, permanent environmental effect of the animal and cytoplasmic effects. Estimates of genetic parameters will be obtained from appropriate model choices.
2. To obtain genetic, environmental and phenotypic covariances and correlations between all possible pairwise combinations of the traits from bivariate analysis.
3. Analysis of scrapie genotype data to estimate allele frequencies and the consequences of selecting for resistance to scrapie.
4. To use the results of univariate and bivariate analysis to construct a selection index.

1.2 An Outline of the Thesis

Following a general introduction (Chapter 1) the thesis is divided into 11 chapters, starting with a review of literature. This chapter introduces the relevant aspects of hill sheep production systems, animal breeding theory, breeding value estimation, selection schemes and objectives, economic values and construction of selection indices. The general view is supplemented in each chapter by a more detailed review related to each chapter topic. Chapter 3 describes the sheep breeding schemes that are employed in the analyses, and general aspects of methodology. Individual chapters go into further detail of methodology.

Chapters 4 and 5 describe the use of data from the CAMDA flock to determine the procedures to be performed in later stages of the work, described in subsequent chapters. Chapter 4 investigates the need for data editing in the file types obtained from the MLC. Chapter 5 evaluates models for univariate analysis of weight and ultrasonically-scanned traits.

Chapters 6 and 7 describe use of the procedures developed in Chapters 4 and 5, for analysing data from three Welsh Mountain breeding groups and the Beulah Sire Referencing Scheme. Separate datasets of the two breeds, both for weight and ultrasonically-scanned traits, were analysed and estimates of variance components and heritabilities were obtained. In Chapter 8 use of the same datasets to determine variance components and heritabilities for litter size born, litter size reared, total litter weight, and mature weight is described. Permanent environmental effect of the animal is also investigated for the first three traits and maternal effects for mature weight.

Chapter 9 examines the estimation of genetic, residual, and phenotypic covariances and correlations between all possible pairwise combinations of the above eight traits. Models chosen for bivariate analysis are based upon the model found to be the most appropriate for univariate analysis of each trait.

An additional possible maternal effect is examined in chapter 10. The significance of cytoplasmic inheritance is examined for weight and ultrasonically-scanned traits using the Welsh Mountain dataset.

Chapter 11 uses available scrapie genotype data for the CAMDA flock. Allele and genotype frequencies are reported and the associations between PrP genotype and both weight and ultrasonically-scanned traits are examined. The implications of the National Scrapie Plan are discussed.

The final chapter includes a general discussion of results from all previous experimental chapters. Conclusions are drawn and areas for further work identified. The effect of combining estimated genetic parameters from previous chapters with relative economic weights into a selection index are investigated. Lastly, appendices providing further detail of the work described in the different chapters are given.

A Review of Literature

2.1 AN OVERVIEW OF SHEEP PRODUCTION

In the world there are over 1,000 million sheep, and over eight billion tonnes of lamb and mutton were produced in 2005 (FAO, 2006). Domesticated sheep, *Ovis aries*, are classified as a member of the family Bovidae and of the order Artiodactyla.

Phylogeny		Genus Ovis
Kingdom:	Animalia	*Ovis aries* (domesticated)
Phylum:	Chordata	*Ovis ammon* (argali)
Subphylum:	Vertebrata	*Ovis canadensis* (bighorn sheep)
Class:	Mammalia	*Ovis montana dalli* (thinhorn sheep)
Order:	Artiodactyla	*Ovis musimon* (European mouflon)
Suborder:	Ruminantia	*Ovis nivicola* (snow sheep)
Family:	Bovidae	*Ovis orientalis* (Asian mouflon)
Subfamily:	Caprinae	*Ovis polii* †
Genus:	*Ovis*	*Ovis vignei* (urial)
Species:	***Ovis aries***	† considered variety of argali

Sheep were one of the first animals to be domesticated and domestication is thought to have occurred 9000-11000 years ago in South-western Asia (Bruford *et al*, 2003; Maijala, 1997). Since then, sheep have been a source of meat, wool, milk and hides. The taxonomy of the genus *Ovis* is contentious, and several wild sheep species or subspecies have been proposed as ancestors of domestic sheep, or as contributors to specific breeds. As all 'species' appear to be able to interbreed it could be argued that they are races of the same species (Franklin, 1997). As domestication first took place in the urial area, where *Ovis urial* occurs, this species was thought to be the main ancestor of domesticated sheep. The mouflon (*Ovis orientalis*) was thought to have contributed to European breeds and the argali (*Ovis ammon*). However, analysis of chromosome number suggests that domesticated breeds arose from the Asian mouflon (*Ovis orientalis*), or a hybridisation of the Asian mouflon with possibly another wild type (Maijala, 1997). This suggestion concurs with results of mitochondrial DNA analysis (Hiendleder *et al*, 2002; Hiendleder *et al*, 1998).

Sheep are widespread throughout the world in both developed and developing countries, and survive in a wide range of environmental conditions ranging from temperate mountain forests to desert habitats, common in areas of high ground and semi-arid parts of the world. The main sheep producing countries are China (over 170 million animals), Australia (106 million), India (62.5 million), Iran (54 million), Sudan (48 million), New Zealand (40 million), and the UK (over 35 million) (FAO, 2006).

2.1.1 Breeds of sheep

Domestication was followed by the creation of many breeds as a result of selection for different traits. There are 800-1000 domesticated sheep breeds in the world (Franklin, 1997). Maijala (1997) listed the features that define a breed of animal. A breed can be described as a homogeneous group of livestock with definable and identifiable external characteristics that allow it to be separated visually from other groups within the same species. Breeds have been developed as a result of geographical and cultural differences and to meet human food and agricultural requirements. In the UK the main development of sheep breeds took place in the eighteenth and nineteenth centuries. The plethora of breeds in the UK partly reflects the many invasions during UK history. Sheep first reached Britain around 3000 BC when Neolithic settlers crossed the English Channel (Ryder, 1964). These sheep were small-bodied, horned, had hairy fleeces, and closely resembled the present-day breeds of Soay and St. Kilda. Movements into Europe of white-faced horned and non-horned sheep from the east and south-east of the Mediterranean occurred during the time of the Roman Empire, following the movements of occupying armies. Danish invaders brought black-faced, horned sheep formerly from the Baltic regions into eastern Britain by 1000 AD. The Vikings followed, bringing sheep from northern and eastern France. In the thirteenth century wool production was a major source of wealth and income in Britain, which had gained a reputation for the most and finest wool; thus efforts to improve wool quality were initiated and the finer wool sheep of Spain were imported up until the sixteenth century. By the seventeenth century, interbreeding of imported sheep and indigenous British sheep produced two main groups, the white-faced and black-faced. The Herdwick breed remained distinct.

The eighteenth century witnessed rapid development of different breeds within the two groups and these became genetically fixed (Hannam, 1995). The developments of different breeds have resulted in differences in the expression of traits and in their management (Goddard *et al*, 2006).

2.1.2 Sheep farming systems in the UK

The total agricultural area in the UK is 18.55 million hectares and is split into the western grasslands, hill and uplands and the eastern arable, grass crop and horticultural lowlands. Generally dairy cattle and lowland sheep are found on the western grasslands, whereas upland and hill sheep, suckler beef cattle and farmed deer are concentrated in the western hills and uplands. In the East, intensive beef, pig, and poultry systems predominate, associated with arable production (DEFRA, 2002).

The Domesday survey of 1086 revealed that at that time in England the majority of livestock were sheep and their main purpose was to provide milk; in order of worth wool, manure, and meat were by-products (Ryder, 1964). In the fourteenth century it was common for wether lambs to be retained for wool production and ewes were expected to rear one lamb a year merely to replenish numbers. However, in the 1750s a law prohibited the export of wool resulted in falling prices, and farmers turned to mutton production instead. By the 1770s sheep were being genetically improved, flushed before mating to produce twin lambs, and fed on clover and winter crops; meat quality improved but wool quality declined.

Presently in the UK, meat production in the form of lean 15-22 kg carcasses is the primary objective of the sheep industry. The UK is the largest producer of sheep meat in Europe and one of the largest specialised sheep meat producers in the world, with a breeding flock of about 15.2 million ewes in 2003 (Pollott, 2006). Of the sheep meat produced, 66 % supplies the domestic market and 34 % is exported; 34 % is also imported due to the seasonal nature of lamb production. Much less emphasis is placed on milk or wool production (Maniatis and Pollott, 1998). There are approximately 200 flocks of dairy sheep, totalling

12,000 ewes (SAC, 2006). Globally wool prices are poor and the market for sheep skins can be volatile; it shrank dramatically after the collapse of the Russian economy in the late 1990s, falling from as high as £11 per skin to zero (EBLEX, 2005). Since concerns over BSE, UK regulations for removing Specified Risk Materials (SRM) from slaughter sheep have caused increased abattoir costs, and reduced the value of cull ewes.

The UK sheep industry is particularly varied and has a uniquely stratified structure, with many breeds and crosses suited to the many different systems and environments, which developed after the First World War period (Croston and Pollott, 1985) following the introduction of the Hill Farming Act in 1946. The industry is characterised by considerable movement of breeding sheep between farms. The core commercial ewe and lamb populations are crosses between various breeds. Stratification is said to have both advantages and disadvantages. Advantages include optimum use of national grazing resources from employing different breeds in different areas according to their particular strengths, as well as exploiting hybrid vigour. The crossing of hill breeds utilizes breeding stock that are produced quite cheaply on the hills and the process of crossing changes the performance characteristics, providing a cross-bred ewe that is more suitable for better conditions (King, 1979). Hill breeds are hardy and have good mothering ability. The longwool breeds are prolific and are good milkers. The Down breeds give good conformation, quick growth rate and quality meat. The stratified structure also enables breeders to concentrate on a limited number of objectives and to use the most suitable farming system for their land. However, it has also been argued that too many breeds make up the national flock and that improvements could be more easily made if efforts were concentrated on just a few key breeds (McGuirk, 2000). The diversity of breeds in the UK, the different conditions in which they live and the different objectives of sheep farming make selection and breeding complicated.

There are about 90 pure breeds, nine-half breeds and many crossbred types recognised in the UK (Pollott, 2006). However, most breeds are confined locally and comprise few individuals with only a small number of breeds that make a significant contribution on the total slaughter generation (MLC, 1994). Breeds

tend to be categorised as hill, longwool crossing, terminal sire, longwool ewe, or shortwool ewe breeds (Pollott, 1998). Breeds with the largest ewe populations are hill breeds: the Scottish Blackface, Welsh Mountain, Swaledale, Beulah Speckled Face and North Country Cheviot. Crossbreds have become a major influence and now comprise 50 % of the national flock; the North Country Mule (Blue Faced Leicester * Swaledale) is the most abundant, with about two million ewes mated anually. Rams are dominated by the terminal sire breeds Texel (24.4 % of the total), Suffolk (22.8 %), Charollais (7.5 %) and Bluefaced Leicester (7.5 %), followed by the three main hill breeds (Pollott, 2006). All these breed types make important contributions to the genetic make-up of slaughter lambs; of these come from 47 % terminal sire, 27 % hill, 15 % longwool crossing, 8 % shortwool, and 4 % from longwool ewe breeds (Pollott, 2006).

Choice of breeds and crossbred groups generally depends on farm altitude and pasture quality, which can be used to define three systems: lowlands under 240 m, uplands 240-300 m and hill > 300 m (Speedy, 1982), as shown in Figure 2.1.

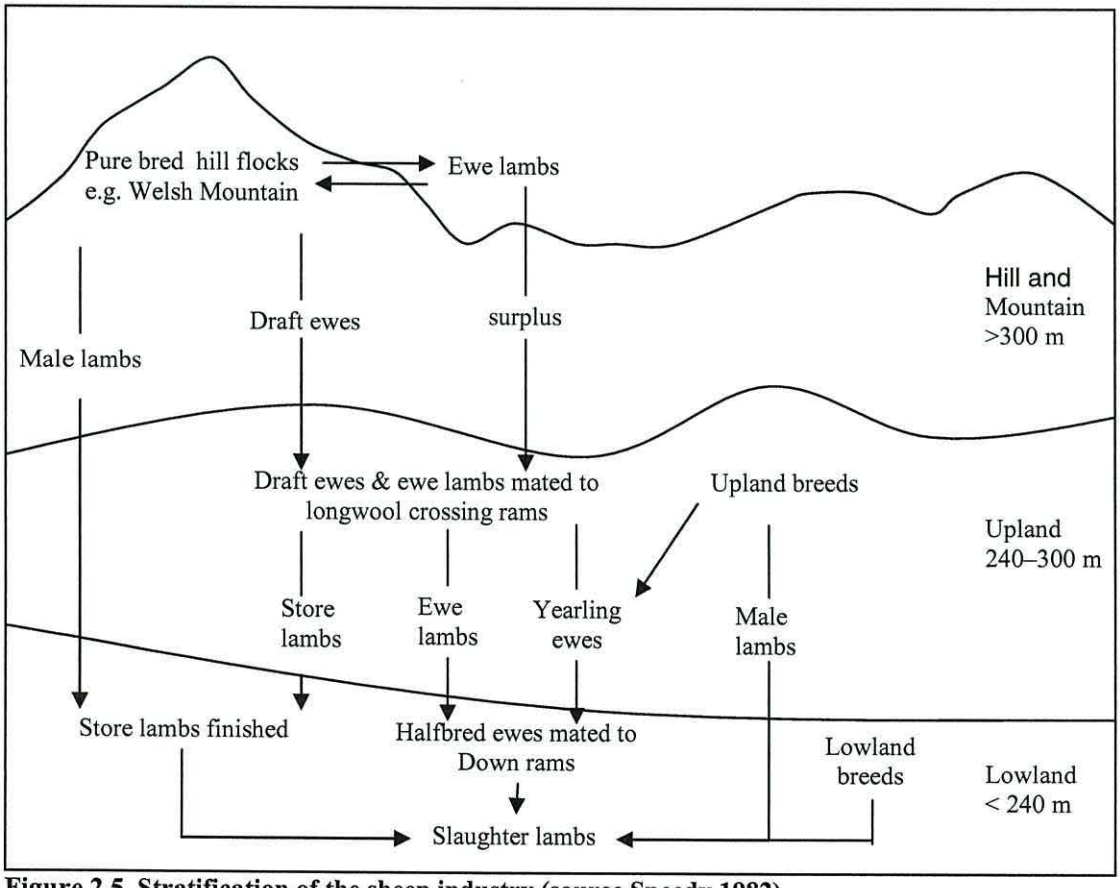


Figure 2.5 Stratification of the sheep industry (source Speedy 1982)

Older, draft ewes from the hills are commonly transferred to more favourable conditions of the uplands after four or five lamb crops. The ewes are crossed with longwool rams, commonly the Blue-faced Leicester or Border Leicester. Longwool upland breeds, such as the Border Leicester, Blue-faced Leicester, Wensleydale and Teeswater, are larger than the hill breeds and are generally kept in small flocks. They are highly prolific and capable of rearing two lambs a year. Draft hill ewes mated with longwool sires give rise to progeny (F1) and generate dam lines of animals that are larger than the hill breed and highly prolific. The halfbred females resulting from these matings are then sold to lowland farmers. These halfbreds form the core of the commercial sheep industry, producing the largest proportion of total sheep meat in the UK. They are mated to terminal sire breeds such as Down breeds (e.g. Suffolk) and European imported breeds (e.g. Charollais and Texel) that are specialised meat breeds to produce the slaughter generation of lambs that meet the quality requirements of the market (HCC, 2004d; Johnston, 1983; Speedy, 1982). Terminal sire breeds account for a small percentage of the breeding ewe flock, but rams from the terminal sire breeds sire 71 % of all lambs slaughtered in Britain (Pollott, 2006).

2.1.3 Hill farming and the contribution of hill sheep breeds

In many remote areas sheep production in the UK is the only feasible form of livestock production due to the severity of the environment; in other areas, sheep integrate resourcefully in mixed farming systems, sometimes utilising arable by-products. Less Favoured Areas (LFA) account for 53 % of UK farmland and the sheep industry is found predominantly in these areas (DEFRA, 2001a). The first stage of the stratified system shown in Figure 2.1 is based upon hill farming. Hill farms have a relatively high proportion of rough grazing and may suffer from low temperatures, high rainfall, acidic soil, impeded drainage and steep terrain. In the UK about a third of the total agricultural land area is classified as rough grazing. There is a distinctive geographical distribution of hill sheep breeds across hill regions in the UK due to the variable local environments and adaptation of breeds to the environment over years of selective breeding.

The main hill breeds, the Scottish Blackface, Welsh Mountain and Swaledale have estimated numbers of 1.7 million, 1.6 million and 1 million ewes respectively (Pollott, 2006). Despite the poorer performance of sheep on the hills than on lowland farms, sheep production remains a major enterprise in these less fertile areas. These hill breeds are adapted to survive the extreme climatic conditions and the poorest quality grazing of the high elevation areas of Wales, England and Scotland. The hill breeds are generally farmed in large flocks, kept pure and breed their own replacements. They are generally smaller in size than lowland breeds, and hence have smaller maintenance requirements and lower feed intake, they are not very prolific due to the conditions in which they live, but may produce twins on bye land (improved pasture). Hill breeds account for about 40 % of breeding ewes and are considered to be the most important sector for producing breeding ewes, pure or crossbred, contributing proportionately 48 % of the genes of all breeding ewes in the UK (Conington *et al*, 1995; Pollott, 2006).

Considering the large number of hill ewes, they contribute relatively little directly to lamb production, due to the low productivity of the hill areas and the need to retain a high proportion of ewe lambs as breeding stock (King, 1979). However, after terminal sire breeds, hill breeds are the second most important contributors to lamb carcass production. Much of the total supply of lamb is sourced directly or as a component of lowland crossbred ewes.

2.1.4 Sheep farming in Wales and Welsh Mountain sheep

Sheep farming is a major land use in Wales. In 2005 there were over 15,000 holdings that kept sheep totalling 4.7 million breeding ewes, and a total population of 9.5 million animals (National Assembly for Wales, 2005a; National Assembly for Wales, 2005b). The climate of Wales, particularly in the mountain areas, is characterised by heavy rainfall and cold winds, and these conditions mean that there is little agricultural alternative to the rearing of sheep. Eighty percent of agricultural land is designated as a Less Favoured Area, and it carries 87 % of all breeding ewes in Wales (DEFRA, 2001a; DEFRA, 2001b).

A survey in 2001 found that 63 % of the Welsh flock was pure bred, of which the main breeds were Welsh Mountain (62 %) and Speckled Face (27 %) (HCC, 2004d). Welsh Mountain is a collective name covering several breeds associated with the Welsh highlands. The original type was the now-extinct tan-faced Rhiw and Card sheep, which had resulted from the interbreeding of the Roman white-faced sheep and the Soay (Ryder, 1964). Several closely-related breeds within the Welsh Mountain group emerged from this intercrossing (Alderson, 1978; Williams-Davies, 1981): the Hardy Welsh, Improved Welsh (or Aberwystwyth), South Wales Mountain (or Nelson), Black Welsh Mountain, and Badger-faced sheep (or Defaid Torddu). The Hardy Welsh is confined to North Wales, the Improved Welsh (Aberystwyth) variety lacks hardiness but is larger in size and more docile than the Hardy Welsh, whilst the South Wales Mountain is the largest and kept in the southern hills of Glamorgan, Monmouth and Brecon. In the Welsh hills the Welsh Mountain breed represents the main grazing animal and the main source of income. It also contributes to upland and lowland sheep systems though sales of draft ewes and crosses (Saatci *et al*, 1999).

2.1.4.1 History of breeding and selection in Welsh Mountain sheep

In 1880 lowland farmers with hill flocks started improvement programmes by selecting the best hill ewes and mating them to the best lowland rams, and then continued breeding from the best available progeny. These small nucleus flocks placed emphasis on characters such as improved conformation, wool and retention of hardiness, based largely on visual assessment. The first Welsh Mountain flock book was compiled in 1905 to register pedigrees of the foundation animals that performed well under poor mountain conditions. As breeding progressed, however, the pedigree nucleus flocks expanded and became virtually independent. This meant selection took place within the nucleus without the utilisation of native stock from the hill, and without animals being challenged by the hill environment. In 1946 a group of Caernarfonshire hill farmers formed a society for the improvement of Welsh Mountain flocks with particular emphasis on retaining hardiness. In 1958 the society split into two, forming the pedigree and the hill flock societies (Dalton, 1959).

Work from the 1920s to 1950s showed that the most important attributes of the Welsh Mountain were body size, fleece weight, milk yield and hardiness (Doney, 1958). The Welsh Mountain was developed to survive harsh hill environments, and during selection emphasis has been placed upon hardiness, mothering ability and lamb survival. The average mature ewe bodyweight is between 35 and 48 kg, and rams weigh between 45 and 80 kg. The ewes are not prolific, averaging 1.13 lambs per ewe (Saatci, 1998; Speedy, 1982). Purebred lambs achieve carcass weights of 12-16 kg (NSA, 1982). A characteristic of the breed is the ability of the ewe to provide a heavy flow of milk to the lamb off poor pastures. The sale of draft ewes a common feature, with 400,000 drafted each year. Draft ewes are crossed, usually with a Border Leicester ram, producing the Welsh half-breds that are then employed in lowland flocks.

2.2 Animal Breeding Theory

Ollivier (1999) defined animal breeding as the optimal exploitation of the species' biological variation, under constraints of reproductive capacity, using appropriate breed estimation tools. Genetic improvement of livestock is an effective, sustainable and cost-effective means of enhancing the efficiency and quality of livestock systems (Haley, 2000), and genetic technologies range from simple to sophisticated (Bishop, 2004). Genetic improvement through selective breeding is permanent, and although the annual rate may be slow it is a cumulative method of altering performance of farmed livestock, because once changes are achieved no further contribution is required for their maintenance and further genetic improvements can be built on those made previously (Piper, 1989; Simm, 2000). Genetic improvement has brought about both farming efficiency and better quality products, for instance leaner meat with less fat. There are two types of selection in animal breeding, natural and artificial. Artificial selection or selective breeding is defined as any act that restricts the random mating of individuals in a population. Animal breeding is generally viewed as simply choosing the best individuals to act as parents of the next generation. Thus, selective breeding is seen to be acceptable by the consumer as it merely means choosing the best of the naturally-occurring animals as parents, and possibly culling the worst. This results in a shift in the allele frequencies and

with continued selection eventual fixation of the desirable allele at a locus would occur.

2.2.1 History of animal breeding

Emphasis on selective breeding increased in the eighteenth century due to an increase in the human population and a greater demand for milk and meat production. At that time selection was done visually, by choosing the 'best' animals to be parents of the next generation.

Robert Bakewell (1725 to 1795), sometimes referred as the founder of animal breeding, is generally given credit for setting the pattern of modern animal breeding. An important element in his procedure was the deliberate and intense use of inbreeding, achieved by the mating of closely-related animals. To assist selection decisions he also measured and recorded the performance of his stock of Old Longhorn cattle, Leicester sheep and shire horses. The work of Charles Darwin and Gregor Mendel in the nineteenth century made further foundations for the development of animal breeding. Additional scientific advances of the twentieth century in genetics, statistics and reproductive biology have further aided understanding of selective breeding processes. Great progress has been achieved in identifying genetically-elite animals through the phenotype (performance and physical characteristics) and of their relatives, particularly their offspring. Better understanding of the genome and technological advances are providing further possibilities for direct identification and selection of animals with the best genes, and future selection may increasingly be based upon genotype (Haley and Visscher, 1999).

2.2.2 Quantitative genetics theory and definitions of terms

The genome holds all the genetic information about an organism and consists of base pairs of DNA containing genes that represent the blueprint for the organism. The performance of an animal is determined by the blueprint defined in the genes inherited from parents, together with environmental factors. A diploid animal (such as a sheep) inherits two copies of each gene, one from each parent (apart from those on the sex chromosome). These two copies may differ in their DNA

sequence (i.e. be different alleles). Some differences have no effect on phenotype, but when alternative alleles do cause different proteins to be produced or control alternative expression of genes, this may cause variation in performance between animals (Haley and Visscher, 1999).

2.2.2.1 Quantitative and qualitative traits

The application of quantitative genetics theory to animal breeding has had a substantial influence. A number of the most important traits in domesticated livestock are quantitative, so that they vary between individuals in a continuous way. Quantitative traits are typically those that are measured rather than scored and variation is usually affected by many genes rather than single genes. These traits may also be influenced by non-genetic factors in the environment. Examples of influencing environmental factors include the management of the animal, standard of feeding or housing, maternal care, geographical factors such as climate and chance influences such as exposure to disease (Simm, 2000).

Qualitative characteristics or traits are those that can be scored, and for which animals can be divided into discrete types with no intermediates. They are generally under total control of a single gene and are less affected by non-genetic factors.

2.2.2.2 Partitioning variation

The phenotype *(P)* is the observed and measured performance of an animal and depends upon the genotype *(G)*, the assemblage of genes inherited from parents and the environment *(E)*, which include all the non-genetic influences it receives. The calculation, in its simplest form is: -

Equation 2.1

$$P = G + E$$

Genotype (G) can be further split into components: -

Equation 2.2

$$G = A + NA$$

or

Equation 2.3

$$G = A + D + I$$

The additive effect *(A)* is the combined effect of all genes that act additively on the trait of interest. The non-additive *(NA)* component is due to dominance and epistasis. Dominance *(D)* deviations are due to interactions between alleles at the same locus. Epistatic effects *(I)* are due to the interactions between alleles at different loci. Direct additive genetic effects are of most interest to animal breeders as they are stable and passed from one generation to the next, and the main cause for resemblance between relatives.

Environmental effects can be divided into permanent environmental effects (also known as general environmental effects) and maternal temporary environmental effects (also known as common environmental effects).

In mammals, there are frequently maternal effects on offspring, both pre-natal and post-natal. These are mainly nutritional effects; however, behaviour of the mother towards the offspring may contribute to environmental variance. Maternal effects can be further assigned to causes due to maternal genotype, maternal permanent environment or maternal temporary environment effects. For example, maternal permanent environmental effects are those effects experienced by offspring of the dam from different parities, and maternal temporary environmental effects are those effects experienced by members of the same litter growing from conception to weaning in a common environment. Age of the mother and the parity are also factors that could contribute to variation among offspring.

Measurement errors are also sources of variation and are a potential problem for traits that are difficult to measure, requiring subjective judgement such as classifying observations into groups. The amount of variation in a population is expressed as the variance, and in the study of variation it is generally partitioned into its components, attributed to different causes (Falconer and Mackay, 1996). R.A. Fisher was the first to partition genetic variance into its components (additive, dominance, and epistatic), and to distinguish between genetic and environmental variances (Ollivier, 1999). Phenotypic variance (V_P) can be partitioned into genotypic variance (V_G), additive variance (V_A), dominance

variance *(V_D)*, interaction variance *(V_I)* and environmental variance *(V_E)*. The last three types are also grouped as non-additive variance *(V_{NA})*.

Sometimes correlations are observed between genotype and environment. Then, the calculation for phenotypic variance is:

Equation 2.4

$$V_P = V_G + V_E + 2cov_{GE}$$

When an interaction between genotypes and environment is present, an interaction component *(V_{GE})* is added to the previous calculation, as shown:

Equation 2.5

$$V_P = V_G + V_E + 2cov_{GE} + V_{GE}$$

2.2.2.3 Heritability

Koch and Clark (1955) defined heritability (h^2) as the proportion represented by the direct additive genetic variance *(V_A)* of the total phenotypic variance *(V_P)*.

Equation 2.6

$$h^2 = \frac{V_A}{V_P}$$

Knowledge of the heritability of a trait is very important in genetic improvement programmes as it indicates whether selection will lead to genetic gains, and at what rate. Falconer and Mackay (1996) describe two types of heritability, termed 'broad sense' and 'narrow sense'. The first expresses the extent to which phenotypes are determined by genotypes, whilst the latter, more valuable in animal breeding, expresses the extent to which phenotypes are determined by genes transmitted from the parents. Equation 2.6, above, is for the calculation of narrow sense heritability.

Heritability is expressed on a scale of 0 - 1. Three groupings have been identified to describe heritability: low (0.0 - 0.1), medium (0.1 - 0.3) and high (0.3 – 1.0) (Willis, 1998). A low heritability means that phenotypic values are less useful for establishing the genetic (breeding) values of animals in order to select those that would make the best parents. As a result, genetic change will be slow. When traits have low heritability, a producer may improve animal performance through management rather than genetically through selection

(Bourdon, 1997). However, when heritability values are high an animal's performance is a good guide of genetic (breeding) value, and genetic gains should be high.

To estimate variance components and heritabilities large datasets containing accurate pedigrees and details of the traits of interest are required.

2.2.2.4 Repeatability

Repeatability *(R)*, expressed as a value in the range 0 - 1, refers to the correlation between repeated records of the same trait in the same individual, and provides an indication of how an animal will perform, in a particular trait, over a lifetime. Traits such as birth weight and weaning weight that only occur once in an animal's lifetime are repeatable when considered as a characteristic of the dam. Repeatability is calculated as: -

Equation 2.7

$$R = \frac{V_A + V_{PEA}}{V_P}$$

where V_{PEA} is the permanent environmental variance of the animal

When repeatability values are high, a single record of performance from an animal should be a good indicator of the animal's overall producing ability, and this is particularly valuable when selection decisions need to be taken early in life.

Heritability is lower than or, very rarely, equal to, but never higher than the repeatability. Repeated measurements reduce the influence of environmental effects and increase the estimate of direct additive genetic variance, thus increasing the accuracy and value of the heritability of the trait and providing a better prediction of genetic (breeding) value (Falconer and Mackay, 1996). The different measurements should have equal variances and represent the same character genetically.

2.2.3 Breeding value estimation

Detection and best use of genetically superior animals has for a long time played a key role in livestock breeding schemes and will continue to do so in future. In the past, intuition of the breeder mainly determined what type of animal chosen, based on the phenotype of individual animals or their ancestors. In most current programmes of genetic improvement this approach has been replaced by estimation of breeding values. Estimated breeding value (EBV) is the predicted value of an animal as a parent and is calculated as the phenotypic deviation of the animal from the average of a population of other potential parents or contemporaries, multiplied by the heritability of the trait concerned (Simm, 2000). Estimated breeding values are ranked and allow the identification and selection of potential parents with the greatest likelihood of producing superior offspring, so increasing average production from the present generation to the next.

The breeding value of an individual can only be determined if individuals are compared with others treated in a similar way at the same time, for example, if they were born over the same time period, and fed and managed in the same way, on the same farm. Similar individuals are called contemporaries and form contemporary groups.

2.2.3.1 Adjustment of values

In breeding programmes the aim is to separate the effects of genes and environment so that selection for animals with high genetic merit is done fairly. Phenotypic values are adjusted by the estimated average effect of an environmental factor in a contemporary group. Such factors could include dam age, birth type or rearing type, lactation number, birth date, age at measurement and presence of sub-clinical disease. Adjusting records of performance may be done by using additive or multiplicative correction factors. Additionally, animals available for selection are not always from the same farm, but live in different environments and over different years. This is where Sire Referencing Schemes (SRS) and the use of statistical procedures, such as Best Linear Unbiased

Prediction (BLUP), can assist the calculation of EBVs. These are described in further detail in sections 2.2.3.2 and 2.4.2.2. Failure to adjust performance records for environmental effects can result in less accurate estimation of EBVs and a decrease in the rate of annual improvement.

2.2.3.2 Best Linear Unbiased Prediction (BLUP)

The theory underlying BLUP was proposed first in 1949, but it was not widely applied to livestock breeding, until some 20-30 years later when computer technology became available (Henderson and Quass, 1976). BLUP is a statistical technique based upon mixed models and produces accurate breeding values by disentangling genetic from environmental effects, such as dam age, birth or rearing type. BLUP also identifies related animals from different contemporary groups and is able to generate genetic links between them. The main BLUP models are sire models, sire-maternal models and individual animal models (Simm, 2000).

2.2.3.3 Sources for estimating breeding values

Breeding values are only estimates, but the more information that they are based upon the more accurate they are likely to be. Pedigree records with information on animals and their relatives are utilised to predict breeding values. The simplest EBV, based solely on individual performance, is calculated as:

Equation 2.8

$$EBV = h^2 * (measured\ performance - flock\ mean - environmental\ effects)$$

Repeated records from the same animal improve the accuracy of EBV, and hence increases the response to selection, as does including as much information as possible on the performance of relatives. Records of performance from relatives are more beneficial and relevant when the individual and relative have a higher proportion of genes in common; progeny records are the most valuable. As the number of records obtained increases, predicted and true breeding value become more closely correlated (Simm, 2000).

2.3 SELECTION SCHEMES AND OBJECTIVES

Sheep are farmed for meat, fibre and to a lesser extent milk, in a wide range of environments throughout the world. Some production systems, such as those in Europe for sheep meat production, use high inputs, whilst other systems such as those in less developed arid zone countries have very low inputs. Selection decisions can be made at three levels; between species, breed choice within species and within-breed selection. Decisions depend upon the objectives of the production system and could be made for economic, aesthetic or sentimental reasons (James, 1986; Ollivier, 1999). Of most interest to animal geneticists is the lowest level of diversity, that occurring within breeds.

2.3.1 Selection between breeds

If the genetic differences between breeds are great, direct substitution of a breed may improve a system significantly and could save generations of selection within a breed (Webb, 1989). The UK industry makes extensive use of cross-breeding, which takes advantage of breed complementarity and heterosis, exploiting differences in maternal and juvenile attributes, as well as environmental adaptations (Bishop, 2004; McGuirk, 2000). Several studies have examined the possibilities of cross-breeding for improving the profitability of sheep in extensive systems (Dawson *et al*, 2004; Elizalde *et al*, 2006; McLean *et al*, 2006).

Breed types chosen for particular systems may change over time as a result of consumer or market demands, new policies, or increasing knowledge of other breeds. In the UK, breed substitution has taken place with the introduction of Continental European breeds, such as the Texel or Charollais as terminal sire breeds, and the replacement of the Border Leicester with the more prolific Bluefaced Leicester as the dominant longwool crossing breed (Haresign and Wolf, 2002; Simm, 2000). The Texel was introduced on to UK farms in 1973 from France and is now very prominent in the industry, as the most numerous ram breed and the largest lowland purebred ewe breed (Pollott, 2006; Texel Sheep Society, 2006). However, breed choice in many sectors is often a matter

of tradition (Haresign and Wolf, 2002). The primary consideration for breed choices should be genotype adaptation to the environment, considering constraints such as disease, so that breeds are suitably matched to particular production systems (Bishop, 2004; Simm *et al*, 1996).

2.3.2 Selection within breeds

Selection within breeds, assisted by suitable breeding scheme design and use of statistical technologies, is widely practised and involves making comparisons of animals of the same breed to produce the next generation (Bishop, 2004). A number of breeding schemes exist in the UK, and breeding goals tend to reflect their place in stratification (Figure 2.1). For instance, in terminal sire breeds emphasis is on improving efficiency of lean growth, whereas in maternal breeds breeding goals include traits affecting female reproductive and rearing ability. Many sheep breeds have a conventional pyramid breeding structure, with a small number of elite pedigree breeders who have the greatest influence on the direction and rate of genetic change. Genetic improvement is transferred by migration of animals to commercial flocks often via at least one multiplier (Webb, 1989). The original motivation for setting up sheep improvement programmes was to provide breeders with a more reliable measure of performance of potential breeding stock (Atkins *et al*, 1986). The initial aim of schemes was to provide the breeder with more precise information than could be obtained from visual assessment of an animal's merit. In the UK, genetic improvement in sheep is based mainly upon on-farm performance and recording. Schemes based on these practices were first initiated in the 1970s after the formation of the Meat and Livestock Commission (MLC) set up under the 1967 Agricultural Act. Since 1995 Signet, a company jointly owned by the MLC and Scottish Agricultural College (SAC), became responsible for delivering breeding evaluations for sheep and cattle. Performance recording first started with weight, recorded at eight weeks and 20-21 weeks. In the 1980s ultrasonic scanning for fat and muscle depths was started. Signet's Sheepbreeder scheme is based upon on-farm recording of pedigree information, litter size, live weights at a range of ages from weaning to breeding, and ultrasonic measurements (Simm, 2000).

Sheep improvement programs are often restricted by the low use of performance recording, relatively small sized-flocks and the lack of across-flock genetic evaluation (Simm *et al*, 2001). There are reasons for the low level of performance recording. The gain from genetic improvement of objective measures may not be as apparent as it is with other farm animals such as dairy cattle. Much additional effort and considerable indirect costs are involved in recording individual ewe and lamb performance, to ensure that accurate records of pedigree and performance are obtained. Recording is mostly done outdoors, which requires added commitment, especially in extreme climates. Schemes were developed to assist to a certain extent in solving these problems, such as the establishment of Group or Cooperative Breeding Schemes and Sire Referencing Schemes (see sections 2.3.2.1 and 2.3.2.2). Terminal sire breeds are more commonly recorded because their single-purpose role means that selection is simpler, and because they are often bred in more favourable locations and kept in smaller flock sizes. In the Signet scheme about 600 flocks participate and about 75 % of these flocks are from terminal sire breeds (Simm, 2000).

2.3.2.1 Group Breeding Schemes

Group Breeding Schemes allow several small-scale breeders to combine into an effective breeding group to promote within-breed improvement (Owen, 1987). They were established first in New Zealand in 1967 by commercial sheep and beef producers, and were also widely used in Australia at that time. CAMDA (acronym for Cymdeithas Amcanu Magu Defaid Amgenach), set up in 1976, is the longest established and the first Group Breeding Scheme in the UK.

2.3.2.2 Sire Referencing Schemes

The MLC set up the first Sire Referencing Scheme (SRS) in 1989 and there are now over 20 schemes for sheep breeds (MLC, 1989; Simm *et al*, 2001). The general aim of SRSs is to increase the rate of genetic improvement in members' flocks, by increasing selection intensity and generation turnover. SRS are similar to Group Breeding Schemes, but instead of central nucleus flocks, genetic links are formed across member flocks by using AI (artificial insemination) rams or shared rams on a portion of ewes in each flock. A group of reference sires are

chosen for use across members' flocks, and these should have high EBVs or index scores. Strong genetic links between related animals in different flocks enables fair comparisons of estimated breeding values across flocks when statistical techniques such as Best Linear Unbiased Prediction (BLUP) are used (Simm *et al*, 2001). This increases the numbers of animals that can be compared, and therefore increases both selection intensity and genetic gain. Recently many more Sire Reference Schemes have been established in Wales, with eight different breeds involved (HCC, 2006a).

2.3.2.3 Marker-assisted and gene-assisted selection

Recent mapping of quantitative trait loci (QTLs) for many economically-important traits in livestock species is thought to have the potential to revolutionise the industry (Georges, 1999; Georges, 2001; Maddox *et al*, 2001). This technology can aid selection procedures and speed up genetic progress as it locates some of the genes conferring merit. Marker-assisted selection is the use of genetic markers which are in close proximity to genes controlling particular traits, and which imply the existence of other genes of interest. Markers are particularly beneficial in selection for traits difficult or expensive to measure (e.g. carcass quality, disease resistance and meat quality traits (van der Waaij *et al*, 2002)), selection of juveniles for traits that are expressed after sexual maturity (Verrier, 2001), sex-linked traits and traits of low heritability (Bishop, 2004; DEFRA, undated; Dekkers, 2004; Haley and Visscher, 1998; Ruane and Colleau, 1995; Steinheuer *et al*, 2003; van der Werf and Kinghorn, 2000). However, there are few examples of this technology being implemented (Dekkers, 2004). Gene-assisted selection is more direct as the gene of interest is known. Examples of direct genetic markers are the halothane gene in pigs (ryanodine receptor gene), the double-muscling gene in cattle (myostatin gene), and resistance to scrapie in sheep (PrP gene) (Band *et al*, 2005; Belt *et al*, 1995; Laplanche *et al*, 1993; McPherron and Lee, 1997).

2.3.3 Selection Objectives and Criteria

2.3.3.1 Breeding Objectives

The objective of most animal breeding programs is to provide a new generation of animals that produce more efficiently under future farm economic and social circumstances than the present generation (Hazel, 1943). The initial step in devising a livestock improvement plan is to define the breeding objective. The breeding objective is a list of traits that need to be improved, including their economic importance ordered by relative economic value. The demand for a product by consumers should define the breeding objective and social factors mainly determine the type of products sought. James (1986) stated that efficiency should be the aim of the breeder, and that improvement of traits would either boost farm income or reduce costs. It was also suggested by James (1986) that all traits of economic importance should be included in the breeding objective, even if they are difficult to measure. The traits must be heritable if selection of parents is to result in improved progeny, and estimates must be made of their relative economic value. Traits such as lamb viability, longevity, disease resistance, and easy-care traits are important factors affecting efficiency (James, 1986) but have had little attention until recently, either because heritabilities are low or because reliable data are not available.

2.3.3.2 Selection criteria

The traits in the breeding objective may be different from those used as selection criteria. Selection criteria are measured characteristics that are correlated with traits of the selection objective; they form the basis of selection decisions and the number of traits may vary. It is important to determine the contribution that the measured criterion has on the trait in the breeding objective. If the correlation between the objective trait and selection criterion is low the response in the trait will be low and will not substantially improve overall genetic merit. Examples of selection criteria are ultrasonic muscle and fat depth of the live animal, which are used to assess the trait of carcass composition.

2.4 CONSTRUCTION OF A SELECTION INDEX

2.4.1 Selection for more than one trait

In some cases a single trait may be of overriding importance, but in most cases many traits will influence an animal's practical value, and do so to varying degrees (Hazel, 1943). All such traits should be considered in breeding programmes (Atkins *et al*, 1986). Numbers of objective and criteria traits included in breeding programmes have increased over recent years. Some traits affect economic merit whilst others improve the accuracy of selection. The drawback of disregarding some traits is that breeding values may be estimated with less accuracy (Van Arendonk *et al*, 1998). The information available for different traits may vary and may be taken from the animal's own performance or from that of relatives. Traits can be selected for individually, using, independent culling levels, but these are inefficient for the selection of many traits at a time and not appropriate for breeding programs that aim to improve several characters at once. This aim is best accomplished by combining traits into an overall score of genetic merit. The method expected to give the most rapid improvement of economic value is the selection index method, which forms the basis for nearly all breeding schemes, for farm animals (Hazel *et al*, 1994; Weller, 2001). Lush and Hazel (Hazel, 1943) devised the principles of index selection and suggested that more emphasis was placed on those traits of greater economic importance.

However, selection indexes have the disadvantage of being highly complex, requiring comprehensive data on both genetic and economic parameters (Willis, 1998). In many practical situations it may be more cost effective for breeders to cull a proportion of their young stock (particularly rams) to eliminate the costs of retaining the animals until the conventional age of selection and reduce measurement costs (Atkins *et al*, 1986; Xu and Muir, 1992).

The net economic improvement that can be made by selecting among a group of animals is the sum of the economic gains made from the traits that are under genetic control. Each trait is weighted by the relative economic value of that trait,

which in turn depends upon the amount of profit that is expected to increase by for each unit of improvement in the particular trait. Estimations of relative economic values could be obtained from long-term price averages and cost of production figures. Economic values may vary from breed to breed or region to region and may change whilst the breeding program is in development (Hazel, 1943). It is essential to anticipate future needs as breeding strategies can take a long time. Economic values are most useful if they are based upon likely conditions in the future, as several generations are necessary for appreciable genetic change. However, because selection indexes can be adapted as circumstances change they are a method of responding to changing objectives gradually.

An index combines genetic parameters for traits of economic importance into a final score, which gives an assessment of an individual. To construct a selection index accurate information on heritability and phenotypic variances of traits, the genetic and phenotypic correlations between traits and their relative economic values is required for traits included in the index. Traits that are commonly included in a selection index often are maternal traits (e.g. mature size, litter size and maternal ability) and growth and carcass traits (e.g. eight week weight and scan weight (20/21 weeks), muscle and fat depth).

Simm and Dingwall (1989) constructed the lean index, widely used in terminal sire breeds, which involved ultrasound measurements of muscle and fat depths, and relative economic values (REV) of muscle and fat depth of +3 and -1, respectively. Van Heelsum *et al.* (2004) developed an index for selecting hill-crossing breeds with aims of improving muscle depth and conformation, by combining EBVs for scan live weight, ultrasound muscle and fat depth, conformation and litter size. Muscle depth and conformation were positively weighted with REVs (relative economic values) of +3 and +2 respectively, while fat was negatively weighted as –1; the index was designed so that litter size remained unaltered. The Hill 2 Index and the Welsh Index are two breeding indexes designed for the hill sector and used by Signet. The purpose of the Hill 2 Index is to improve overall ewe productivity by increasing the number of lambs reared to weaning and enhancing lamb weaning weights, whilst minimising

increases in ewe size. The Welsh Hill Index has a 25 % weighting for maternal traits and 75 % weighting for growth and carcass traits (taken from the lean index), and is designed to improve the mothering ability of breeding ewes, whilst increasing lamb growth rates and carcase values. Conington *et al.* (2001) derived three selection indexes for purebred hill sheep, for intensive, semi-intensive and extensive farming systems. Objective traits included lamb performance, maternal performance, fleece weight, mature size, and longevity.

2.4.2 Traits of interest in selection indices

Due to the diversity of climates, management and production systems under which sheep are kept, a wealth of breeds and strains exist, for which there may be very different breeding objectives (Ponzoni, 1986). It has been suggested that narrow breeding objectives that have particular emphasis on high production and efficiency can lead to undesirable outcomes, such as behavioural, physiological and immunological problems, examples being found particularly in poultry, pigs and dairy cattle (Rauw *et al*, 1998). There is a move towards broader breeding goals that do not solely consider production traits, but include health and welfare traits. Lawrence *et al.* (2004) reported that the inclusion of health and fitness traits into breeding indexes had proven to be more profitable than selecting for production traits alone. Breeding goals are dependent upon environmental constraints, particularly when considering hill breeds in hill environments (Beilharz, 1998; Conington *et al*, 2001). Financial pressures on sheep production are likely to lead to a reduction in labour, and it is vitally important that welfare is not compromised.

2.4.2.1 Survival

The survival of lambs to weaning is dependent on a successful partnership between the ewe and lamb during gestation, parturition and lactation, and is influenced both by the lamb's capacity to survive (viability) and the dam's rearing ability (Haughey and George, 1982; Piper *et al*, 1982). Lamb survival and the rearing ability of the dam have both been shown to be heritable and repeatable, thus offering opportunities for reducing high perinatal lamb mortality (Atkins, 1980; Donnelly, 1982; Haughey, 1983; Haughey and George, 1982).

Mortality can be a major concern in sheep production and can be the result of foeto-pelvic disproportion (arising from a small maternal pelvis, foetal oversize, or both, leading to injury, still birth or neonatal death), abnormal maternal or neonatal behaviour, low resistance to cold, inadequate milk supply and teat udder abnormalities. Some or all these defects may have a heritable basis. The size of lambs at birth is an important influence on mortality and it has been recommended that birth weight should be parameterised as a trait of the lamb with a maternal component (DEFRA, 2003a). Very small lambs (weighing less than 2 or 3 kg) can easily suffer from cold and are prone to starvation, whereas oversized lambs may cause birthing difficulties (dystocia). Through genetic improvement programs there have been small increases in birth weight as a result of selection for carcass traits (Anon, 2001), which may ultimately lead to fewer small lambs and lower mortalities. Mortality of lambs oversized at birth is thought to be less of a problem, as selection indexes would be expected to increase the mature size of ewes. Lambe *et al.* (2006) found that selection for carcass and maternal traits in Scottish Blackface ewes caused no significant change in the incidence of ewes requiring assistance when lambing. It had been proposed that if the objective is to increase the number of lambs weaned, selection should be for survival rather than prolificacy, as increasing prolificacy can result in competition for milk and reduced birth weights in multiple births (Conington *et al*, 2004; Welsh *et al*, 2003). It has been reported that lamb genetic effect ($h^2 = 0.27$) is stronger than the maternal effect ($m^2 = 0.07$) for lamb losses; in breeding programmes survival should therefore be treated as a trait of the lamb with a maternal genetic component, rather than as a dam trait (DEFRA, 2003a). It has been suggested that brown fat in newborn lambs is a component of cold resistance, could be correlated with lamb survival, and could be used as predictor if measured by CT scanning (DEFRA, 2003a).

2.4.2.2 Longevity

Improving longevity has been shown to be important for livestock profitability and evaluations of the trait have been used in dairy cow breeding programmes (Veerkamp *et al*, 1995). In dairy cows the heritability of longevity was found to be 0.06 (Brotherstone *et al*, 1997). The benefits from longer herd life include

lower replacement costs, increased income due to the number of animals producing at the mature level, fewer resources used on non-producing heifers, more opportunities for culling low-producing animals, and improved health resulting in lower veterinary costs. Selection of high-producing animals with a greater requirement for nutrients may lead to reduced longevity in harsh conditions, given the effect of rearing twins on a ewe's body condition and subsequent performance. Selection for longevity could best be achieved by identifying characteristics that leads to premature culling, such as teeth wear or mastitis, which are major criterion for culling ewes. Meyer *et al.* (1983) reported a heritability of 0.46 +/- 0.13 for wear rate of permanent incisors in young ewes. Conington *et al.* (2001) incorporated longevity in a multi-trait index for sheep.

2.4.2.3 Growth and carcass characteristics - muscle and fat

Carcass traits are important from both a farm and a strategic point of view. It is desirable to increase lamb carcass weight without an increase in fat, so that desired carcass grades are achieved. However, results from index calculations show that the current industry payment structure for lamb carcasses is unsuccessful at providing clear signals to the farmer for reducing fatness in lambs (Jones *et al*, 2004).

2.4.2.3.1 Assessment of carcass traits

In the UK, the MLC provides a carcase classification system that allows understanding of specifications in the marketing chain (Table 2.1 and Figure 2.2). The classification system consists of five conformation classes based upon the distribution of meat on the carcase and five fat classes according to the amount of fat. The conformation classes are called E, U, R, O and P, with E being the best conformation and P the poorest. Fatness is assessed on a scale of 1-5, class 1 being extremely lean and class 5 being very fat.

Table 2.1 Classification grid for conformation and fatness showing percentage distribution of all carcasses in 2000. Source (MLC, 2001).

Fat Class

Increasing fatness →

Conformation Class (*Increasing Conformation* ↑)	1	2	3L	3H	4L	4H	5
E	**0.0**	**0.1**	**0.5**	0.2	0.1	0.0	0.0
U	**0.0**	**1.5**	**7.3**	4.5	1.4	0.6	0.3
R	**0.1**	**9.1**	**30.0**	12.9	3.2	1.2	0.4
O	0.4	7.8	10.6	3.3	0.7	0.2	0.1
P	3						

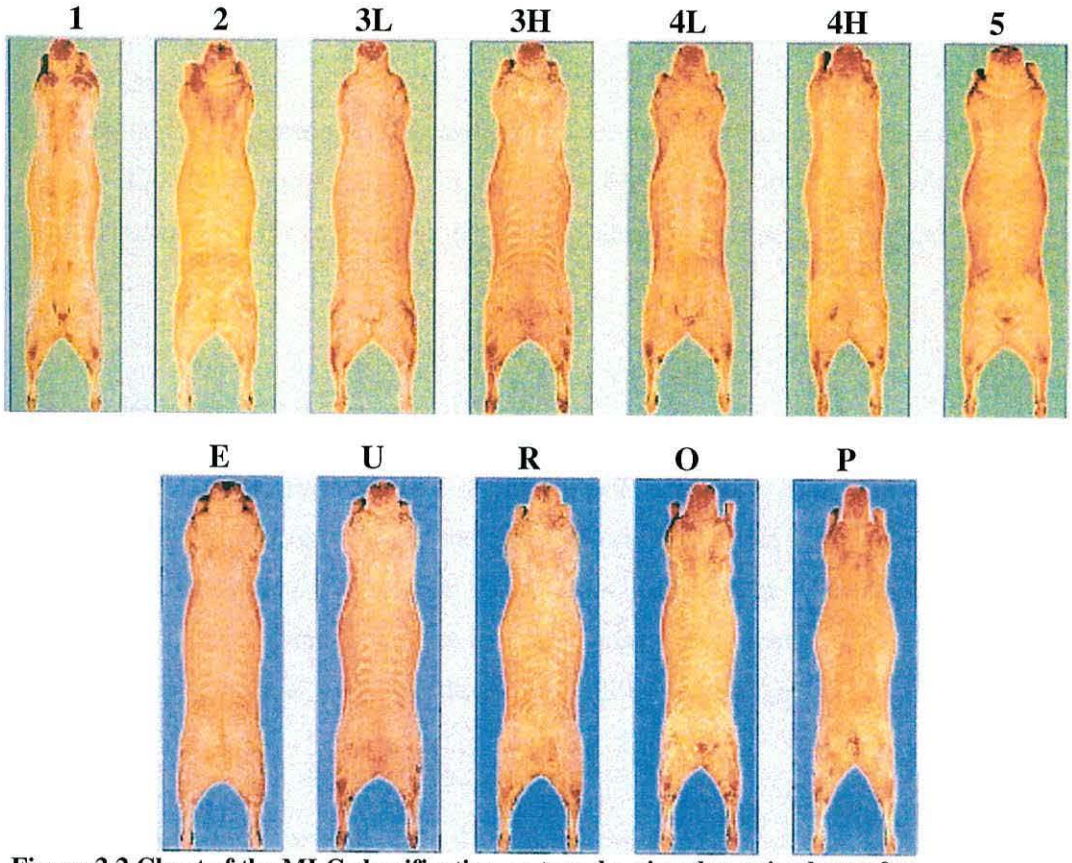


Figure 2.2 Chart of the MLC classification system showing the main classes for conformation and fatness. Source (MLC, 2001).

The classification of carcasses are judged subjectively by experts, though new technology such as Video Imaging Analysis (VIA) that is currently being evaluated at Welsh Country Foods, Anglesey, could contribute to the efficiency and consistency of classification, in addition to giving increased confidence in the classification system (HCC, 2006b).

The main retail market is for 16 – 21.9 kg carcasses, and 63 % of Welsh lambs fitted this weight range in 2005. Lambs that are slaughtered from the UK national flock can be described as providing a variable product (see Table 2.1), which reflects the breeds and crosses used and the different systems of production (King, 1979). Consumer demand is reflected in the fact that abattoirs penalise producers with over-fat lambs. Excess fat means unnecessary costs in terms of energy and money (Gooden *et al*, 1980), as the excess will be trimmed off before being sold to the consumer. Findings of Hybu Cig Cymru revealed that over half of all lambs slaughtered in Wales meet the specification of E, U, or R for conformation and 1, 2 or 3L for fatness, and that 20 % of Welsh lambs do not achieve target grades because they are over fat (HCC, 2006c).

Lambs from hill breeds tend to reach desired fatness (MLC fat class 2 to 3L) at light weights, because of their small mature size (Conington *et al*, 1995). It has been reported in MAFF funded research that only 20% of Welsh Mountain lambs fall into the desired carcass category of EUR 2-3L (MAFF, undated). This leads to financial penalties unless specialist markets for light lamb are developed (Conington *et al*, 1998). One-quarter of Welsh lambs fit the specifications for the Mediterranean market, where lean, light lambs (under 16 kg) are required and conformation is less important (HCC, 2006c). Over-fatness is not just a problem for hill sheep farmers, but affects much of the sheep industry due to the large proportion of hill breeds and their influence on the genotypes of slaughter lambs in each sector. Therefore, a breeding program to improve carcass quality should benefit all levels of the stratified sheep production industry and ultimately the consumer. Management and nutritional measures may influence carcass fatness, but genetic improvement through selection of breeding stock offers a permanent, practical and usually cost-effective way of improving carcass composition (Simm and Dingwall, 1989).

2.4.2.4 Quality and healthiness of meat

There is intense competition in the meat industry, particularly from imports from countries that can produce meat much more cheaply than in the UK. The UK industry might benefit from improving meat quality traits if the consumer is

willing to pay more for those. Meat quality traits affecting appearance and eating quality have been shown to be heritable (DEFRA, undated; Fernandez *et al*, 2003; Suzuki *et al*, 2005). Tenderness is the most important aspect of eating quality and high heritabilities have been reported for this trait (DEFRA, 2005; Suzuki *et al*, 2005). Intramuscular fat is thought to play a role in meat tenderness, juiciness, and flavour (Cameron and Enser, 1991; DEFRA, undated) and it has been suggested that an increase in carcass leanness would change the fatty acid composition of intra-muscular fat, leading to a reduction in juiciness and tenderness (Cameron and Enser, 1991). Kerth (1999) observed that the presence of the Callipyge gene, which controls muscle mass, also reduced the tenderness of longissimus muscle. However, Suzuki *et al.* (2005) reported that tenderness was related to water-holding capacity associated with increased collagen content and suggested that collagen content, as well as electric impedance, should be included in an index to improve meat quality. Recently the presence in meat of beneficial fats, such as Omega 3 fatty acids, has been promoted in meat. Fernandez *et al.* (2003) reported heritabilities of various fatty acids to range from 0.29 – 0.41 in Iberian pigs.

Meat quality traits are expensive and difficult to measure. Utilisation of genetic markers or candidate genes to predict meat quality traits might be the most promising way of incorporating them in breeding programs (Fernandez *et al*, 2003). Genetic improvement of meat quality would benefit the consumer but not necessarily the breeder at present, so breeders and producers would need an incentive to include the extra traits in selection indices. Many meat quality traits are more influenced by production factors, such as nutrition and meat processing, than by genetics (Cameron *et al*, 2000), so it might be worth making changes in these domains.

2.4.2.5 Maternal traits: fertility, litter size, and maternal ability

Ewe prolificacy, expressed as a trait of the dam, is a major determinant of profitability, particularly in lowland systems. However, it has been suggested that it is more cost effective to farm ewes with the ability to rear more of their lambs, rather than increasing prolificacy (Conington *et al*, 2001). Rearing ability

is defined as the ratio of the number of lambs weaned to the number of lambs born (LW/LB) (Piper *et al*, 1982). Costs of supplementary feeding of ewes that are carrying higher litter sizes during winter would be lower if the selection emphasis was placed on the ewe's ability to rear lambs that they have given birth, rather than increasing their litter size born. EBVs in cattle include udder and teat scores to prevent suckling difficulties or infection (Roughsedge *et al*, 2004).

2.4.2.5.1 Maternal ability and behaviour

The environment provided by the dam is important for the survival and growth of the offspring. Basically, maternal ability represents the dam's willingness to sacrifice time, energy and resources to the rearing and protection of the offspring (Stookey, 1997). There appears to be less variability in maternal behaviour in hill breeds and it tends to be at the good end of the spectrum (Hinch, 1997). It has been suggested that hill sheep, reared in and adapted to harsh conditions, have evolved more efficient behavioural and physiological mechanisms to improve lamb survival than intensively managed lowland breeds (Dwyer and Lawrence, 2005). Lambs of hill and feral breeds are reported to be able to find the udder more quickly than lowland breeds (Slee and Springbett, 1986). Several behavioural traits, such as responsiveness towards signals from offspring, aggressive behaviour towards offspring, nursing behaviour, and fear responses determine the offspring's survival and ability to make a good start in life, and some of these traits are partly genetically controlled (Grandinson, 2005). Variation in maternal ability has been noted between breeds (Dwyer and Lawrence, 1998; Dwyer and Lawrence, 2000); the Merino ewe in Australia, for example, is widely recognised as a poor mother (Nowak, 1996). In addition to differences in maternal ability between breeds, studies have shown within breed variation (Cloete and Scholtz, 1998; Lambe *et al*, 2001). Lambe *et al.* (2001) found that the heritability of maternal behaviour score (a score to assess flight distance of ewes when lambs were first handled) was 0.13 in Scottish Blackface sheep. A close ewe-lamb spatial relationship is associated with improved lamb survival, as it facilitates lamb sucking, lamb learning and is indicative of maternal protectiveness against predators (Dwyer and Lawrence, 2005). Fear responses can be advantageous in the wild: ewes selected downwards for

responsiveness to humans have been shown to exhibit stronger maternal behaviour than their counterparts selected upwards (Boissy *et al*, 2005). However, when animals need to be handled or to be housed indoors at lambing fear reactions can lead to reduced productivity and welfare (Viérin and Bouissou, 2002). The stockperson's work is made easier if animals are easier to handle and there is a positive human: animal bond. Animals that do not cooperate when handled tend to require more time (Goddard *et al*, 2006).

Many maternal behaviour traits are difficult to use as selection traits because births are not always supervised, and it would be impractical, time consuming or difficult to measure such traits on a large scale. However, behaviour variables could be measured using tests, or subjectively judged by the farmer. Previous studies have indicated that it is not necessary to include maternal behaviour score in an index to improve overall productivity (DEFRA, 2003a) as it has low heritability and is not related with other production traits. However, in experiments it has been shown that ewes, which have the lowest maternal score, which flee at the approach of an observer and which show no interest in lambs until the observer has left, have reduced lamb survival (DEFRA, 2003a). It is suggested that these ewes should not be used for breeding again.

Milk production is a component of maternal ability. However, it is a trait that is difficult to measure directly without interfering with normal lamb suckling behaviour, and is generally measured in terms of lamb growth.

2.4.2.6 Feed conversion ratio

Feed can account for a large proportion of costs, particularly in pork and milk production enterprises, and feed efficiency as a selection objective has been incorporated in pig breeding programmes (Cameron, 1998). In more extensive systems such as in beef and sheep production this would be more difficult to measure, but it could be assessed indirectly by rate of lean growth.

2.4.2.7 Wool

Wool production is not a priority for most sheep breeders in the UK as it provides little income, particularly in coarse-wool breeds. Thus, inclusion of wool traits such as fleece weight in a selection index may be inefficient because of the physical and financial effort of recording fleece weight. Conington *et al.* (2001) indicated that the accuracy of an index was slightly decreased by excluding fleece weight from the breeding goal. It was suggested that fleece weight should be included as a goal trait, but not recorded; thus a more reliable estimate of the economic benefit of the index would be achieved (Conington and Murphy, 2003).

2.4.2.8 Easy care traits to reduce labour requirements

The advantages of easy care are the reductions in production costs, particularly labour, and increased productivity through reduced lamb and adult mortality. The objective is to produce sheep with a minimum of human assistance or intervention, especially at lambing (Bradford and Meyer, 1986). 'Easy care' has been defined as those sheep that are able to adapt and survive to climatic conditions and successfully rear at least one lamb without assistance (Goddard *et al*, 2006). Such sheep have higher survival rates, lower lamb mortality, and require less shepherding (Goddard, 2002). Lambing difficulty is associated with added labour and often linked with increased lamb mortality. The easy care approach could result in the practice of culling animals that require assistance at birth. As a trait of the dam, dystocia has been found to have low heritability and low repeatability (DEFRA, 2003a); therefore, the culling of ewes in this instance may not be sensible. Natural selection would have strongly favoured easy care ewes in the past. However, since intensification in management of animals the provision of shelter, supervision and artificial rearing has increased the survival of lambs that would otherwise die. In addition, artificial selection for particular traits has made sheep increasingly dependent upon human input. Easy care traits could include adaptation, hardiness, disease resistance or tolerance, maternal ability, shedding of wool, and would vary upon breed types and the environment. Movement towards extensification may increase welfare problems in the short-

term if breeds that have been intensively managed for generations have become increasingly reliant on human input and may lack the skills necessary for survival in extensive systems (Dwyer and Lawrence, 2005).

2.4.2.9 Disease resistance

Disease causes problems in livestock production systems including production loss, uncertain food security, lost income due to mortalities, veterinary and drug costs, and increased work in animal management. It can also have a direct impact on human health (Baker, 1991). Within the livestock sector partial costing estimates of the losses due to disease in developed and developing countries have been suggested as 17 % and 35-50 % of turnover respectively (Bishop, 2004). Niewhof and Bishop (2005) estimated the costs of the three major diseases in Great Britain; gastro-intestinal parasites, footrot, and scab were estimated to have annual costs of £84 million, £24 million, and £8 million, respectively.

There are a number of management options for eliminating diseases; these include vaccination, chemotherapy, improved husbandry, genetic change or a combination of these. In livestock production reliance on medication, vaccination and management techniques have been important for the control of animal health, and as a result health-related traits have played a minor role in breeding goals (Knap and Bishop, 2000). However, it has been suggested that many of the disease management strategies in present use are not biologically sustainable (Bishop, undated).

There is genetic variation in resistance to or tolerance of over 40 livestock diseases (Bishop *et al*, 2002). Variation in resistance to disease in livestock is well documented; it has long been observed that symptoms seldom develop in all individuals of a population exposed to disease (Adams and Templeton, 1998). Genetic improvement of disease resistance could be achieved by selection for phenotype, genetic markers or specific genes. Selection based on phenotype is appropriate when the presence of the infection is a feature of the production system (Bishop, 2004), such as nematode parasite infections in sheep. However,

for epidemic or sporadic diseases, genetic markers are likely to be more appropriate for disease resistance selection, as they allow selection of animals in the absence of infection challenge. Resistance to gastrointestinal parasites is measured by fecal egg count but the method is expensive and time consuming, so genetic markers could be more effective (Davies *et al*, 2006). Genetic approaches have shown to be effective in managing diseases including tick infestations, helminth disease (Gasbarre and Miller, 1999) and Marek's disease. Diseases for which genetic resistance is currently used as part of disease control strategies include trypanosomosis (d'Ieteren *et al*, 1999), mastitis (Heringstad *et al*, 2000; Owen *et al*, 1999), scrapie (Dawson *et al*, 1998) and E.coli diarrhoea in pigs (Edfors-Lilja and Wallgren, 1999). Use of appropriate breeds may be effective if some breeds are more resistant than others to particular strains of disease (Good *et al*, 2006). Native breeds may be more resistant to various diseases than imported breeds (Miller *et al*, 1998).

The future for selective breeding schemes designed to improve disease resistance depends upon both the efficiency of non-genetic approaches and the costs of breeding for resistance, which include direct costs, such as laboratory analysis and genotyping, and indirect costs, for example, negative effects on production traits or loss in selection pressure for other traits. Some studies have observed correlations (both desirable and undesirable) between disease resistance and production traits. In Merino sheep, Pollott and Greeff (2004) concluded that the increase of genetically-based host resistance to parasites should have no detrimental effect on production characteristics. There are ongoing investigations into whether there are any associations between scrapie genotype and production traits (Bossers *et al*, 2000; De Vries *et al*, 2004a; De Vries *et al*, 2005; De Vries *et al*, 2004b).

There is concern over the risk that pathogens may co-evolve with the host in response to genetic changes (Bishop and MacKenzie, 2003), which would reduce the effectiveness of genetically-based resistance. When resistance is due to a single gene, there is less of a challenge to the parasite than that posed by multifactorial resistance, such as that observed for resistance to nematodes (Bishop *et al*, 2002; Bishop and Gettinby, 2000).

Breeding for resistance is one of a number of approaches for controlling disease, and is of particular importance when other measures of control fail because they are ineffective, unsustainable or uneconomic. In the control of worms in sheep it is suggested that three methods (killing worms, avoiding contamination and improving host response) should be combined, and that it would be unsustainable to solely concentrate on one approach (Waller, 2006). Selection for resistance to one species can confer resistance to other species if there are strong underlying genetic correlations (Gruner *et al*, 2004; Raadsma *et al*, 1997; Woolaston *et al*, 1990). Once genetic resistance is established in a production system input and maintenance costs are low because of reduced reliance on chemicals, hence contributing to sustainable disease management. The permanence and consistency of the genetic effect may lead to eradication of a disease, such as being currently attempted by breeding sheep for resistance against scrapie.

2.4.3 Method of constructing a selection index

Selection for several objectives simultaneously involves knowledge of certain genetic parameters if success is to be achieved. Genes affecting a particular trait may also affect other traits. Relationships between traits can be quantified by calculating the correlations between them; these range from -1.0 to +1.0. Loss of genetic merit is possible when there is genetic antagonism between a selected and an important but possibly unselected trait, for example, an increase in growth rate may lead to excess fat. Restricted selection indexes are used to maintain optimal levels for some traits while improving other traits with which there is some degree of genetic antagonism. To construct a selection index, the following are required: -

1. economic values for each of the selection objectives
2. genetic variances for each of the selection criteria
3. genetic covariances between the selection criteria
4. genetic covariances between the criteria and objectives
5. phenotypic variances for each of the selection criteria
6. phenotypic covariances between the selection criteria.

The index takes the form of: -

Equation 2.9

$$I = b_1 EBV_1 + b_2 EBV_2 + b_3 EBV_3 + b_4 EBV_4 + \ldots\ldots\ldots b_n EBV_n$$

where I = index score for individual animal; b = index weight on EBV i; EBV i = estimated breeding value for trait i. Schneeberger *et al.* (1992) presented a method for computing index weights from estimated breeding values from different selection criteria, using the equation

Equation 2.10

$$b = G_{11}^{-1} G_{12} v$$

where b is the vector for index weights; G_{11} is the genetic variance-covariance matrix of the criteria in the index; G_{12} is the genetic covariance matrix between the selection criteria in the index and the traits in the objective; and v is the economic weights for the traits in the objective. If values in 11 are equal to the criteria in 12, then $b = v$.

2.4.4 Assessing the response from selection

Ponzoni (1986) stated that the success of a breeding program is enhanced if the following steps are taken in order: 1) definition of the breeding objective; 2) choice of selection criteria; 3) organisation of the performance recording scheme; 4) use of the information recorded to make selection decisions; and lastly 5) use of selected individuals. The rate of response to selection within a population depends on the following: variation in breeding values, generation interval, selection intensity, effective population size and accuracy of selection (Nicholas, 1987). Selection is more effective in males than females as fewer males are required to produce the same number of offspring, and therefore greater selection intensity can be practiced. Multiple ovulation and embryo transfer (MOET) can increase genetic progress from selection of females. Genetic gain per generation is calculated as

Equation 2.11

$$\textit{Genetic gain / generation} = \textit{heritability} \times \textit{selection differential}^{1}$$

and genetic gain per year as

Equation 2.12

$$\textit{Genetic gain / year} = (\textit{heritability} \times \textit{selection differential}) / \textit{generation interval}$$

[1] Selection differential = selection intensity × phenotypic standard deviation

Conington *et al.* (2006) investigated the response to selection after the use of two selection indices for five years in hill sheep and concluded that the multi-trait selection indices had been successful and proved to be a viable, long-term strategy to improve levels of production.

2.5 ECONOMIC VALUES

The challenge for livestock production in developed countries is to continue to be sustainable and competitive in the face of declining prices, higher costs, competition and public pressures (Bishop, 2004). Social factors mainly determine the type of products produced, and the demand for products from consumers should define breeding objectives. Breeding objectives for most farm animals are to increase profits by improving production efficiency. Breeding objectives are expressed by a profit function which uses genetic values as inputs and profits as outputs (Charfeddine, 2000). Despite the emphasis placed on the selection for particular traits in many breeding schemes, in many instances farmers will choose an animal they consider to look more attractive, regardless of the animal's value for those traits that affect economic performance. Varying market signals cause breeders to concentrate on aesthetic qualities in order to sell more animals to more farmers, even though processors and consumers are more interested in other qualities. The marketing system in the UK, under which animals are still sold live in auctions as well as dead-weight, may be one reason why farmers see little reason for improving, for instance, carcass traits; no report is returned with slaughter information for animals, and there may be little variation in prices. When price signals are not passed from consumers to breeders, economic weights can become distorted (Goddard, 1998). Weller (1994), however, suggests that 'animal appearance' is a trait of economic importance if appearance will cause a buyer to pay more or less for an animal.

To construct a selection index, economic values (EVs) are needed for each trait in the breeding objective so that selection emphasis is proportional to the economic importance of each trait. The economic value of a trait can be defined as the marginal profit as a consequence of genetic change in one unit of the trait considered (Simm, 2000). The profit function is also used to define economic

weights of traits contributing to economic genetic improvement, and the traits must be related as directly as possible to all sources of income and costs. Profit is defined as a function of direct additive genetic values of aggregate genotype traits for a given set of management and economic parameters.

Equation 2.13

$$Profit\ (P) = f(g_1, g_2, g_3, \ldots\ldots g_n)$$

Where g_1 is the direct additive genetic value of trait one; g_2 is the direct additive genetic value of trait two etc.

Charfeddine (2000) stated that traits should not be kept out of profit functions because of lack of information but should be excluded if they show no genetic variation, otherwise sub-optimal decisions could result.

The profit equation should have the following minimal characteristics:

1. change in profit should be a function of genetic change rather than change in phenotype
2. management conditions should be relevant to the population in which genetic change is to be used at the time genetic change is used
3. economic parameters should reflect the marketing and management system.

The general form of the profit equation to maximise profit $P = R - C$

(P = Profit, R = returns, C = Cost)

There are also questions about whether the profit equation be viewed from the perspective of the farmer, industry or the consumer, and whether the objective should be to maximise profit or return on investment, or to minimise cost per unit production.

Bright (1991) recommended that when an economic weight refers to more than one production period, future economic weights should be discounted by an appropriate rate of interest and summed to give their net present value. Time of expression (e.g. lamb or adult) and the number of times an animal expresses the trait (once per animal for slaughter traits, repeatedly for reproductive traits) are then accounted for. Ignoring cumulative discounted expressions could lead to

bias in relative selection emphasis on traits and to non-optimum genetic responses (Charfeddine, 2000). Multiplying the economic value by the cumulative discounted expression gives the discounted economic value.

Equation 2.14

$$a_1 = c_1 + v_1$$

where c_1 = cumulative discounted expression for trait 1; v_1 = economic value of trait 1.

The aggregate genotype *(H)* that represents the economic merit of an animal is the sum of its genotypes for several traits, all with its own discounted economic value.

Equation 2.15

$$\textit{(Aggregate genotype)}\ H = a_1BV_1 + a_2BV_2 \ldots\ldots + a_nBV_n$$

where BV_1 = the breeding value for trait 1; a_1 = the discounted economic value for trait 1.

Charfeddine (2000) stated that selection that is genetically and socio-economically balanced requires correct economic values, and can then give optimum levels of genetic improvement with regard to future production circumstances. Deriving economic values requires use of appropriate methodology, including modelling of production, economics, and social factors, with suitable assumptions about future production circumstances. Increasingly, bio-economic models that account for genetic, nutritional, management and economic factors are used for estimating economic values for traits, and in addition are valuable for exploring the robustness of values when adjustments are made to the factors (Conington *et al*, 2000; Conington *et al*, 2004; Jones *et al*, 2004).

One weakness in deriving economic values of traits is that often observed or historical values are used, whilst breeding is future-oriented. Prices fluctuate within and across years (see Figure 2.2), and in some years there may be extremes due to sudden food scares or disease outbreaks, such as the outbreak of Foot and Mouth Disease in 2001. Future production and economic circumstances are uncertain and difficult to predict. Jones *et al.* (2004) suggested

that when choosing economic values it is best to use an average value across years, possibly excluding values from extreme years. They also suggested that once an index is derived, the more extreme values could be used to test the sensitivity of the index to changes in market prices. Kulak *et al.* (2003) suggested that uncertainty over future product prices ought to be considered when estimating economic weights, and evaluated a risk-related profit model for doing this. Often prices of inputs and outputs are not known for certain when decisions need to be made, and increasingly producers are exposed to changeable competitive markets for inputs and outputs, so often there is an element of risk. Kulak *et al.* (2003) recommended that economic models should take into consideration the fact that knowledge is not perfect and that economic circumstances change over time.

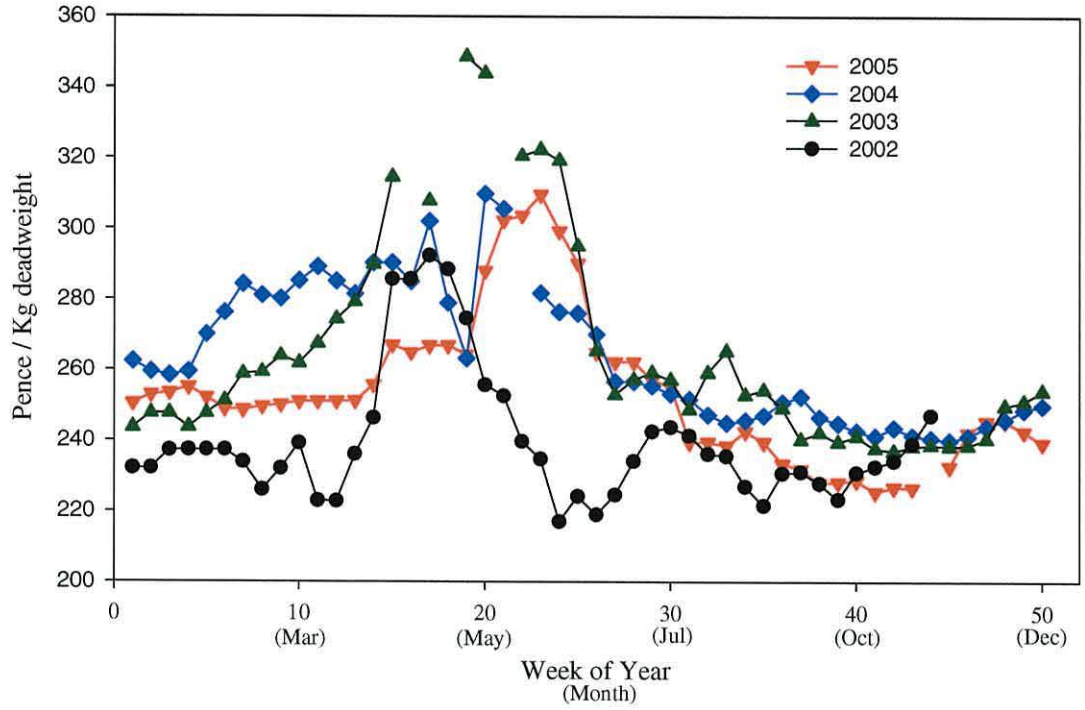


Figure 2.3 Deadweight lamb prices during years 2002 to 2005

2.5.1 Hill breeds

In the UK sheep form an important part of the rural economy in the hill and upland areas. Grazing by sheep is also important for maintaining habitats and landscapes that form part of the national heritage, which in turn generates income through tourism, recreation, sport and hunting. Defining breeding goals is more complicated for hill breeds than for other sectors of the industry as they supply

breeding females as well as slaughter lambs (Conington *et al*, 2000). Economic values differ between production systems due to diversity in the physical constraints of farm size, pasture availability and the biological limits of sheep in extensive rearing environments. Conington *et al.* (2000) derived economic values for three types of hill production system (intensive, semi-intensive and extensive) using Scottish Blackface sheep. It was concluded that there may be economic limitations to genetic improvement where environments are harsh; for example, increasing the number of lambs reared in such environments resulted in economic loss.

CHAPTER 3

General Materials and Methods

This chapter provides a general explanation of the materials and methods common to the work described in chapters 4-11. Further descriptions of methods are given in these chapters relating to individual studies in detail.

3.1 SOURCE OF ANIMALS AND DATA

3.1.1 The sheep flocks

With the agreement of four breeding groups in Wales (Figure 3.1), data from their flocks were obtained from MLC/Signet. All flocks were of Welsh sheep breeds and were located in Wales. The Group Breeding Schemes CAMDA, CAMP, and Llysfasi provided data for the Welsh Mountain breed. Data for the Beulah Speckled Face breed was obtained from the Beulah Sire Referencing Scheme.

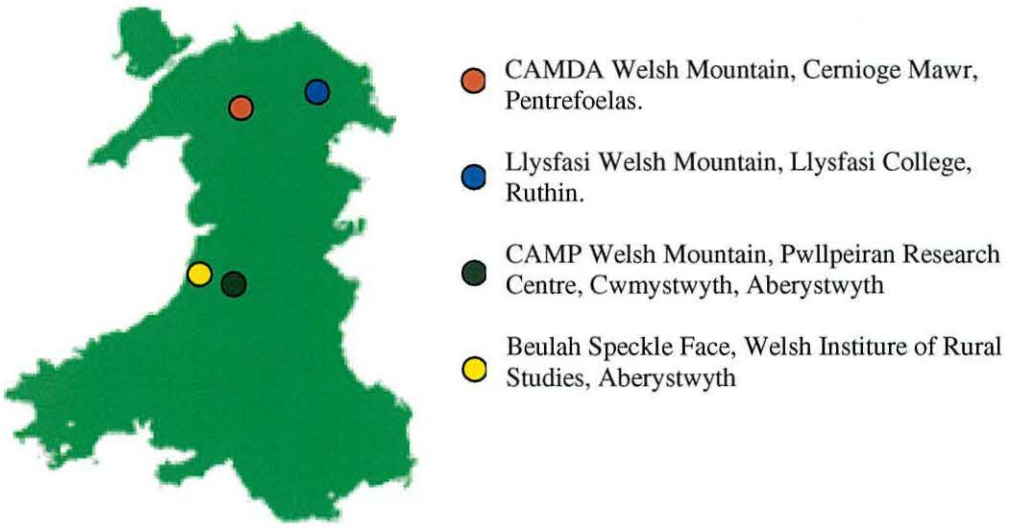


Figure 3. 1: Location of breeding groups in Wales

3.1.1.1 Cymdeithas Amcanu Magu Defaid Amgenach (CAMDA)

CAMDA, set up in 1976, is the longest-established and the first Group Breeding Scheme in the UK. It was set up at the Animal Breeding Research Organisation's Rhydyglafes, Cynwyd farm by Welsh Mountain sheep breeders from Caernarfon, Denbigh and Merioneth. The members were upland farmers with hill flocks of the Welsh Mountain sheep breed. The basis of the scheme was to set up a central nucleus to provide a source of superior rams for members and for sale. The nucleus flock was established over three years by selecting the best 40 ewes based on MLC records from each of the 10 members flocks, and by 1978 the nucleus had 400 breeding ewes. Since 1982 the flock has been located at Ceirnioge Mawr, Pentrefoelas, in North Wales.

Initially three selection lines were designed, a genetic control line, a nucleus line and a commercial control line (Saatci *et al*, 1999). The genetic control line operated until autumn 1995 and was based on animals originally chosen from the foundation flock, with replacements selected randomly afterwards. The nucleus line was based on the replacements produced in the nucleus flock and until 1982 females were also transferred from the members. The commercial line was based on imported rams from commercial flocks outside the scheme.

Early in the scheme there was close cooperation with the MLC, followed by Signet, and their indices have been used to aid selection. Breeding objectives for the group are to produce slightly heavier ewes that lamb easily and rear heavier lambs on hill pastures and also retain the beneficial characteristics of Welsh Mountain sheep such as hardiness. Selection is based on MLC recording with a multi-trait index based on lamb growth (60%), mature size (15%), maternal ability (24%) and litter size (1%). At CAMDA lambs are fully recorded at birth, which requires tagging each lamb and recording its dam and sire identity, date of birth, sex and birth type (single/twin). Lambs are weighed at 12 weeks of age and again in September when they are also ultrasonically-scanned for back fat and eye muscle depth. Estimated breeding values (EBVs) are combined into an index for each lamb. In 1994 the index for the flock was set at 100 and has since

progressed to 143 in 2001. Analysis of data showed that genetic progress for weaning weight in the nucleus averaged 145 g/year; 117 g/year was through improvements in direct lamb growth and 28 g/year was from changes in maternal ability. Since 1977 the adjusted 12-week weights of lambs had increased by 2.94 kg and ewe mature weight was 3.5 kg more than control ewes (CAMDA, 2003). Rams were also involved in an annual performance test at the University of Wales, Bangor that included rams from other commercial flocks. Results showed that CAMDA rams were consistently heavier than the mean of other rams in the test period (CAMDA, 2000).

3.1.1.2 Cynllun Grŵp Bridio Defaid Mynydd Cymru / CAMP Welsh Mountain Group Breeding Scheme

Fifteen North Ceredigion hill farmers set up the nucleus flock for this scheme at an Experimental Husbandry Farm, ADAS Pwllpeiran, Cwmystwyth in 1990. Each member contributed 20 in-lamb ewes to establish the 300-ewe flock. The breeders aims were to improve the percentage of lambs in the higher classification grades for conformation and to increase carcass weight, without forfeiting hardiness and mothering ability. Signet uses the Welsh Selection Index for the flock. Annually about 15 ram lambs are selected, and are further scrutinised the following autumn. Of these, two or three are used on the nucleus flock, whilst the others are used on the members flocks. Ewe lambs from the top half of the index are selected as breeding replacements. Progress in the flock amounted to a gain of 1 kg in weaning weight within the first five lamb crops. In addition, the percentage of lambs classified 'R' increased from 29 % to 53 % in 2003 (HCC, 2004b).

3.1.1.3 Grwp Magu Defaid Mynydd Cymreig Llysfasi / Llysfasi Welsh Mountain Group Breeding Scheme

This scheme was set up by ten members who established a 250-ewe nucleus flock in 1990 at Llysfasi College, Denbighshire, North Wales. Selection of animals is based upon the index used by Signet and breed type. The aim is to keep the characteristics of hardiness and mothering ability, as well as improving lambing percentage, tooth retention, longevity, conformation, and lamb and ewe

size (HCC, 2004c). Longevity is important as older ewes from the flock are retained to produce Welsh Halfbreds. Cervical AI has been used in recent years to enable members to improve their flocks. Most rams would traditionally only serve one flock per season but with the use of AI technology they can now be used on the members flocks as well as the college flock in the same season thus improving the flocks on a wider scale and at a greater pace.

3.1.1.4 Cynllun Cyfeirnod Hyrddod Penfrith Beulah / Beulah Sire Referencing Scheme

Ten members, who supplied a total of 100 ewes for a nucleus flock, set up the Llanarth Beulah Group Breeding Scheme in 1979. The initial aim was to increase prolificacy, and once this was achieved efforts were directed towards improving carcase quality. In 1996 a Sire Referencing Scheme was set up, and included the Llanarth flock as a founder member. The Welsh hill index is used and care is taken to maintain breed type. Since establishment the scheme has made more genetic progress than any other breed within Wales (HCC, 2004a). This is principally the result of strict selection of rams on index, as well as maintaining good breed type.

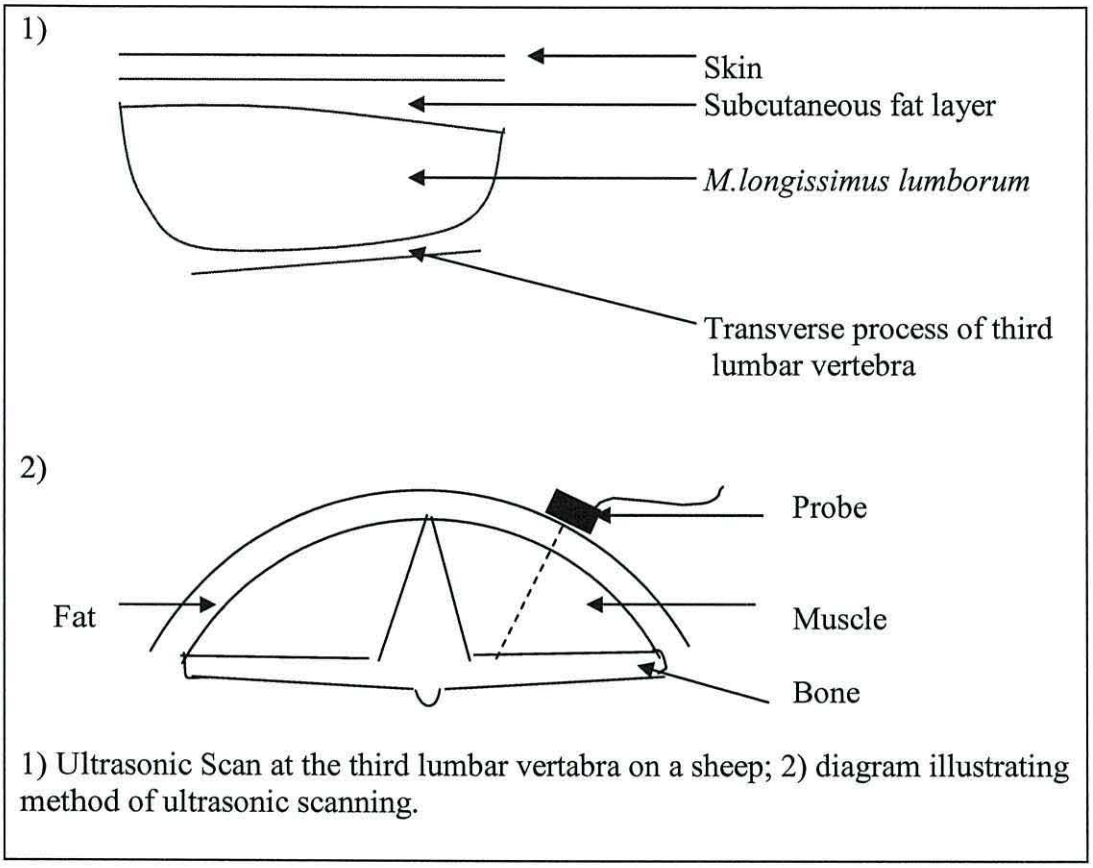
3.1.2 Collection of data

Signet follows strict protocols when animals are weighed and scanned. Signet suggests that the breeder weighs lambs at eight weeks of age. Weights are then sent to Signet and adjusted to eight-weeks if necessary. At 20/21 weeks lambs are weighed again and a technician from Signet records ultrasonic scanning measurements of muscle and fat depths.

3.1.3 Scanning method

The scanning technique (Figure 3.2) involves parting the wool over the third lumbar vertebra and the application of liquid paraffin oil to the skin to ensure acoustic contact. When the animal is suitably relaxed the transducer is placed on the prepared area and adjusted until a clear picture is obtained of the vertebra, and the eye muscle and fat layer covering it can be seen on the machine. The

image is frozen and linear measurements are taken of muscle and fat depth from the screen using a cursor. The fat depth measurement is obtained by averaging three measurements of the distance between the skin-fat interface and the interface between fat and muscle. Muscle depth is measured at its maximum point. This information is then downloaded into a computer and stored, or recorded on paper.



1) Ultrasonic Scan at the third lumbar vertabra on a sheep; 2) diagram illustrating method of ultrasonic scanning.

Figure 3.2 Diagrams illustrating the method of ultrasonic scanning. Source Simm (1987).

3.1.4 Computer Software

The data collected by Signet from all breeding groups and schemes were provided in electronic format by the MLC. For each group/scheme a PEST file of the measurement data and a pedigree file were sent. The data were transferred into Microsoft Access for cleaning and editing, and the procedures used are described in Chapter 4. MINITAB (Minitab Release 13 for Windows) was used to obtain descriptive statistics for the datasets and to test the growth and carcass trait data for normality. Following editing and preliminary analysis, models chosen to estimating variance components were evaluated using ASReml (Gilmour *et al*, 2002), and details are provided in Chapter 5.

CHAPTER 4

Preparation of Data for Analysis

ABSTRACT

Accurate genetic merit estimates can only be obtained by using appropriate models and quality data. The latter were explored for animals of the CAMDA flock. Software used included Minitab for statistical analysis and data validation, and Microsoft Access for editing. Entries for 15121 individuals in the original dataset were reduced to 11751 by data editing. Problems arose due to unrecorded data and duplicated identities. Duplicate identities of lambs were mainly between animals born in different years rather than the same year, due to the type of tag code given. This problem was resolved by recoding current identity to include birth year and the sex of the animal.

4.1 INTRODUCTION

A successful estimate of genetic merit for selection and marketing purposes, providing the most accurate predictions of merit of future progeny, depends upon use of an appropriate model and adequate, high quality data from which the estimate can be made (Bertrand and Wiggans, 1998). This latter requirement has led to the adoption of data editing as an important step between data collection and analysis. Some errors in collecting and recording of field data are to be expected. Therefore checks are necessary to ensure consistency and to allow errors to be corrected or eliminated (Bertrand and Wiggans, 1998).

It is vital that datasets of pedigree and performance are free of major errors before data analysis, as errors could result in biased estimates of genetic values, thereby reducing the accuracy of predicted responses to selection (Mackay and Caligari, 1999). Van Vleck (1970) reported in studies of dairy cattle that inclusion of misidentified records in the analysis led to biases in estimates of variance components, correlations between estimated and true genetic values, and genetic progress.

Data are eliminated for four main reasons: if there are missing values; if there are reasons to suspect that records are unreliable; if values are extreme; or if they are few in number. There may be good reasons for a low number of observations (for instance, one individual weighed at birth while the majority of animals are weighed at six months), but such records can cause computational problems if left in the analysis.

Outliers could be mistakes in data recording or entry or may be accurate records of naturally-occurring, unusual values. Outlier errors resulting from misplacing the decimal point or double entry of numbers can be easily detected in relation to the rest of the data and checked against values that are believable or physiologically possible. Source records can be used to verify that a mistake has occurred, and incorrect values can be removed or corrected. Outliers can present problems in statistical tests based upon sample means and variances (High, 2000); these can be distorted by outliers, biasing the results of tests and leading to unreliable conclusions.

Brown *et al.* (2000) stated that it is necessary for observations to lie within a biologically meaningful range and for information on animals to be biologically consistent. Before analysis of continuous data, records are often eliminated when they exceed two or three standard deviations of the mean. However, this process of elimination could remove genuinely elite animals from analysis, and there will be no estimates of their breeding value or worth. LAMBPLAN, an Australian breeding programme and genetic evaluation system, performs checks on data beyond three standard deviations of the group mean (Brown *et al*, 2000). Bertrand and Wiggins (1998) used 3.5 - 4 standard deviations as the cut off for eliminating animals of contemporary groups when editing records for beef and dairy cattle for genetic evaluation. The aim was elimination of animals that could have been sick, preferentially treated or placed in the wrong contemporary group. Maniatis and Pollott (2002b) rejected animals with weights over four standard deviations from the mean, whilst Hussain *et al.* (2006) defined outliers as observations more than 4.5 deviations from the mean. Mackay and Calgari (1999) expressed concern about recording errors that have large effect, but do not appear as outliers, as these are considerably more difficult to detect.

Maniatis and Pollott (2002b) excluded animals if information on age of dam or type of birth was missing. Additionally, animals reared artificially or fostered were eliminated. In the study of Maniatis and Pollott (2002b) contemporary groups (lambs born in the same year) that had fewer than ten animals were omitted from analysis. Hussain *et al.* (2006) deleted data from lambs with sires that had fewer than five recorded progeny.

It is essential that basic information about the animal, for instance sex and breed codes are correct; if suspect, the record should be rejected. For instance, during data validation records were encountered of scrotal circumference on ewes (Brown *et al*, 2000), bulling and calving dates for male cattle, and calving dates or gestation periods that were physiologically impossible (Ap Dewi and Pritchard, 2004). The latter are often due to data entry of the wrong years.

ASReml, a statistical program that fits linear models using Residual Maximum Likelihood (REML) techniques, has been under development since 1993 by Arthur Gilmour and co-workers of NSW Agriculture and IACR-Rothamsted, and is licensed by VSN International. The program is particularly useful for large datasets, and specifically caters for livestock data that are analysed using a wide range of complex variance models (Gilmour *et al*, 2002). For genetic analysis using an animal model, an information file is required containing variates, covariates, factors and traits. A pedigree file is needed when analysing animals that are genetically linked, and contains three columns: the individual, its sire and its dam. Finally a command file specifies the model used. Prior to data being analysed, other software is used to recode character fields, to validate data and eliminate non-contributing animals, in a process referred to as cleaning or pruning.

The objectives of the work described in this chapter were to prepare a data file containing data obtained from MLC on the CAMDA flock that would be appropriate for ASReml analysis, to examine problems with the dataset provided by MLC, and to make recommendations for possible solutions.

4.2 METHODS

4.2.1 Source of animals and data

Two datasets, referred to as Camda and Camdadam, from a breeding group of Welsh Mountain Sheep (CAMDA, see section 3.1.1.1) were provided by Signet. A pedigree file was also provided with sire, dam, and animal identities. Data came from lambing years 1977 to 2003. The main source of information was the Camda dataset, which originally contained data on 15121 individuals. Information and data available in the dataset were lamb, sire, and dam identification; date of birth; sex; birth litter size; rearing litter size; adjusted eight week weight; age and weight at the time of ultrasonic scanning; and measurements for ultrasonic muscle and fat depths. There was additional information in the Camdadam dataset on fostering and genetic dams, and this was utilised in the main file (see section 4.2.2.1).

4.2.2 Data editing

Microsoft Access was used to eliminate records and to construct additional columns for year of birth, dam age, birth rearing type, litter codes and new identity codes for all animals. Minitab 13 was used for statistical description of data.

Year of birth was created from date of birth. Dam and sire identity codes were obtained from the pedigree file, which had previously been recoded to include sex and year of birth. Birth rearing type was a new descriptor created to describe litter size at birth and litter size during rearing, and were as follows: single born – single reared (S:S); twinborn – single reared (T:S); twin born – twin reared (T:T). Dam age was calculated by retrieving year of birth of dam from the dam's identity code. Dam ages greater than five years were recoded to 5. Litter codes were constructed from year of birth and dam identity; thus animals born to the same dam in the same litter year had a unique code.

To help solve a problem of duplicate identities (Section 4.2.2.4) a new identity for each animal was created which combined the year of birth with the original

identity; for example 979M:C456 born in 2003 became 03:979M:C456. Sex of the animal (F, M) was also incorporated into the new identity, for example F_03:979M:C456.

4.2.2.1 Combining datasets

Most of the information and data needed for analysis were contained in the Camda dataset. The Camdadam dataset was required to identify animals that were not reared by their genetic dams, and these were later eliminated from the Camda dataset. For this to be possible the identity codes of the animals had to be the same for both datasets. New identities were therefore constructed in the Camdadam dataset by including year of birth in the code, as described above. However, information on the sex of animal was not available. Therefore, elimination of animals reared by non-genetic rearing dams was done prior to the stage of incorporating the code for sex into the new identity.

4.2.2.2 Duplicate records

Each animal of the CAMDA flock had an identification code containing numbers and letters, for example '979M:C456.' The first part of the code (before the colon) shows that the animal originates from CAMDA. The letter after the colon represents the year in which the animal was born, for example those born in 1999, 2000, 2001 were given the letters W, X and Z respectively. The numbers following the letter should be unique for each animal.

However, in the data file received from Signet, a substantial number of duplicate records for animals were noticed. Three types of duplicate records were observed. The vast majority were due to a repetition of the identities of animals born in different years. Because CAMDA has long been established, the letters referring to animal year of birth were repeated, and duplicate or triplicate identities were found in the dataset. For instance, in the CAMDA system 'T' corresponds to both 1981 and 1997. Therefore identical identities could be found in these two years, although the animals were born sixteen years apart.

The other two types of duplicate records occurred within the same year of birth. One type resulted from reporting of the same animal more than once, and in this case all the records for the animal were identical in the entries. The other type of duplicate was more problematic, and occurred when animal identities were the same but the records in the duplicate entries were different. This suggested that the animals were different and that one identity had been entered wrongly, but it was impossible to decide which one was correct.

4.2.2.3 Reasons for elimination

Those individuals that had duplicate identities, incomplete records or data values more than three standard deviations from the mean were eliminated before calculating descriptive statistics. After this, 11751 individuals remained for analysis, i.e. 22.3% of the records had been eliminated. Presented in Table 4.1 are explanations for eliminations.

Table 4.1 Reasons for eliminations of entries (animals) in data cleaning. The original dataset contained information on 15121 individuals.

Reason for elimination	No. eliminated	No. remaining in dataset
Duplicate identities	1312	13809
Foster/genetic dams	303	13506
Triplets/quadruplets/missing	745	12761
Early years with few records	0*	12761
Missing dams/ Missing sires	302	12459
Control sires	628	11831
Dam age <2 years	5	11826
Scan age > 3 sd.	33	11793
8-wk weight > 3sd	37	11756
Scan weight > 3sd	1	11755
Muscle depth > 3 sd	1	11754
Remove birth rearing type	3	11751

* Animals were present in the original dataset but table shows none eliminated because they were eliminated on the basis of other criteria.

4.2.2.3.1 Eliminations due to a low number of animals in a class

There was one record for a one-year old dam, which was eliminated due to its rarity. Triplets and quadruplets were present in the original dataset for the variables litter size at birth and litter size at rearing, and these were also eliminated as they represented a small proportion of the population (triplets 1.2 % and quadruplets 0.04 %). It would be expected that animals from these multiple births would receive preferential treatment such as being bottle fed, and

it would therefore not be appropriate for them to be kept in the analysis. For a few animals birth-rearing type was classified as single born - twin reared. However, this is unlikely to have happened in practice in the CAMDA flock, and because there were relatively few of them, these animals were eliminated from the dataset. The dataset originally contained data from years from 1972 to 2003. However, there were few records of animals born in the years up until 1977 (0.2%); for instance in both 1972 and 1974 there were records for only one individual. The decision was therefore taken to use only the data from 1977 onwards.

4.2.2.3.2 Eliminations due to an absence of records

Individuals with missing identities for sires and dams, and with no records for size of litter at birth or rearing (1.4%) were eliminated.

4.2.2.3.3 Eliminations due to inconsistencies, outliers, and differences in management

Some sires in the data were from the control group (Section 3.1.1.1) and offspring of these sires were also eliminated. In the dataset there were 196 records for genetic dams, which meant that offspring were a result of embryo transfer, in 1994, 1998 and 2003. It was thought that information on whether the dam was a genetic or foster dam was not consistently recorded, and could pose problems, and perhaps should be considered in a separate analysis; thus animals with records indicating either fostering or embryo transfer were eliminated. Animals with eight-week weights, scan-weights, ultrasonic muscle depths and fat depths more than three standard deviations from the mean were eliminated. The original dataset contained a wide range of scanning dates (from 121 days to 929 days), and three distinct groupings of age were observed. The main scanning age range was 121 to 189 days (4-6 months), and other scanning ages for males were at 536 to 556 days (18 months) and 909 to 926 days (30 months). It would clearly be impractical to scan animals at a precise age because individuals are born at different times, mainly throughout April but also in March and May. Recording carried out by Signet for weights and ultrasonically-scanned traits takes place ideally at 20/21 weeks of age, but because individuals are not all born

at the same time and scanning may only be performed on a single day a range of scanning dates is to be expected. Scanning performed by Signet takes place in September/October. The scanning of older (yearling or two-year-old) rams would have been done when the main scanning was performed on lambs at 20/21 weeks. As those older animals accounted for only a small proportion of the dataset and their scanning age was more than three standard deviations (327.8 days) from the mean they were eliminated.

4.3 RESULTS

Animal. There were 11751 individuals in the edited dataset. Details of fixed effects, basic statistics for each trait and the covariate age at scanning are presented in Tables 4.2 and 4.3.

Sex. There were 5490 records for males (46.7 %) and 6261 for females (53.3 %). No castrates were recorded.

Sire and dam information. All individuals had information on the identities of their sires and dams. There were 221 sires and 3664 dams represented in the dataset. The number of offspring per dam ranged from 1 to 12 lambs, and the average number of progeny per dam was 3.2. Ninety-two percent (3366) of dams had at least two lambs, and approximately 46 % of these (1696) had a maximum of six lambs. Dam age ranged from two to 11 years (mean age 3.6 years). The numbers of ewes in an age group decreased with age; the most common ages of dams were two (27.2 %), three (25.4 %) and four (22.3 %) years. The number of progeny per sire ranged from 1 to 235, with an average of 53.17. Number of progeny per sire per year group ranged from 1 to 105 lambs.

Birth-rearing type. Single-born, single-reared lambs made up 36.4 % of the total, twin born – single reared lambs 7.5 %, and twin born – twin reared lambs 56.1 %. Although the majority of lambs are born as twins, nearly 12 % of these are reared as single lambs.

Litter groups. In total there were 8402 different litter groups. Litter groups consist of those animals born to and reared by the same dam in the same year.

Year of birth. Year of birth ranged from 1977 to 2003. Years 1985 onwards had a higher number of records than previous years.

Table 4.2 Count of fixed effects in the dataset.

Year of Birth	No.	Year of Birth	No.
1977	40	1998	481
1978	69	1999	614
1979	66	2000	620
1980	65	2001	586
1981	78	2002	666
1982	86	2003	633
1983	152		
1984	152	**Dam age**	
1985	536	2	3199
1986	569	3	2984
1987	620	4	2620
1988	627	5	2948
1989	516		
1990	530	**Sex**	
1991	536	Male	5490
1992	560	Female	6261
1993	607		
1994	633	**Birth: Rearing type**	
1995	560	Single: Single	4276
1996	584	Twin: Single	883
1997	565	Twin: Twin	6592

Eight-week weight. There were 10667 records of eight-week weight. The mean weight was 20.9 kg, with minimum and maximum values of 10.1 kg and 31.7 kg respectively (Table 4.3).

Scan age and scan weight. There were 1656 records for age at scanning and scan weight, for years 2000 to 2003 only. The mean age of scanning was 156 days (approximately five months), with minimum and maximum values of 121 and 189 days respectively. The mean scan weight was 30.1 kg, with minimum and maximum values of 12 kg and 47 kg respectively (Table 4.3).

Ultrasonic scanned muscle and fat depths. There were 750 records for both muscle depth and fat depth, for years 2000 to 2003. The majority of records

came from female lambs (82.4 %). The mean muscle depth was 20.5 mm, with minimum and maximum values of 14.6 mm and 29.2 mm respectively. The mean fat depth was 3.5 mm, with minimum and maximum values of 1.1 mm and 8.1 mm respectively (Table 4.3).

Table 4.3 Descriptive statistics for each trait and the covariate age at scanning.

	Count	Mean	St. Dev.	Minimum	Maximum
Trait					
8-week weight (kg)	10677	20.90	3.573	10.1	31.7
Scan weight (kg)	1656	30.11	5.028	12	47
Muscle depth (mm)	750	20.50	2.686	14.6	29.2
Fat depth (mm)	750	3.51	1.215	1.1	8.1
Covariate					
Age at scanning (days)	1656	156.3	11.03	121	189

4.4 DISCUSSION

4.4.1 Comments on original records

Ap Dewi *et al.* (2002) reported more observations for scanning data of the CAMDA flock, from the years 1987-1988. These records were not included here because generally scanning was done on the mature animal (average scan age 437 days) and over a wider age range. In Ap Dewi *et al.*'s (2002) study males were scanned at about 12 to 13 months and females between 12 and 20 months. In the cleaned dataset used in this study scanning age is consistent with Signet Protocols of around 20 to 21 weeks of age.

4.4.1.1 Editing

From a total of 15121 individuals, 11751 animals remained in the dataset after editing. Some data were eliminated because groups were represented by very few records, such as the single ewe recorded to have progeny when one year old. Some types of records were rare and were eliminated because they were thought to be errors. For instance, a few animals in the dataset were described as being single born – twin reared. On some farms it is common for ewes that bear a single lamb to have another lamb fostered onto it, if the ewe has plenty of milk to support two lambs; this is particularly likely to happen on lowland farms and when ewes are lambed indoors. However, this was unlikely to have occurred in

the CAMDA flock and so the records were eliminated from the dataset. Some sires appeared to have had very few progeny, sometimes as few as one. This was unlikely to be a true representation of the situation and could be explained either by a failure to enter sires for some animals, or perhaps by incorrect data entry.

Major problems were encountered with identities that were duplicated in the dataset. Some of these may have been due to incorrect data entry. Cases occurred when animals born in the same year had the same identity code, but were clearly different animals. Errors in data recording for these animals could have taken place either on the farm (when reading ear tag numbers, writing tag numbers or writing performance records down at time of recording) or when reading from paper-based records and re-entering data into computer files. If various people carried out different tasks during the stages of collecting and recording data, errors are more likely to have arisen. Identification of an animal throughout its lifetime is crucial. When identification is by use of ear tags, problems can arise when ear tags fall or get ripped out. The farmer may be able to identify the animal, and tag it with the same number, but otherwise it will be given a new number and previous data on the animal will effectively be lost.

Furthermore, it was noticed that flock identities had been repeated and even triplicated due to the use of letters to represent year within the identity codes. For instance, in the CAMDA system, 'T' corresponds to both years 1981 and 1997. Duplicate identities could cause major problems if data were not edited before analysis to distinguish between animals born at different times, and therefore a new identity that included year of birth in the code was created. Most animals in the dataset were born in the CAMDA flock and had a known date of birth; in these cases the construction of the new identity was straightforward. However, it was very difficult to determine year of birth of sires and dams, particularly if their identities as lambs were not present in the dataset. To deduce year of birth from the letter on the tag was not always reliable, because not all tag letters corresponded to a year or single year (see above). Difficulties in determining identities increased, for example, when bought-in animals had different types of identity codes, or if an animal with a lost ear tag had been given another identity, for instance with a tag where the letter did not

correspond with its year of birth, but the year it lost its tag. Therefore, identities for sires and dams in the pedigree file, which already used the format of the new identity codes, replaced original entries in the dataset. The pedigree file was one used by (Saatci, 1998) and was updated with data from recent years.

4.4.2 Importance of data editing

Animal recording is necessary to assess the performance of animals and for the prediction of breeding values. Comparing differences in performance records is fundamental in selecting genetically superior animals, and records in turn depend upon accurate data collection and appropriate use of the data. Data editing is a necessary part of the process of assessment. Original data should be checked for completeness and validity, and cleaning may follow this. Records may also have to be recoded, before analysis, into the format specific to the software used. Preparation of the dataset used for analysis here was quite complex and time consuming. In the version of the file received from Signet there were discrepancies, such as the presence of duplicate identities, which necessitated changing animal identities. During a later visit to the MLC it was learnt that when records of new animals arrive to be entered in their database, they were recoded with new identities. This eliminates the problem of duplicate identities in their analyses. After analysis the recoded identities are converted back to the original identities and the results are returned to the farmer.

4.4.2.1 Potential impact of errors

Errors in data or animals with missing records can have an impact on the accuracy of genetic parameter and breeding value estimation. Maher (1994) stated that errors in data can be costly in terms of the time required to recollect data or because of inefficiencies when decisions are based upon data with undetected errors. Animals for which data are suspect or incomplete are less valuable for breeding estimation and are often excluded from analysis. In breeding programmes it is useful to have full records and as much data as possible, but it is also accepted that in some situations this is not practical, for reasons of cost and time. Some measurements of traits also need particular expertise and equipment. Genetic evaluation of livestock ordinarily involves

evaluation of several traits together. An animal for which some data are missing may be eliminated from analyses, cannot then be selected and could be a loss to improvement programs if they were animals of high genetic merit. Alternatively, animals with incomplete records could remain in the dataset for analyses, and it may be possible to estimate their values for the non-recorded traits indirectly (from relatives or from records of other traits where these are correlated genetically). However, an estimate of a non-recorded trait is likely to be less accurate than a direct measurement of the trait (Bates, undated).

Maniatis and Pollott (2003) emphasized the importance of recording pedigree information. They found that the number of progeny per dam and the proportion of mothers that had their own entry in a dataset influenced parameter estimates greatly. Direct-maternal genetic correlations have often been found to have high negative values that are difficult to explain, and seem biologically impossible (Meyer, 1992). Maniatis and Pollott (2003) put forward the idea that increasing the number of dams with performance records lowered the negative direct-maternal genetic correlation. The disentangling of the maternal genetic component and maternal permanent environmental effects requires repeated records for individual dams. Hence, the ideal is for individuals to have records for sires and dams, and for dams to have all their progeny recorded.

4.4.3 Reducing errors

For the purpose of tracing animals, tagging of sheep has recently become necessary for commercial farmers as well as pedigree breeders. Current proposals from the European Commission are for Electronic Identification (EID) to be made mandatory from 1 January 2008 (DEFRA, 2005) and pilot trials are currently taking place to find out whether it would be practical and effective for use in the UK (Plate 4.1). The use of EID could eliminate identification errors, as identity would be permanent and could not be changed. The EID would not be lost as an ear tag would, unless the ear is torn off. Similarly, rumen boluses are a form of electronic identification in animals, particularly as part of the National Scrapie Plan. However, boluses can be regurgitated, especially if small, and might not to be suitable for administering to lambs as they could choke. In cattle, Fallon *et al.* (undated) found that the most suitable site for implantation of

electronic chips was under the scutellar of the ear. A scanner is used to read the identity electronically, thereby eliminating human error. To further reduce errors the scanner should be connected to a computer system, so as to directly input the data, thereby eliminating more of the stages where errors can take place. The Pig Improvement Company has used this recording protocol with software developed by Pigtales (Maher, 1994). Menus and lists in the software program would be beneficial, to prompt the user during data collection, to ensure data are entered in the way that is required, or as a point of data validation.

Plate 4.1 Ewe with electronic identification in ear (DEFRA, 2005)

The long-standing connection between the University of Wales Bangor and the CAMDA Group Breeding Scheme was very valuable in this study, as there was first-hand knowledge of control animals, foster and genetic dams that allowed some entries to be taken out of the dataset. There is less familiarity with the other breeding schemes that provided data for analyses in later chapters 6 - 11.

Signet is a reputable company, part of the MLC, and is responsible for delivering breeding evaluations to the sheep and beef sector throughout the UK, so would be expected to be dependable. It was thought that for the analyses in chapters 6 – 11 it would be most straightforward to use the PEST files that are used by Signet to estimate breeding values. In these files identities are recoded uniquely, and there is no problem of duplicate identities from different years. Additionally, this approach would mean there would be consistency when compiling further datasets for analysis, as the data from all breeding groups used the same file format.

CHAPTER 5

Evaluation of Models to Estimate Variance Components due to Direct and Maternal Effects on Eight-week, Scan weight, Ultrasonic Muscle and Fat depths of Welsh Mountain Lambs

ABSTRACT

Six models were evaluated, ranging from a simple model, which included only direct additive effects of the animal as a random factor, to more complex models taking account of additive maternal genetic effect, maternal permanent environmental effect, maternal temporary environmental effect and the covariance between direct and maternal genetic effects. The most appropriate model for eight-week weight was one that contained all effects except direct-maternal genetic covariance, and for scan weight it was a model with animal and maternal genetic effect; whereas for the traits muscle depth and fat depth the simplest model was adequate. Direct heritability estimates for eight-week weight, scan weight, muscle and fat depth were 0.18, 0.23, 0.23 and 0.25, respectively. Maternal heritability for eight-week weight and scan weight were 0.09 and 0.17, respectively. The results show that it is important to choose a model that suitably reflects the conditions in which an animal is raised. There are considerable differences in heritability estimates depending whether maternal effects are included in the model, and the simple model alone can produce inflated estimates of heritability. In cases where the environment due to the dam affects the lamb during early growth, choosing the wrong model may result in biased estimates of heritability, which may result in progress in genetic gain to be less than or different from that anticipated.

5.1 INTRODUCTION

The amount of variation observed in a phenotypic trait in a population can be quantified as its variance (Falconer and Mackay, 1996). The partitioning of variance into components, due to genetic and environmental causes, allows estimation of their relative importance in determining phenotype, and knowledge of variance components is fundamental in breeding programs. Components of variance are described in more detail in section 2.2.2.2.

5.1.1 The importance of maternal effects

In animals where family members are dependent on or in close proximity to one another, the variance of a trait could be made up of several components that reflect contributions from related individuals (Willham, 1963; Willham, 1972). Offspring inherit genes affecting performance from both parents (direct additive genetic effect), and will perform better or worse than others depending on this, their dam's maternal ability, and environmental influences. Maternal ability is a genetic trait passed to offspring from both sire and dam; however, it is only expressed in females when they have offspring.

In many species, the dam's contribution to the phenotype of her progeny is much greater than the sire's (Ferraz Filho *et al*, 2004), and it is suggested that the dam's phenotype is the most important environmental condition experienced by an individual during its development (Wade, 1998). As well as the dam contributing half her genes to the next generation, the dam provides an environment for the offspring as it develops. The individual's phenotype is determined not by just its own genotype and the environmental conditions it experiences during development, but is also influenced by the phenotype or environment of its mother (Wade, 1998). The maternal effect is an environmental influence relative to the offspring, but the phenotypic differences between dams for the maternal effect are shown in the phenotypic values of the offspring (Willham, 1963). Milk production and mothering ability are the main characteristics of the dam affecting the offspring's environment; however,

uterine environment and extra-chromosomal inheritance may also play a part (Meyer, 1992).

The variation between dams in their maternal performance may arise from genetic or environmental causes, and therefore maternal phenotypic variation that has effects on offspring phenotypes can be divided into genetic and environmental components, as illustrated in Figure 5.1. Genetic factors affecting the individual can therefore be partitioned into direct additive genetic and additive maternal genetic effects. Environmental maternal effects can be divided into two types, maternal permanent environmental effect (or general effects) and maternal temporary environmental effect (also referred as immediate, common, or litter effects). Maternal permanent environmental effect is an effect due to the dam that is consistent across all litters born during the dam's lifetime. For example, a dam with only one side of its udder in working order as a result of mastitis would provide poorer nutrition to all lambs since mastitis occurring. Maternal temporary environmental effect is an environmental effect that would be experienced by lambs of the same dam in the same year; however, the effect may not necessarily be the same each year. For instance, a ewe may consume less food in one particular year, and her lambs will receive less nourishment. This could be due to age, for instance yearling ewes with fewer teeth or older ewes with worn teeth, or to disease, such as footrot. Ekiz *et al.* (2004) suggest that maternal environmental effects on birth weight is largely determined by uterine capacity, feeding level at late gestation and the maternal behaviour of the dam, and that weaning weight is largely determined by the milk production of the dam.

It is expected that maternal effects will be more important in sheep than cattle or pigs. Compared with cattle there is greater relative variation in litter size at birth in sheep, and in many production systems lambs are dependent on their mother's milk supply until very close to the time of marketing, or until they have achieved a high proportion of their slaughter weight (Bradford, 1972).

Wade (1998) distinguished between prezygotic, postzygotic-prenatal and postzygotic-postnatal maternal effects. Maternal effects play a significant role in

postnatal growth, and this influence tends to decrease after weaning as the genes of the offspring have an increasingly important direct effect on growth. Passive immunity, transferred from dam to offspring via the placenta or colostrum, is very important for early survival, and its influence, like other maternal effects, diminishes as the offspring increases in age and produces its own antibodies. In addition to the nourishment a dam provides to her offspring, the behaviour of the dam is important in providing protection from predators, seeking shelter, and finding suitable areas for water and grazing. Although the offspring's dependence on the dam decreases with time and terminates at weaning, it is nevertheless likely that for certain traits maternal effects persist after weaning.

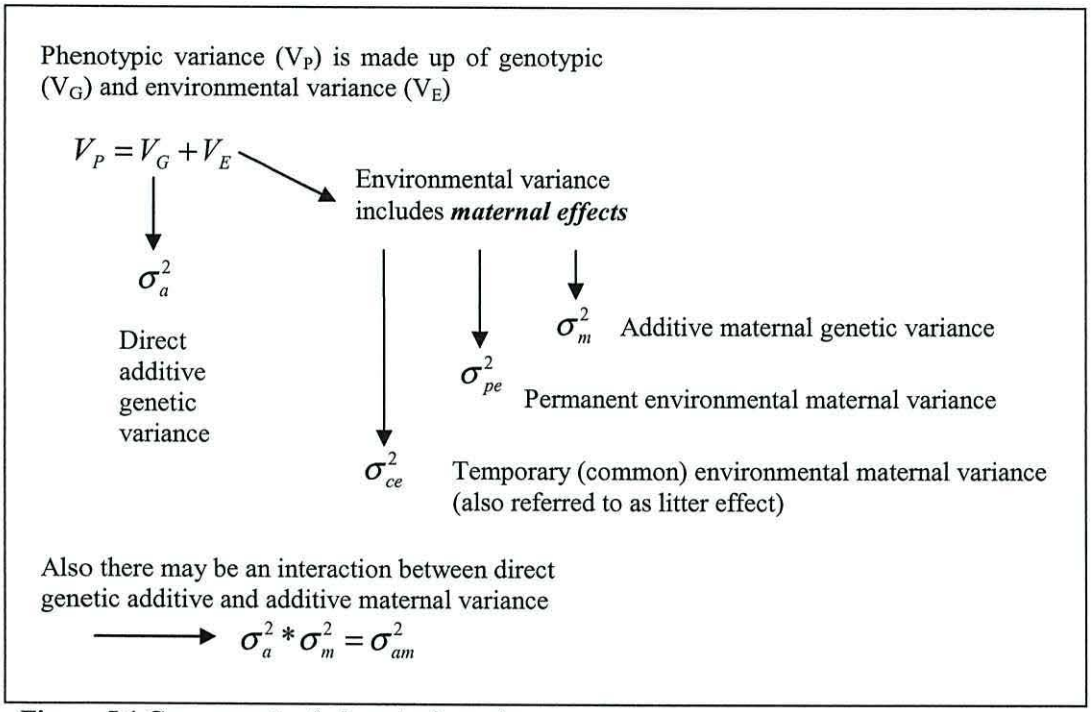


Figure 5.1 Components of phenotypic variance

Wade (1998) suggested that maternal effects could be equal to or more important than the genes of the offspring during the early post-natal growth period, up to at least six weeks of age, during which the mothers nurse their young. Tosh and Kemp (1994) showed the importance of maternal effects for lamb weight at an age of 100 days for Hampshire and Polled Dorset sheep breeds. Solanes *et al.* (2004) suggested that in pigs, early growth should be treated as a maternal trait, but that late and overall growth rate should be treated as a direct trait, in breeding evaluations. Robison (1981) indicated the importance of maternal effects in some adult traits. In beef cattle, Prayaga (2003) found that maternal additive effects were highly significant for weaning weight and pre-weaning average

daily gain, and suggested possible carry-over effects to yearling weight. Nasholm and Danell (1996), working with lambs, observed high maternal genetic correlations between both birth weight with 120 day weight and slaughter weight (mean age of 174 days), and suggested that maternal effects on later weights were, in part, effects carried on from the pre-natal period.

5.1.2 Importance of including maternal effects in breeding programs

Many studies have concluded that maternal components of variability as well as direct effects should be accounted for to achieve optimum genetic progress in breeding programs, particularly when antagonisms exist between the direct and maternal components (Robison, 1981). Maternal effects are well recognised, and they are often considered as complications that make interpreting biological data more difficult. Estimation of maternal effects and covariance components is difficult because direct and maternal effects are generally confounded, expressed only by females, occur late in life, and lag one generation (Willham, 1980).

Understanding of the genetic variation in maternal effects and the relationship between direct genetic and maternal effects is crucial for planning breeding programs, as heritability estimates may otherwise be biased due to the presence of maternal effects. Several studies have included maternal environmental, additive maternal genetic and the covariance between direct and maternal additive genetic effects into models estimating heritabilities; they include studies by Maniatis and Pollott (2002b) for early growth traits in sheep, and by Meyer (1992) for growth traits in beef cattle. Both studies concluded that models were significantly improved by the inclusion of maternal effects and that their exclusion would cause heritabilities to be overestimated. Clément *et al.* (2001) reported that when maternal effects existed, but were not accounted for, direct heritability could be inflated by more than 100 %, and the bias was influenced by the genetic correlation between direct and maternal effects. Hanford *et al.* (2003) stated that use of direct and maternal genetic effects and, as appropriate, either

direct[1] or maternal permanent environmental effects in standard models is adequate for some production traits. However, only when there are several generations of data can maternal genetic effects be accurately estimated (DEFRA, 2003a).

5.1.3 Use of models

Use of the REML (Restricted Maximum Likelihood) method in an animal model forms the basis of estimating variance components and BLUP breeding values. Genetic analysis using a simple animal model includes only the direct additive genetic component, which is the sum of parental gamete contribution, as a random effect (Maniatis, 2000). Development of more sophisticated models has allowed phenotypic variance to be partitioned into its variance components and determination of indirect effects, such as maternal effects. Naal-Castillo and Segura-Correa (2004) indicated that no particular type of model should be used for any given set of data, but suggested that, in order to estimate reliable heritabilities, the best model should account for all genetic and environmental effects of the population. Misztal (1994) stated that the best type of model for analysing data was species-dependent. For instance, in dairy cattle a single trait repeatability model is generally used for production data and a multitrait (repeatability) model for conformation data. The preferred model for pigs and poultry is the multitrait model. In beef cattle, models are multitrait with maternal effects included.

Conington *et al.* (1995) accounted for maternal effects, although the maternal genetic component was also confounded with the maternal temporary environmental effect. Saatci *et al.* (1999) employed 12 models for variance component analysis. These were based upon models of Meyer (1992), modified to enable a maternal temporary environment effect to be included with or without a maternal permanent effect. Maniatis and Pollott (2002a) considered nine models in an analysis of the eight-week weight, scan weight, muscle and fat

[1] Direct permanent environmental effects of the animal are included in models where there are repeated records for a trait, for example litter size, milk yield and fleece weight are traits that could be recorded each year for the same animal.

depth in Suffolk lambs that were part of a sire referencing scheme. In addition to the animal-maternal models described above, sire interactions with year, flock and flock-year were examined to determine the extent of genotype-environment interactions. Similarly, Hagger (1998) evaluated 12 models that included terms such as flock-year and ram-flock effects. An additional feature of some models is the inclusion of the effect of mitochondrial inheritance (Hanford *et al*, 2003; Maniatis and Pollott, 2002b; Snowder *et al*, 2004; Van Vleck *et al*, 2005; Van Vleck *et al*, 2002). Clément *et al.* (2001) reported that the omission of one random effect can lead to incorrect estimation of the other components. Results from various studies of direct heritability and maternal genetic heritability for weight traits and ultrasonically-scanned traits are shown in Table A.1 in Appendix A. The results for different breeds show the importance of obtaining breed-specific parameters in the design of optimal breeding programmes (Ap Dewi *et al*, 2002; Nsoso *et al*, 2004; Prayaga, 2003). Safari *et al.* (2005) reviewed the literature on various breeds and presented mean heritability estimates of traits. For meat breeds direct heritability estimates for weaning weight, muscle depth, and fat depth were 0.18, 0.26, and 0.24, respectively.

Saatci (1998) recommended that the fixed effects birth year, rearing type, dam age, and age of animal should be used to estimate genetic parameters for weaning weight. Birth year reflects the environmental differences between years, for example the weather (which affects grass growth) and differences in location of certain groups of animals (which may result in differences in pasture quality). Inexperienced maiden dams can explain some of the effects of dam age on growth traits; these dams have lower milk yields and hence their lambs have lower weights. Furthermore, poorer nutrition of older ewes due to their worn teeth can result in lighter lambs. Rearing type also affects the nutrition of lambs, due to competition between littermates and the lighter birth weights of multiple litters. It is also widely reported that there are significant differences in growth between males, females, and castrates. Age, as expected, is required as a covariate in data analysis when animals are measured at different times, as weight generally increases with age. Saatci (1998) reported that the interactions between the factors were also important.

The objectives of the work described in this chapter were to compare models that differed in the random effects included, using the cleaned CAMDA data described in Chapter 4, and to identify the most appropriate models for analysing data on the traits eight-week weight, scan weight, muscle depth and fat depth.

5.2 METHODS

5.2.1 Source of animals and data

Data were obtained from the CAMDA flock of Welsh Mountain sheep described in section 3.1.1.1. The editing and cleaning of the data were described in Chapter 4. Eight-week weight, scan weight, muscle and fat depths were recorded by Signet as part of a recording scheme.

5.2.1.1 Description of the traits

Eight-week weight (kg) is a measure for growth rate up to eight weeks of age as well as an assessment of the maternal ability of the ewe. Lambs can be weighed between 42 and 84 days of age and the weights are adjusted to eight weeks.

Scan weight (kg) is a measure of growth rate to 21 weeks of age taken at the time of ultrasonic scanning. Selection for heavier scan weights results in animals with heavier carcasses at a constant fat class or leaner carcasses at a constant age.

Muscle depth (mm) is measured by one ultrasound measurement across the third lumbar vertebra at 21 weeks (section 3.1.3) and is an assessment of loin muscle depth and is used as a predictor for carcase muscling i.e. likely lean meat yield

Fat depth (mm) is measured by the average of three ultrasound measurements taken across the third lumbar vertebra at 21 weeks (section 3.1.3) and is an assessment of leanness. Low fat levels should produce leaner carcasses that can be taken to heavier weights without becoming too overfat.

Eight-week weight had been adjusted by Signet for age. Records for eight-week weight were from years 1977-2003, whereas records for scan weight, muscle and

fat depth were from years 2000-2003. The mean age for the scanning of lambs was 156 days (approximately 22 weeks), as shown in Table 4.3 (Chapter 4). Normality of the data for the four traits was assessed using Minitab 14. All traits showed significant ($P \leq 0.01$) deviations from normality using the Kolmogorov-Smirnof test. However, the traits presented fairly normal distributions when assessed visually, so data were not transformed (Figure A.1, Appendix 1).

5.2.2 Description of the models used

The models used for analysis of variance were mixed models, including fixed and random effects (Ap Dewi, undated). Birth year, dam age, sex, birth rearing type and interactions between these, with the exception of dam age, were treated as fixed effects, based upon commonly accepted procedures of other authors (Ap Dewi *et al*, 2002; Saatci, 1998). The number of animals in the dataset for birth year, dam age, sex and birth rearing type are given in Table 4.2 (Chapter 4). Scan age was included as a covariate in the analysis of scan weight, muscle depth, and fat depth.

Model 1 was the simplest, with the direct additive genetic effect (σ^2_a) as the only random factor. The following model was used:

Equation 5. 1

$$Y_{ijklm} = \mu + a_i + b_j + c_k + d_l + f_m + b_j c_k + b_j d_l + c_k d_l + b_j c_k d_l + z_m + e_{ijklm}$$

where μ = overall mean of eight-week weight, scan weight, muscle depth or fat depth; a_i = fixed effect of rearing dam age (i= 2-5); b_j = fixed effect of lamb sex (j= male/female); c_k fixed effect of birth rearing type (k= S:S, T:S, T:T (Section 4.3.2)); d_l = fixed effect of year of birth (l= 1977 to 2003); f_m = is lamb age as a covariate (not needed for eight-week weight); $b_j c_k$ = the interaction between j^{th} sex of animal and k^{th} birth rearing type; $b_j d_l$ = the interaction between j^{th} sex of animal and l^{th} year of birth; $c_k d_l$ the interaction between k^{th} birth rearing type and l^{th} year of birth; $b_j c_k d_l$ = interaction between j^{th} sex of animal, k^{th} birth rearing type, and l^{th} year of birth; z_m = random effect of animal m; e_{ijklmn} = random environmental effect.

Model 2 was Model 1 plus the additive maternal genetic effect (σ^2_m) as an additional random effect.

Equation 5. 2

$$Y_{ijklmn} = \mu + a_i + b_j + c_k + d_l + f_m + b_j c_k + b_j d_l + c_k d_l + b_j c_k d_l + z_m + x_n + e_{ijklmn}$$

where x_n = the random maternal additive genetic effect of the n^{th} dam.

Model 3 was Model 2 with the addition of permanent environmental effect (σ^2_{pe}) due to the dam.

Equation 5. 3

$$Y_{ijklmn} = \mu + a_i + b_j + c_k + d_l + f_m + b_j c_k + b_j d_l + c_k d_l + b_j c_k d_l + z_m + x_n + w_n + e_{ijklmn}$$

where w_n = the random maternal permanent environmental effect of the n^{th} dam.

Model 4 was the addition of litter or the maternal temporary environment effect (σ^2_{ce}) to Model 2, as an additional random factor.

Equation 5. 4

$$Y_{ijklmn} = \mu + a_i + b_j + c_k + d_l + f_m + b_j c_k + b_j d_l + c_k d_l + b_j c_k d_l + z_m + x_n + v_{nl} + e_{ijklmn}$$

where v_{nl} = the random maternal temporary environmental effect of the n^{th} dam in the l^{th} year.

Model 5 was created by the addition of litter or the maternal temporary environment effect to Model 3, as an additional random factor. Model 5 could be compared with both Models 3 and 4.

Equation 5. 5

$$Y_{ijklmn} = \mu + a_i + b_j + c_k + d_l + f_m + b_j c_k + b_j d_l + c_k d_l + b_j c_k d_l + z_m + x_n + w_n + v_{nl} + e_{ijklmn}$$

Model 6 was created by the addition of the covariance between direct and maternal additive genetic effects (σ^2_{am}).

Equation 5. 6

$$Y_{ijklmn} = \mu + a_i + b_j + c_k + d_l + f_m + b_j c_k + b_j d_l + c_k d_l + b_j c_k d_l + z_m + x_n + w_n + v_{nl} + u_{mn} + e_{ijklmn}$$

where u_{mn} = the random direct-maternal interaction between the m^{th} animal and n^{th} dam.

5.2.2.1 Estimation of genetic parameters

Variance components for direct and maternal effects and covariance components between these effects were estimated in ASReml (Gilmour *et al*, 2002) for the four measured traits. Convergence of log likelihood (logL) was reached for each model run in ASReml. Variance components were then used to calculate phenotypic variances (σ_p^2) and to estimate direct (h^2) and maternal heritabilities (m^2) for each model and trait.

Equation 5. 7

Phenotypic variance (σ_p^2) $= \sigma_a^2 + \sigma_m^2 + \sigma_{pe}^2 + \sigma_{ce}^2 + \sigma_{am}^2 + \sigma_e^2$

Equation 5. 8

Direct heritability $(h^2) = \frac{\sigma_a^2}{\sigma_p^2}$

Equation 5.9

Maternal heritability $(m^2) = \frac{\sigma_m^2}{\sigma_p^2}$

The proportion of phenotypic variance due to maternal environmental effects was calculated for both permanent and temporary environmental effects

Equation 5.10

For maternal permanent environment $(pe^2) = \frac{\sigma_{pe}^2}{\sigma_p^2}$

Equation 5.11

For maternal temporary environment $(ce^2) = \frac{\sigma_{ce}^2}{\sigma_p^2}$

Direct-maternal relationships were examined by calculating the genetic direct-maternal covariance (C_{am}) and the direct-maternal additive genetic correlation (R_{am}).

Equation 5.12

Genetic direct-maternal covariance $(C_{am}) = \frac{\sigma_{am}^2}{\sigma_p^2}$

Equation 5.13

Direct-maternal additive genetic correlation (R_{am}) $= \frac{C_{am}}{\sqrt{h^2 * m^2}}$

The total additive genetic influence of parents on offspring was expressed by total heritability (h_T^2).

Equation 5.14

$$\text{Total heritability } (h_T^2) = \frac{(\sigma_a^2 + 0.5\sigma_m^2 + 1.5\sigma_{am}^2)}{\sigma_p^2}$$

5.2.2.2 Model Selection

The procedure used by Ap Dewi *et al.* (2002) was used to determine whether components of variance were significant. Each component was divided by its standard error (C/se) and when the ratio was greater than or equal to 2, it was considered significant. Values of C/se less than 0.5 were considered as non-significant and the significance of values between 0.5 and 2 were determined using a likelihood ratio test (P = 0.05), and models were compared with or without the effect.

To determine the most appropriate model, log likelihood ratio (logL) tests were used for each trait. An effect was considered to have a significant influence when its addition caused a significant increase in the logL value (generally logL values tend to be negative therefore models with values closer to zero are chosen), compared to a model without the effect. Only models that differed by one parameter (neighbouring models) were compared. If the difference in logL between two models was greater than 3.84 (χ^2, 1 degree of freedom, P > 0.05), the effect of the added parameter was considered to be significant. When log likelihoods did not differ significantly (P > 0.05), the model with fewest parameters was selected as the most appropriate model.

5.3 RESULTS

5.3.1 Eight-week weight

Descriptive statistics for fixed effects are shown in Table 5.1.

Table 5.1 Counts, means and standard deviations of fixed effects year, sex, dam age and birth rearing type (Brt) for eight-week weight.

Trait	Count	Mean (kg)	Sd (kg)	Trait	Count	Mean (kg)	Sd (kg)
Year				**Sex**			
1977	38	18.19	2.798	Male	4993	22.31	3.645
1978	67	17.73	2.69	Female	5674	19.65	3.000
1979	62	16.52	2.621				
1980	64	20.25	2.238	**Dam age**			
1981	76	18.18	2.201	2	2906	20.03	3.464
1982	78	20.39	3.191	3	2717	21.32	3.504
1983	147	19.32	2.084	4	2353	21.31	3.509
1984	151	19.8	2.559	5 +	2691	21.04	3.650
1985	525	20.44	3.841				
1986	560	19.59	3.282	**Brt**			
1987	593	20.25	3.288	S:S	3947	22.32	3.655
1988	608	19.14	3.297	T:S	509	20.86	3.735
1989	489	20.64	3.525	T:T	6211	19.99	3.191
1990	501	21.26	3.232				
1991	503	21.5	3.447				
1992	522	19	2.863				
1993	480	22.12	3.321				
1994	561	20.31	3.565				
1995	502	21.73	3.45				
1996	519	22.28	3.732				
1997	514	21.43	3.615				
1998	427	23.41	3.475				
1999	567	20.83	3.35				
2000	605	21.96	3.207				
2001	579	20.3	3.575				
2002	411	21.62	2.938				
2003	518	22.87	3.356				

S:S single born -single reared; T:S twin born -single reared; T:T twin born -twin reared.

Year. Year of birth for the period 1977-2003 was used. There were few records in the early years up until 1982. The lowest mean weight of 16.52 kg was recorded in 1979 and the heaviest mean weight of 23.41 kg in 1998 (Table 5.1).

Sex. Comparison of mean weights showed that males were heavier than females by about 2.6 kg (Table 5.1).

Dam age. Dam aged ranged from 2 to 5 years. Mean weights were lowest (20.0 kg) for the offspring of two-year old dams and heaviest (21.3 kg) for the offspring of three and four-year-old dams (Table 5.1).

Birth-rearing type. Mean weight decreased in the order single born - single reared, twin born - single reared, and twin born - twin reared (Table 5.1).

Estimates of variance components and genetic parameters for eight-week weight together with logL values for all six models are shown in Table 5.2 and illustrated in Figure 5.2. Direct and maternal heritability estimates derived from the models ranged from 0.17 to 0.36 and from 0.08 to 0.18 respectively. Model 5 was chosen as the most appropriate model for analysing eight-week weight data because it had the logL value closest to zero. All models were significantly different from their neighbouring model, and logL moved closer to zero from Model 1 to Model 5. Model 6 had a logL value further from zero than Model 5. Model 5 produced estimates for direct heritability and maternal heritability of 0.18 and 0.09, respectively.

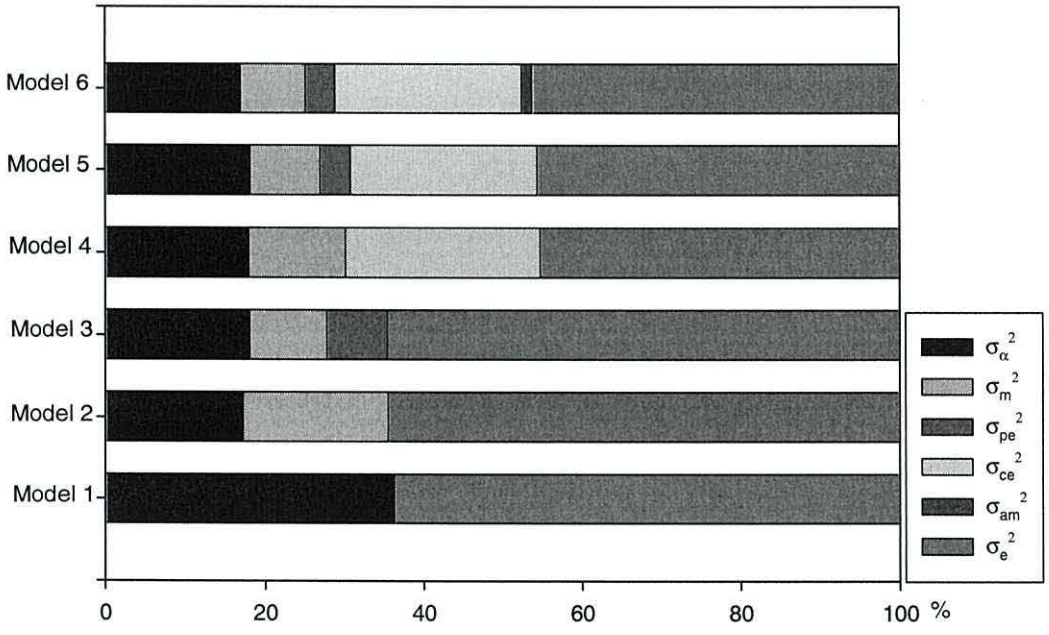


Figure 5.2 Contribution of variance components to phenotypic variance of eight-week weight in models 1-6. See Table 5.2 for definitions of components.

Table 5.2 Models to estimate (co)variance components and genetic parameters for eight-week weight of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	2.71	1.28	1.31	1.30	1.31	1.22
σ^2_m		1.36	0.71	0.89	0.641	0.59
σ^2_{am}						0.09
σ^2_{pe}			0.55		0.28	0.27
σ^2_{ce}				1.79	1.70	1.70
σ^2_e	4.75	4.79	4.67	3.30	3.30	3.34
σ^2_p	7.46 ± 0.13	7.43 ± 0.13	7.24 ± 0.12	7.30 ± 0.13	7.23 ± 0.12	7.23 ± 0.12
h^2	0.362 ± 0.02	0.172 ± 0.02	0.181 ± 0.02	0.180 ± 0.02	0.182 ± 0.02	0.169 ± 0.03
m^2		0.183 ± 0.01	0.098 ± 0.02	0.122 ± 0.03	0.088 ± 0.02	0.082 ± 0.02
pe^2			0.076 ± 0.01		0.038 ± 0.01	0.037 ± 0.01
ce^2				0.246 ±0.02	0.236 ± 0.02	0.236 ± 0.02
C_{AM}						0.013 ± 0.02
r_{AM}						0.110 ± 0.14
h^2_T	0.362	0.271	0.230	0.240	0.225	0.230
logL	-15447.8	-15323.0	-15308.9	-15214.1	-15210.6	-15232.4
diff	0	124.8 (S)	14.1 (S)	108.9 (S)	98.3/3.5 (S)	-21.8

σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{am} direct-maternal genetic covariance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal common environmental variance; σ^2_e error variance; σ^2_p phenotypic variance, h^2 direct heritability, m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal common environmental variance expressed as a proportion of the phenotypic variance, C_{AM} genetic covariance between direct and maternal effects expressed as a proportion of the phenotypic variance; r_{AM} genetic correlation between direct and maternal effects; h^2_T total heritability; logL log likelihood ratio; diff difference between neighbouring models; Model 4 compared with 2, model 5 compared with 3 and 4. S = significant, N.S = non significant.

Model 1 gave the highest estimate of direct heritability (0.36) out of all the models. The model did not account for the additive maternal genetic effect, and by comparing it with Model 2, which included additive maternal genetic effect, it can be seen that the estimates of direct heritability and additive direct effect were inflated in Model 1, due to the compounding of additive direct effect and additive maternal genetic effect.

Including the maternal permanent environmental effect, as in Model 3, resulted in a decrease in the value of the additive maternal genetic effect, and maternal heritability decreased to nearly half of its value in Model 2.

Model 4 replaced the maternal permanent environmental effect of Model 3 with the maternal temporary environmental effect, and showed that the latter was the

more important of the two effects by providing a better fit to the data (logL significantly closer to zero).

The addition of the maternal temporary environmental effect to Model 3 (i.e. Model 5) did not affect direct heritability, but did reduce the estimates of maternal heritabilty, maternal permanent environmental variance and some of the error variance.

Including the covariance between the direct additive genetic effect and direct maternal effects in Model 6 caused additive direct genetic and additive maternal genetic effects to decrease, thus also reducing direct heritability and maternal heritability.

5.3.2 Scan weight

Descriptive statistics for fixed effects are shown in Table 5.3

Table 5.3 Counts, means and standard deviations of fixed effects year, sex, dam age and birth rearing type for scan weight.

Effect	Count	Mean (kg)	Sd. (kg)
Year			
2000	88	28.92	2.870
2001	499	27.98	4.926
2002	542	30.88	4.993
2003	527	31.55	4.725
Sex			
Male	753	32.35	5.175
Female	903	28.25	4.050
Dam age			
2	371	29.20	4.763
3	392	29.90	5.267
4	411	30.21	4.868
5 +	482	30.91	5.045
Birth rearing type			
S:S	623	31.67	5.090
T:S	35	30.64	5.156
T:T	988	29.12	4.731

S:S single born -single reared; T:S twin born -single reared; T:T twin born -twin reared.

Year. Year of birth for the period 2000-2003 was used. The lowest mean scan weight of 27.98 kg was recorded in 2001, and mean values increased to 31.55 kg in 2003 (Table 5.3).

Sex. Comparison of mean weights showed that males were heavier than females by about 4 kg.

Dam age. Age of dam ranged from 2 to 5 years. Mean scan weights increased with dam age, from 29.20 kg for two-year-old dams to 30.91 kg for five-year-old dams (Table 5.3).

Birth-rearing type. Three classes were used, as for eight-week weight, and scan weight decreased in the same order (Tables 5.1 and 5.3).

Estimates of variance components and genetic parameters for scan weight together with logL values for all six models are shown in Table 5.4 and illustrated in Figure 5.3. Direct and maternal heritability estimates derived from the models ranged from 0.23 to 0.60 and from 0.02 to 0.17, respectively. Model 2, which included only the additive direct effect and maternal genetic additive effect, had a logL value that was closer to zero and significantly lower than the logL value for Model 1. Model 2 gave estimates for direct and maternal heritability of 0.23 and 0.17, respectively, and a phenotypic variance of 14.67 kg.

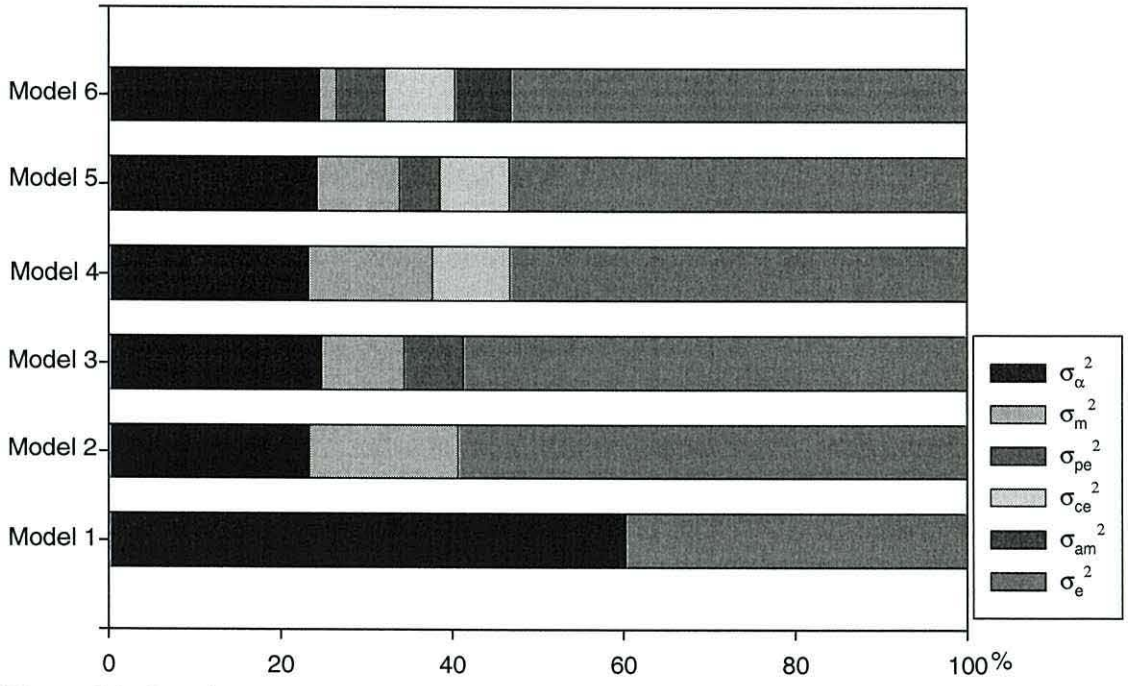


Figure 5.3 Contribution of variance components to phenotypic variance of scan weight in models 1-6. See Table 5.2 for definitions of components.

Table 5.4 Models to estimate (co)variance components and genetic parameters for scan weight of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	9.55	3.42	3.58	3.39	3.51	3.55
σ^2_m		2.55	1.39	2.10	1.38	0.29
σ^2_{am}						0.95
σ^2_{pe}			1.00		0.68	0.82
σ^2_{ce}				1.32	1.18	1.18
σ^2_e	6.28	8.71	8.49	7.75	7.69	7.68
σ^2_p	15.84 ± 0.76	14.67 ± 0.64	14.46 ± 0.64	14.56 ± 0.62	14.45 ± 0.62	14.47 ± 0.62
h^2	0.603 ± 0.07	0.233 ± 0.08	0.248 ± 0.09	0.233 ± 0.09	0.243 ± 0.09	0.246 ± 0.09
m^2		0.174 ± 0.04	0.096 ± 0.06	0.144 ± 0.04	0.096 ± 0.06	0.020 ± 0.07
pe^2			0.069 ± 0.05		0.047 ± 0.05	0.057 ± 0.05
ce^2				0.091 ± 0.05	0.082 ± 0.05	0.081 ± 0.05
C_{AM}						0.066 ± 0.06
r_{AM}						0.948 ± 2.49
h^2_T	0.603	0.320	0.296	0.305	0.291	0.354
logL	-2962.61	-2955.99	-2955.22	-2954.06	-2953.71	-2953.58
diff	0	6.62 (S)	0.77 (N.S)	1.93 (N.S)	1.51/0.35 (N.S)	0.13 (N.S)

See Table 5.2 for definition of abbreviations.

5.3.3 *Ultrasonic scanned muscle and fat depth*

Descriptive statistics for fixed effects are presented in Table 5.5.

Table 5.5 Count, mean and standard deviations of fixed effects year, sex, dam age and birth rearing type for ultrasonic muscle depth and fat depth.

		Muscle depth		Fat depth	
Fixed effects	**Count**	**Mean (mm)**	**St.dev. (mm)**	**Mean (mm)**	**St.dev. (mm)**
Year					
2000	88	18.87	2.139	3.47	1.063
2001	190	18.63	1.916	3.14	0.975
2002	277	20.47	1.841	4.19	1.176
2003	195	23.10	2.447	2.93	1.072
Sex					
Male	132	21.75	2.936	3.34	1.230
Female	618	20.23	2.553	3.55	1.209
Dam age					
2	184	20.19	2.754	3.26	1.066
3	175	20.49	2.696	3.46	1.180
4	192	20.41	2.859	3.53	1.330
5 +	199	20.88	2.400	3.77	1.215
Birth rearing type					
S:S	356	20.79	2.814	3.69	1.303
T:S	10	22.28	2.780	3.36	1.274
T:T	364	20.19	2.515	3.35	1.105

S:S single born -single reared; T:S twin born -single reared; T:T twin born -twin reared.

Year. Year of birth for the period 2000 to 2003 was used. There was an increase in muscle depth from 18.63 mm in 2001 to 23.10 mm in 2003. Mean fat depth varied from year to year; the lowest mean was 2.93 mm in 2003 and the highest mean was 4.19 mm in 2002 (Table 5.5).

Sex. The majority of records were for females. Comparison of sexes showed that mean muscle depth was greater in males by about 1.5 mm and mean fat depth was greater in females by about 0.20 mm (Table 5.5).

Dam age. Age of dam ranged from 2 to 5 years. Greatest mean muscle depth (20.88 mm) came from offspring of dams aged five or more and lowest mean muscle depth (20.19 mm) came from two-year-old dams (Table 5.5).

Birth-rearing type. Twin born - single reared had the greatest mean muscle depth (22.28 mm), but only ten animals were grouped in this category. Fat depth was greatest (3.69 mm) in single born: single reared lambs (Table 5.5).

Estimates of variance components and genetic parameters for muscle depth and fat depth, together with logL values for all six models, are shown in Tables 5.6 and 5.7 and illustrated in Figures 5.4 and 5.5. For muscle depth, direct heritability and maternal heritability ranged from 0.09 to 0.23 and from 0.04 to 0.08, respectively. For muscle depth the most appropriate model appeared to be the simplest model, which only included animal as a random factor (Model 1). The heritability estimate for Model 1 was 0.23 and the phenotypic variance was 4.1 mm. Other models showed no significant improvement in logL values. For fat depth, direct heritability and maternal heritability ranged from 0.20 to 0.25 and from 0.02 to 0.03, respectively. As for muscle depth, the most appropriate model appeared to be the simplest model, which only included animal as a random factor (Model 1). The heritability estimate for Model 1 was 0.25 and the phenotypic variance was 1.0 mm.

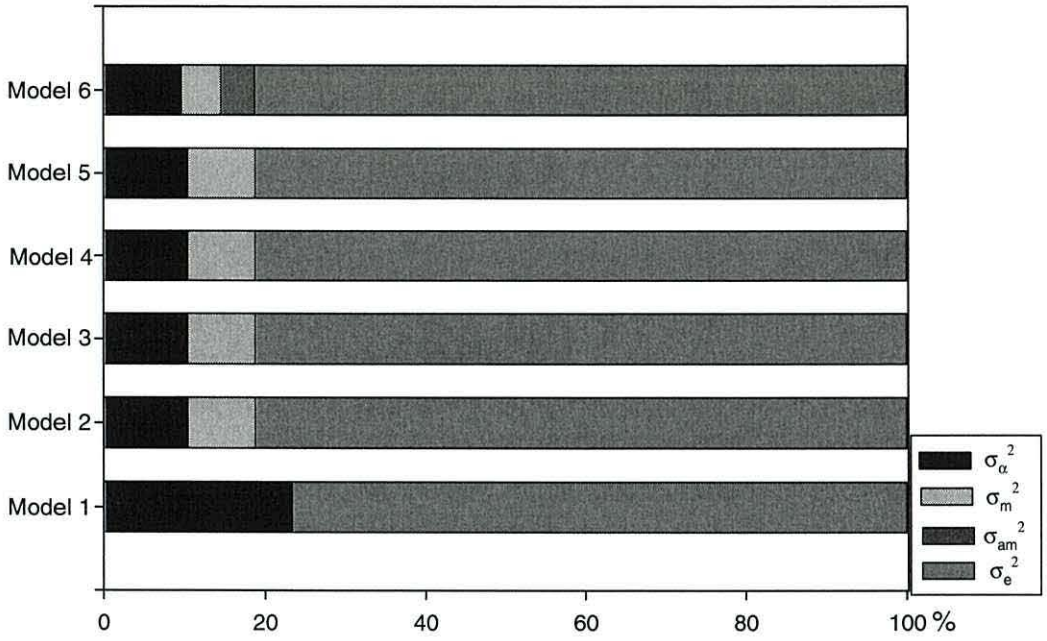


Figure 5.4 Contribution of variance components to phenotypic variance of ultrasonic muscle depth models 1-6. See Table 5.2 for definitions of components.

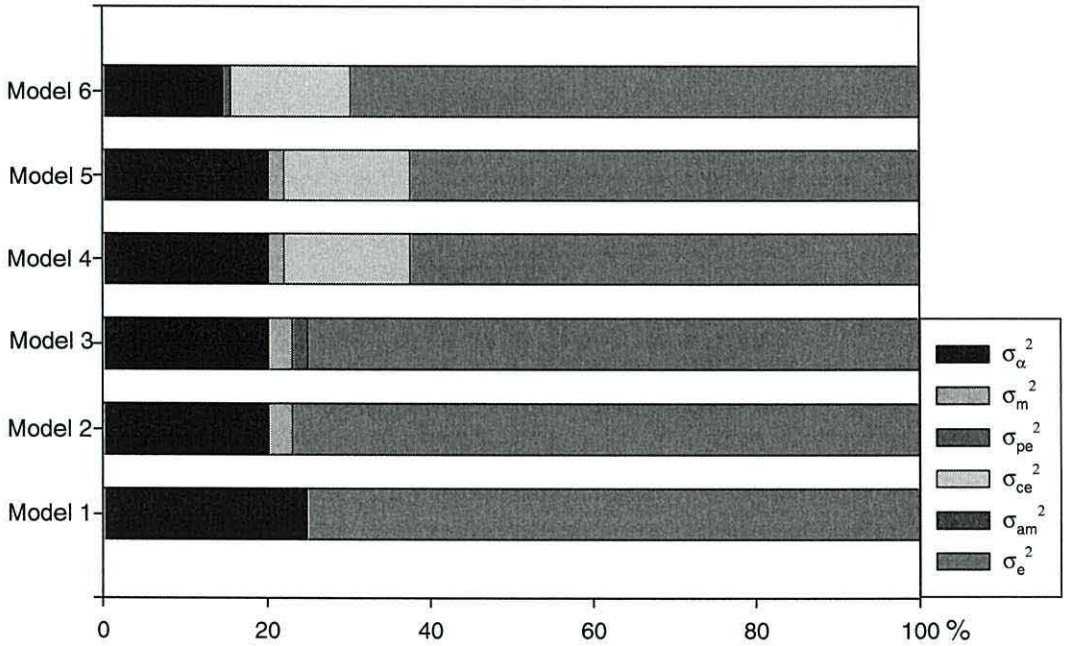


Figure 5.5 Contribution of variance components to phenotypic variance of ultrasonic fat depth models 1-6. See Table 5.2 for definitions of components.

Table 5.6 Models to estimate (co)variance components and genetic parameters for muscle depth of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	0.91	0.40	0.40	0.40	0.40	0.37
σ^2_m		0.32	0.32	0.32	0.32	0.19
σ^2_{am}						0.16
σ^2_{pe}			<0.00		<0.00	<0.00
σ^2_{ce}				<0.00	<0.00	<0.00
σ^2_e	2.98	3.11	3.11	3.11	3.11	3.12
σ^2_p	3.893 ± 0.22	3.829 ± 0.21	3.829 ± 0.21	3.829 ± 0.21	3.829 ± 0.21	3.831 ± 0.21
h^2	0.234 ± 0.091	0.104 ± 0.084	0.104 ± 0.085	0.104 ± 0.085	0.104 ± 0.085	0.095 ± 0.079
m^2		0.083 ± 0.055	0.083 ± 0.055	0.083 ± 0.055	0.083 ± 0.055	0.049 ± 0.075
pe^2			<0.000		<0.000	<0.000
ce^2				<0.000	<0.000	<0.000
C_{AM}						0.042 ± 0.065
r_{AM}						0.990 ± 1.349
h^2_T	0.234	0.145	0.145	0.145	0.145	0.182
logL	-883.095	-881.811	-881.811	-881.811	-881.811	-881.609
diff	0	1.284 (N.S)	0 (N.S)	0 (N.S)	0/0 (N.S)	0.202 (N.S)

See Table 5.2 for definition of abbreviations

Table 5.7 Models to estimate (co)variance components and genetic parameters for fat depth of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	0.26	0.21	0.21	0.21	0.21	0.15
σ^2_m		0.03	0.03	0.02	0.02	<0.00
σ^2_{am}						<0.00
σ^2_{pe}			0.02		<0.00	0.01
σ^2_{ce}				0.16	0.16	0.15
σ^2_e	0.79	0.80	0.79	0.65	0.65	0.72
σ^2_p	1.044 ± 0.06	1.038 ± 0.06	1.038 ± 0.06	1.039 ± 0.05	1.039 ± 0.05	1.023 ± 0.05
h^2	0.247 ± 0.09	0.200 ± 0.102	0.199 ± 0.102	0.201 ± 0.103	0.201 ± 0.103	0.147 ± 0.019
m^2		0.034 ± 0.052	0.028 ± 0.059	0.020 ± 0.050	0.020 ± 0.050	<0.000
pe^2			0.015 ± 0.071		<0.000	0.006 ± 0.068
ce^2				0.149 ± 0.109	0.149 ± 0.109	0.143 ± 0.012
C_{AM}						0.002 ± 0.000
r_{AM}						<0.000
h^2_T	0.247	0.217	0.213	0.211	0.211	0.160
logL	-402.879	-402.643	-402.622	-401.745	-401.741	-402.232
diff	0	0.236 (N.S)	0.021 (N.S)	0.898 (N.S)	0.881/0.004 (N.S)	0.491 (N.S)

See Table 5.2 for definition of abbreviations

5.4 DISCUSSION

5.4.1 Chosen models

Model choice differed for eight-week weight, scan weight, and the ultrasonically measured traits. For eight-week weight a model that included direct additive genetic effect, maternal additive genetic effect, maternal permanent environmental effect and maternal temporary environmental effect (Model 5) gave a significantly lower logL value than the other models used. For scan weight a model including direct additive genetic effect and maternal genetic effect (Model 2) gave the lowest significant logL value. The other models produced logL values that were closer to zero but the differences between logL values were not significantly different.

The simple animal model was found to be adequate for analysing ultrasonically-determined muscle and fat depths. When extra terms were added to the model for the scanned traits there were no significant decreases in the value of logL. Relatively high standard errors for scanned traits, compared to eight-week weight, could be a reflection of the lower number of records for these traits. Saatci *et al.* (1998) used a model that included only the direct additive genetic effect for ultrasonically-scanned traits, but the mean scanning age in that study was 393 days, by which stage it would be anticipated that dam effects would be minimal.

Safari *et al.* (2005) reported that the majority of estimates of genetic parameters for ultrasonic muscle and fat depth have been acquired by using the simple direct additive genetic model. However, in recent studies maternal effects had been reported, so it was suggested by Safari *et al.* (2005) that it is necessary to include these effects when estimating genetic parameters for muscle and fat depth. In the study reported here Model 5 included all maternal effects, was the selected model for eight-week weight, and was not significantly different from the selected models for scan weight and ultrasonically-scanned traits. For practical purposes it would be simpler to use the same model for all data analyses, and in this case Model 5 is recommended. Clément *et al.* (2001) argued that it did not

matter if unnecessary, non-significant random effects were fitted in a model, as they should not yield biased estimates or reduce the accuracy of estimates.

5.4.2 Heritability estimates

5.4.2.1 Direct heritability

Weight was found to be moderately heritable (0.18 to 0.23, see Tables 5.2 and 5.4) and as was expected direct heritability for weight increased with animal age, as shown by results for eight-week weight and scan weight (Tables 5.2 and 5.4), due to the greater independence of lambs from the dam. Previously reported heritability estimates for the CAMDA flock were 0.16 and 0.49 for the traits twelve-week weight and scan weight (Ap Dewi *et al*, 2002). The heritability for scan weight differs a great deal from that formerly reported. This was because the timing of scanning was different. Previously scanning was carried out on those animals kept for breeding, and took place from about twelve months onwards in (mean age in Ap Dewi *et al*'s (2002) study was 436.9 days). In recent years, as in the study reported here, scanning age is more consistent, with scans taken ideally around 20/21 weeks. Maternal effects were not included in the model used for analysis of scan weight by Ap Dewi *et al.* (2002) and it is probable that at the older age at which data were collected in that study these effects were not significant. However, at 20/21 weeks it is likely that maternal effects are present, although diminishing in importance. Direct heritability estimates for muscle and fat depths were found to be moderate (0.23 and 0.25, respectively, see Tables 5.6 and 5.7) and within the range reported by other authors (Safari *et al*, 2005).

5.4.2.2 Maternal heritability

Maternal heritability for the weight traits increased slightly (0.09 to 0.10 Model 5 for both traits) with age. It was expected to decrease with age, as the lamb becomes more dependent upon grass and less upon milk from the dam as it grows. It might also be expected that there would be a maternal influence upon ultrasonic muscle and fat depths because of their relationship with weight; however the models that included maternal effects did not improve logL values. Other authors have studied maternal effects for these traits. Maternal heritability

estimates of muscle and fat depths reported by Larsgard and Olesen (1998), were 0.05 (±0.11) and 0.04 (±0.06) in Norwegian sheep breeds (mean age 144 days), Maniatis and Pollot (2002a) reported values of 0.05 (±0.009) and 0.07 (±0.008) for Suffolk lambs (mean age 146 days), and estimates of Nasholm (2004) ranged from 0.04 to 0.11 and 0.01 to 0.07 in Swedish lambs of White breeds and the Gotland breed (mean age 171-172 days). These results suggest that maternal genetic effects on carcass traits are quite low.

The timing of scanning would influence heritability estimates for the traits. At a young age, maternal effects would generally be greater; however, it is known that the stages of growth of body tissues occur at different times and in a fixed order (Palsson and Verges, 1952). Development of muscle occurs after the stages of growth of bones and internal organs, and the laying down of adipose tissue or fat occurs last of all. There is also variation in the rate of maturity of fat tissues; subcutaneous depots are later maturing, whereas intramuscular depots and kidney fat mature earlier. Hence the reason why maternal effects are low may be that at the later stages of development of carcass tissues the diet relies less upon the dam's milk. Clarke *et al.* (1997) made comparisons of weight-selected Romney hoggets for growth, ultrasonic back fat and eye muscle dimensions, when animals were weighed and scanned at 6, 8, 10 and 14 months. They concluded that selection at the later yearling stage brought about greater improvement in early lamb growth than earlier selection, for example immediately after weaning. Conington *et al.* (2001) suggested that very early recording for fat and muscle in hill flocks could be inappropriate because animals may be too immature to have measurable variation in fatness. Ultrasonic scanning has been assessed many times and results have been encouraging enough for it to be used to predict carcass composition (Huslegge *et al*, 2000; Young and Deaker, 1994; Young *et al*, 1996). However, lower precision has been reported in lambs due to shallow layers of subcutaneous fat (Simm, 1987), the presence of wool and the mobility of the skin (Young and Deaker, 1994).

5.4.2.3 Maternal environmental effects

In addition to additive maternal genetic effect, maternal environmental effects also appear to be important in determining eight-week weight, and it is essential to separate maternal temporary environmental effects (within year) from maternal permanent environmental effects (across years). Maternal permanent environmental effect accounted for about 4-5 % of variance for both weight traits. The addition of maternal permanent environmental effects resulted in significant improvement of the model used for eight-week weight (Table 5.2), but not for scan weight (Table 5.4). In both cases the addition of the effect caused the maternal genetic effect to be reduced by approximately half. Maternal permanent environmental effects could include maternal infections such as mastitis, maternal injuries (for instance damaged teats), or intra-uterine effects.

Maternal temporary environmental effects are particularly important where multiple births are quite common (Safari *et al*, 2005). The addition of maternal temporary environmental effect significantly improved the models for eight-week weight, and accounted for more of the variance than permanent environmental effect (Table 5.2). Maternal temporary environmental variance ranged from 8 % (scan weight, Table 5.4) to 24 % (eight-week weight, Table 5.2). When added to the model, maternal temporary effects reduced the maternal permanent environmental effect by approximately half for both weight traits, but the majority of this change resulted from decrease in the residual variance, which was reduced by 11-19 %. The maternal temporary environmental effect was also quite substantial for fat depth, accounting for 15 % of the phenotypic variance (Table 5.7), but not for muscle depth. The result for maternal temporary environment is similar to that observed by Saatci *et al.* (1999), who also studied the CAMDA flock. Their estimate for maternal temporary environmental effects on twelve-week weight was that it accounted for 20 % of phenotypic variance.

Hagger (1998) investigated average daily weight gain during early growth of lambs and found that maternal temporary environment and permanent environment accounted for 26 to 31 % and 3 to 6 % of the phenotypic variance,

respectively. The results presented here also suggest that both terms should be included in models used for data analysis, and that maternal temporary environment is the more important of the two. Significant variation due to litter effects can be explained by temporary health problems of the ewe (such as footrot, mastitis or digestive disorders), would only affect offspring of a particular litter, and are not accounted by the permanent effect of the ewe (Hagger, 1998). Ap Dewi *et al.* (2002) commented that large litter effects indicate that ewe management within-year could have a considerable impact on the influence a dam exerts on its offspring.

5.4.2.4 Direct-maternal genetic covariance

The inclusion of direct-maternal genetic covariance has been inconsistent across many studies and has resulted in various estimates that have been difficult to interpret. Some studies have noted an antagonism between direct and maternal genetic effects (Robinson, 1996). Maniatis and Pollott (2003) suggested that highly negative results might have been obtained in studies due to problems of data structure. For eight-week weight the inclusion of direct-maternal covariance resulted in a poorer model fit, while its addition was not significant for scan-weight or muscle depth. In addition, the correlations between direct and maternal components were positive. A positive or zero correlation for a trait would not create a problem in terms of selection; for example, an animal selected for higher eight-week weight should not compromise selection for maternal ability. However, a negative correlation could mean genetic progress would be compromised because part of the gain obtained by increasing the animal's growth rate would be associated with a reduction in the dam's maternal ability. Saatci (1998) suggested that negative correlations could be due to low levels of milk production in young dams, large birth rearing groups, or to selection being made without taking account of maternal effects.

5.4.2.4 Total heritability and the importance of maternal effects

Maternal effects are not only important to produce unbiased estimates of direct heritability but also if improvement is made on maternal EBVs as well as direct EBVs then a greater overall response in a trait should result (Roehe and Kennedy,

1993a). Depending on the genetic correlation between direct and maternal additive genetic effects, Roehe and Kennedy (1993b) found that maternal additive genetic effects could be highly influential on genetic improvement of litter size in pigs, even when maternal heritability was low relative to direct heritability. It has been suggested that total heritability, the combination of maternal and direct heritability and their covariance, should be used where traits are influenced by maternal effects (Roehe and Kennedy, 1993a).

Using Model 5 total heritability estimates of eight-week weight, scan weight, muscle depth and fat depth were 0.23, 0.29, 0.15, and 0.21, respectively (Tables 5.2, 5.4, 5.6, 5.7). Comparison of total heritability estimates from Model 1 (direct genetic effect only) and Model 5 shows that the former gave higher estimates. Hence, when maternal effects are unaccounted for, genetic parameters are overestimated and if applied would give unreliable estimates of breeding values. Eight-week weight and scan weight show substantial exaggeration of direct heritability, by 100 % and 150 % respectively. The contribution of total maternal effects (sum of maternal genetic and maternal environmental contribution) to eight-week weight, scan weight, muscle depth and fat depth were 0.36, 0.23, 0.08, and 0.17, respectively, which suggests that it is important to include maternal effects when estimating genetic parameters for these traits.

CHAPTER 6

Estimating Variance Components due to Direct and Maternal Effects on Eight-week weight, Scan weight, Ultrasonic Muscle and Fat depths of Welsh Mountain Lambs

Plate 6.1 Welsh Mountain ewe with lamb on Tryfan

ABSTRACT

Six models were considered for univariate analysis, ranging from a simple model that included animal as the only random factor, to more complex models taking account of maternal genetic effect, maternal permanent environmental effect, maternal temporary environmental effect and the covariance between direct and maternal genetic effects. The most appropriate model for estimating variance components and heritability estimates for eight-week weight, scan weight, ultrasonic muscle and fat depth was one that contained all the factors except the direct-maternal genetic covariance. Direct heritability estimates (h^2) from univariate analysis for eight-week weight (EWW), scan weight (SW), muscle depth (MD) and fat depth (FD) were 0.18, 0.25, 0.24 and 0.21 respectively. Maternal heritability estimates (m^2) for EWW, SW, MD, and FD were 0.06, 0.05, 0.02 and 0.05 respectively. Estimates for maternal permanent environmental effects (pe^2) for EWW, SW, and MD were 0.06, 0.07, and 0.03 respectively. Maternal permanent environmental effect was not significant for FD. Estimates of maternal temporary environmental effects (ce^2) for EWW, SW, MD, and FD were 0.24, 0.14, 0.09, and 0.16 respectively.

6.1 INTRODUCTION

Previous estimates of variance components and heritabilities for the Welsh Mountain breed have used data from the CAMDA flock (Ap Dewi *et al*, 2002; Aslaminejad *et al*, 1999; Saatci *et al*, 1998; Saatci *et al*, 1999), the longest established group breeding scheme in the UK. Since, many more breeding schemes for the breed have been set up, particularly in the last few years.

Development of selection indexes for Welsh Mountain flocks by Roden (1999) used estimates of genetic parameters from studies of the CAMDA flock up until 1998. A weakness of this work was that the dataset was small, and estimates of genetic parameters for carcass traits were scarce. Hence, the results of other studies were used, the genetic parameters for the Welsh Mountain studies were considered to be similar to those for other breeds.

Presently, several breeding schemes for the Welsh Mountain breed operate, namely CAMDA, CAMP, Llysfasi, Tregaron, Pennlle'r Castell, Hafod y Llan, Cwmtawe and Elan Valley. They are managed either as group breeding schemes or sire referencing schemes. The proliferation of breeding schemes of the Welsh Mountain (see Plate 6.1) has increased recording of the breed, improving the scope for producing accurate estimates of genetic parameters from a larger dataset created by combining data from different flocks. However, the most recent sire referencing schemes have only operated for a few years, and individual flocks are small in size; the benefit of putting these flocks into an analysis is limited at present. Data from these flocks were not used in the current study but they should be useful in future analyses when more years of data are available. Instead, data from the CAMDA, CAMP and Llysfasi schemes (sections 3.1.1.1, 3.1.1.2, and 3.1.1.3) were used for estimation of genetic parameters. Between these three flocks it is known that there have been genetic exchanges (See Appendix B, Table B.1).

6.2 METHODS

6.2.1 Source of animals and data

Datafiles for the group breeding schemes for the Welsh Mountain breed were obtained from the MLC in the form of PEST files. Two files were obtained for each breeding scheme, the datafile and the pedigree file. Each datafile was separately edited in Microsoft Access to remove duplicate identities and non-genetic rearing dams. A sire column, containing sire information, taken from the corresponding pedigree file, was added to each datafile. The files were then imported into Minitab for preliminary analysis.

6.2.2 Description of dataset and data editing

The procedures in Chapter 4 were used to edit and clean the data. Initially 28830 animals were in the dataset; this decreased to 24569 animals after cleaning. Uncommon birth rearing types, one-year-old dams, and traits records that were more than three standard deviations from the trait mean were removed from the dataset. There were only two animals with scanning measurements in 1997, so they were removed from the dataset to simplify analysis. One flock was removed containing 2248 animals as it had no sires in common with any of the other flocks. Descriptive statistics of traits, after data editing and cleaning, are presented in Table 6.1.

Normality of the data for the four traits was assessed using Minitab 14. All traits showed significant ($P \leq 0.01$) deviations from normality using the Kolmogorov-Smirnof test. However, the traits presented fairly normal distributions when assessed visually, so data were not transformed (Figures B.1, Appendix B).

Table 6.1 Descriptive statistics for each trait and the covariate age at scanning

	Count	Mean	St. Dev.	Minimum	Maximum
Trait					
Eight-week weight (kg)	24569	18.28	4.532	4.9	32.3
Scan weight (kg)	10509	26.78	5.695	9.5	45
Muscle depth (mm)	8389	20.01	2.878	10	28
Fat depth (mm)	8389	2.56	1.132	0.1	6.27
Covariate					
Age at scanning (days)	10509	151.66	19.15	91	216

Sires and Dams. There were 452 sires and 9883 dams in the dataset. The number of offspring per sire ranged from one to 1089. Genetic links between flocks were determined by investigating the number of sires used across flocks of all three breeding schemes (See Table B.1, Appendix B). The number of offspring per dam ranged from one to 14, and averaged 2.49 lambs. There were 18029 litter groups and these are animals with the same dam of the same year. Number of lambs per litter group ranged from one to two, and average litter size was 1.36 lambs. This litter effect was used as a random effect (maternal temporary environmental effect).

6.2.2.1 Description of fixed effects and covariate

Description of fixed effects are summarised in Table 6.2 and Tables B.2 to B.4 in Appendix B.

Table 6.2 Summary of the classes for each fixed effect

Fixed effect	Number of classes	Range/type
Year of birth	20	1985 - 2004
Sex	2	Male, female
Birth rearing type	3	S:S, T:S, T:T
Dam age	4	2, 3, 4-6, 7
Flock	40	1-40

S:S single born -single reared; T:S twin born -single reared; T:T twin born -twin reared.

Year. Twenty classes. Year of birth (in the period 1985-2004) was used.

Sex. Two classes. Records for both males and females were available. There were no castrates.

Birth-rearing type (BRT): The original dataset had 12 rearing types, but only three types were kept in the dataset, namely: single born - single-reared; twin born - single reared; and twin born - twin reared. The other birth rearing types had small numbers in comparison, and some records were doubtful, for example some litter sizes recorded as many as six lambs.

Dam age. Age of dam (two to seven years) at the time the animal was born. Dam ages of four, five, and six were grouped together in the PEST file received from MLC. Ewes with offspring at age one were removed from the dataset, as

ewes of the Welsh Mountain breed are generally not mated until 18 months, and hence these occurrences were rare (0.12 %).

Flocks. Forty flocks were in the dataset. The largest flock size was that of the CAMDA flock, the longest established flock (Table B.4).

Covariate - animal age. This was the age of the animal, in days, at the time of weighing and ultrasonic scanning for scan weight, muscle depth and fat depth. It was excluded from eight-week weight analysis. Forty-one animals were removed from the dataset because of scanning measurements were taken late in life (536 to 909 days). See sections 4.2.2.5.3 and 4.4.1 for an explanation of these late measurements.

6.2.3 Models

The fixed effects used in all models were dam age and an effect which combined year of birth, sex, birth rearing type and flock, hereafter referred to as YSBF. Inclusion of YSBF in the model allowed for all interactions between the fixed effects to be accounted for. Six models, including the same random effects as in the six models described in Section 5.3.2 and 5.3.2.2 were used for analysis.
The full model (Model 6) was

Equation 6. 1

$$Y_{ijklmno} = \mu + a_i + b_{jklm} + c_n + z_n + x_o + w_o + v_{ol} + u_{no} + e_{ijklmno}$$

where μ = overall mean of eight-week weight, scan weight, muscle depth or fat depth; a_i = fixed effect of rearing dam age ($_i$ = 2-7); b_{ijkl} contemporary group of j^{th} sex (male/female) k^{th} birth rearing type (=1-3) l^{th} year of birth (1985 to 2004) m^{th} flock; c_n = is age at scanning as a covariate (not needed for eight-week weight) of the animal n; z_n = random effect of animal n; x_o = the random maternal additive genetic effect of the o^{th} dam; w_o = the random maternal permanent environmental effect of the o^{th} dam; v_{ol} = the random maternal temporary environmental effect of the o^{th} dam in the l^{th} year; u_{no} = the random direct-maternal interaction between the n^{th} animal and o^{th} dam; $e_{ijklmno}$ = random environmental effect.

The random effects included in each model are shown below.

Model 1 σ_a^2

Model 2 $\sigma_a^2 + \sigma_m^2$

Model 3 $\sigma_a^2 + \sigma_m^2 + \sigma_{pe}^2$

Model 4 $\sigma_a^2 + \sigma_m^2 + \sigma_{ce}^2$

Model 5 $\sigma_a^2 + \sigma_m^2 + \sigma_{pe}^2 + \sigma_{ce}^2$

Model 6 $\sigma_a^2 + \sigma_m^2 + \sigma_{pe}^2 + \sigma_{ce}^2 + \sigma_{am}^2$

where σ_a^2 is the additive direct genetic effect of the animal; σ_m^2 is the additive maternal genetic effect; σ_{pe}^2 is the maternal permanent environmental effect; σ_{ce}^2 is the maternal temporary environmental effect and σ_{am}^2 is the direct-maternal genetic covariance.

6.3 RESULTS

6.3.1 Eight-week weight

Year, sex, birth rearing type, dam age, and flock. Numbers of animals, mean values, and standard deviations are shown in Figures 6.1 to 6.4, and full details are reported in Tables B2 to B4 in Appendix B. Year of birth for the period 1985-2004 was used; the fewest records in years 1985–1992 (Table B.2). Figure 6.1 shows that mean eight-week weight fluctuated between years. The mean weight of males was 1.7 kg more than that of females (Table B.3). The largest proportion of lambs were born and reared as twins (Table B.3), and these had the lowest mean weight (Figure 6.2). The largest age group for dams was the 4-6 year age group (Table B.3). Mean weight was highest in lambs of three-year old dams, and least for seven-year old dams (Figure 6.3). There were 40 flocks and the number of animals per flock included in the analysis ranged from 15 to 11595. Minimum and maximum mean eight-week weights of flocks were 12.13 kg and 21.01 kg, respectively (Figure 6.4, Table B.4).

Estimates of variance components and genetic parameters for eight-week weight for the six models are summarized in Table 6.3. A model that included additive direct genetic, additive maternal genetic, maternal permanent environmental, and maternal temporary environmental effects (Model 5) appeared to be the most suitable because it gave the value of logL closest to zero, with the exception of the model that also included an animal-dam genetic covariance (Model 6). The inclusion of an animal-dam genetic covariance gave a logL value, slightly nearer

to zero, but it was not significantly closer than the value for Model 5. The genetic correlation between additive direct genetic and additive maternal genetic effects was also weak (0.088). The phenotypic variance was 6.56 kg. Direct and maternal heritabilities were 0.18 and 0.06 respectively. Maternal permanent environmental and maternal temporary environmental variances were 0.06 and 0.24 respectively.

6.3.2 Scan weight

Year, sex, birth rearing type, dam age, and flock. Year of birth for the period 1994-2004 was used (Table B.2, Figure 6.1). There were few or no records for 1997 and 1998, so these years were not included in the analysis. There seems to be a decline in mean scan weight over the years (Figure 6.1), but these records have not been adjusted for age at scanning, and it was later found that the mean age at scanning was greater in 1994 and 1995. Males were 3.2 kg heavier than females at scanning (Table B.3). There was about a 2 kg difference between single born – single reared lambs and twin born – twin reared lambs, with twin born - single reared lambs intermediate between the two birth rearing types (Figure 6.2). Lambs with dams aged four to six years produced lambs with higher mean weights, and dams aged two years produced lambs with lightest mean weights (Figure 6.3). There were 37 flocks and number of animals per flock included in the analysis ranged from 5 to 2055 (Table B.4). Minimum and maximum mean scan weights of flocks were 22.20 kg and 37.29 kg, respectively (Figure 6.4).

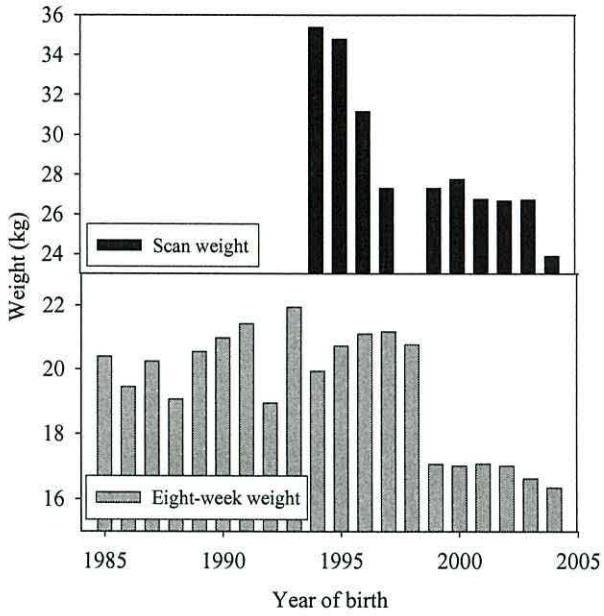


Figure 6.1 Mean eight-week weights and scan weights for the fixed effect year of birth.

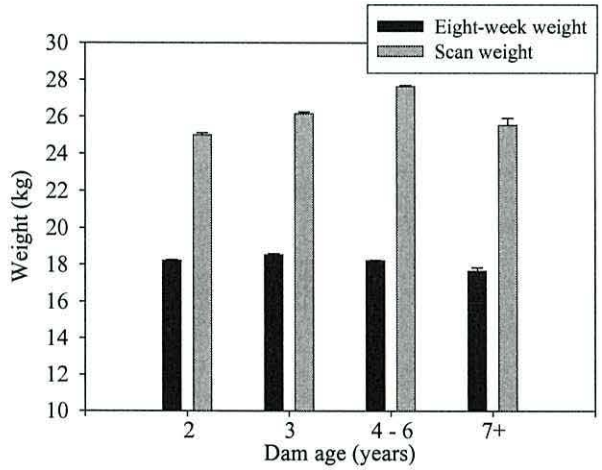


Figure 6.2 Mean eight-week weights and scan weights for the fixed effect dam age.

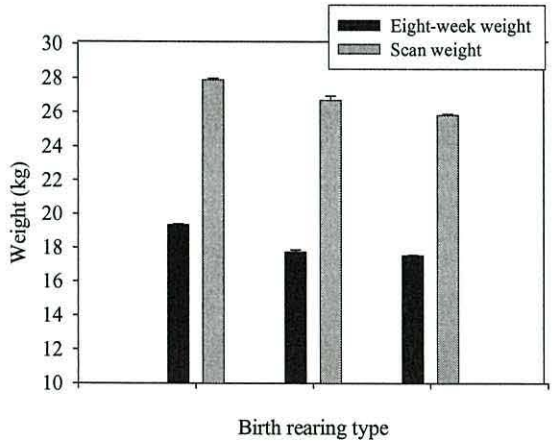


Figure 6.3 Mean eight-week weights and scan weights for the fixed effect birth rearing type.

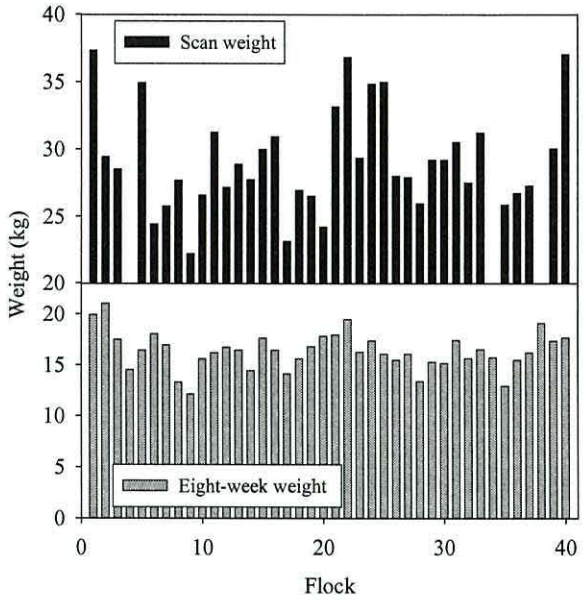


Figure 6.4 Mean eight week weights and scan weights for fixed effect flock.

Estimates of variance components and genetic parameters for scan weight for the six models are summarised in Table 6.4. As for eight-week weight, the model including all effects apart from animal-dam genetic covariance (i.e. Model 5) provided the logL closest to zero. The addition of animal-dam genetic covariance had no effect on logL value. Estimates of direct heritability, maternal heritability, maternal permanent environmental and maternal temporary environmental variances were 0.25, 0.05, 0.07 and 0.14, respectively. The phenotypic variance was 11.51 kg.

Table 6.3. Models to estimate (co)variance components and genetic parameters for eight-week weight of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	2.74	1.21	1.24	1.21	1.21	1.15
σ^2_m		1.08	0.39	0.36	0.36	0.34
σ^2_{am}						0.05
σ^2_{pe}			0.71		0.41	0.41
σ^2_{ce}				1.57	1.56	1.57
σ^2_e	4.12	4.35	4.20	3.01	3.01	3.03
σ^2_p	6.85 ± 0.079	6.65 ± 0.074	6.54 ± 0.072	6.56 ±0.073	6.56 ± 0.073	6.55 ± 0.073
h^2	0.399 ± 0.017	0.182 ± 0.018	0.190 ± 0.018	0.184 ± 0.018	0.184 ± 0.017	0.175 ± 0.021
m^2		0.163 ± 0.010	0.060 ± 0.011	0.055 ± 0.011	0.055 ± 0.011	0.051 ± 0.012
pe^2			0.109 ± 0.011		0.063 ± 0.011	0.062 ± 0.011
ce^2				0.240 ± 0.012	0.239 ± 0.012	0.240 ± 0.012
C_{AM}						0.008 ± 0.012
r_{AM}						0.088 ± 0.131
h^2_T	0.399	0.264	0.219	0.212	0.212	0.213
logL	-34302	-34103.1	-34046	-33839	-33839	-33838.7
diff	0	198.9	57.1	264.1	207/0	0.3

σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{am} direct-maternal genetic covariance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal temporary environmental variance; σ^2_e error variance; σ^2_p phenotypic variance, h^2 direct heritability, m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance, C_{AM} Genetic covariance between direct and maternal effects expressed as a proportion of the phenotypic variance; r_{AM} genetic correlation between direct and maternal effects; h^2_T total heritability; logL log likelihood ratio; diff difference between neighbouring models; Model 4 compared with 2, model 5 compared with 3 and 4. S = significant, N.S = non significant.

Table 6.4. Models to estimate (co)variance components and genetic parameters for scan weight of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	6.55	2.86	3.01	2.87	2.87	2.87
σ^2_m		1.81	0.57	0.55	0.55	0.55
σ^2_{am}						0.01
σ^2_{pe}			1.30		0.84	0.84
σ^2_{ce}				1.58	1.58	1.57
σ^2_e	5.76	6.94	6.66	5.69	5.69	5.67
σ^2_p	12.32 ± 0.230	11.61 ± 0.206	11.53 ± 0.206	11.51 ± 0.203	11.51 ± 0.203	11.51 ± 0.205
h^2	0.532 ± 0.031	0.246 ± 0.038	0.261 ± 0.039	0.250 ± 0.038	0.250 ± 0.037	0.249 ± 0.043
m^2		0.156 ± 0.018	0.049 ± 0.023	0.048 ± 0.022	0.048 ± 0.022	0.048 ± 0.027
pe^2			0.113 ± 0.022		0.073 ± 0.023	0.073 ± 0.023
ce^2				0.137 ± 0.022	0.137 ± 0.022	0.137 ± 0.022
C_{AM}						0.001 ± 0.026
r_{AM}						0.008 ± 0.241
h^2_T	0.532	0.324	0.285	0.274	0.274	0.274
logL	-17294.9	-17249.9	-17237.7	-17227	-17227	-17227
diff	0	45 (S)	12.2 (S)	22.9 (S)	10.7/0 (S/N.S)	0 (N.S)

See Table 6.3 for the definition of abbreviations

6.3.3 Muscle depth and fat depth

Year, sex, birth rearing type, dam age, and flock. There were fewer records available before 1999 for ultrasonic scanning traits (Table B.2, Appendix B). Mean minimum and maximum muscle depths were in 2001 and 1995, respectively. Mean minimum and maximum fat depths were in 2004 and 1994, respectively (Table B.2). In the last few years of recordings, Figure 6.5 shows that there have been an increase in mean muscle depth and a decrease in mean fat depth. Males had higher mean muscle depths, and females higher mean fat depths (Table B.3). Muscle and fat depths appear to follow similar trends, as shown by Figures 6.6 and 6.7, for dam age and birth rearing type. Mean muscle and fat depths declined with increased litter size (Figure 6.7). Mean muscle and fat depths were lowest in dams of two years, and greatest in dams of ages four to six years (Figure 6.6). As for scan weight there were 37 flocks and the number of animals per flock included in the analysis ranged from 5 to 2052. Minimum and maximum mean muscle depths of flocks were 18.96 mm and 23.46 mm, respectively. Minimum and maximum mean fat depths were 1.63 mm and 4.05 mm, respectively (Table B.4, Figure 6.8).

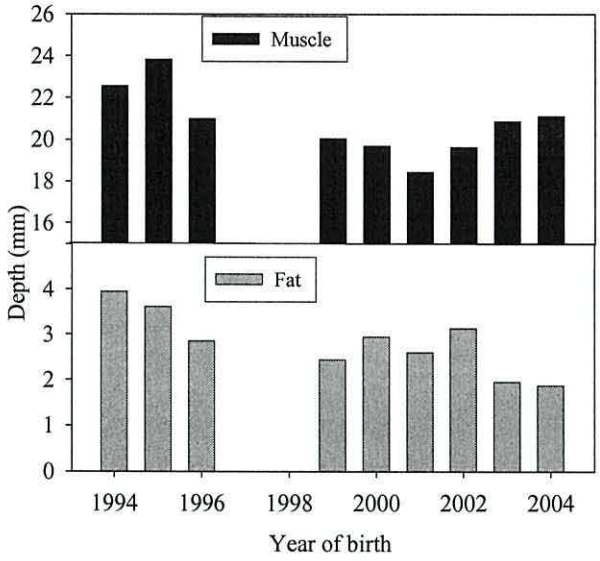


Figure 6.5 Mean muscle and fat depths in years 1994 to 2004

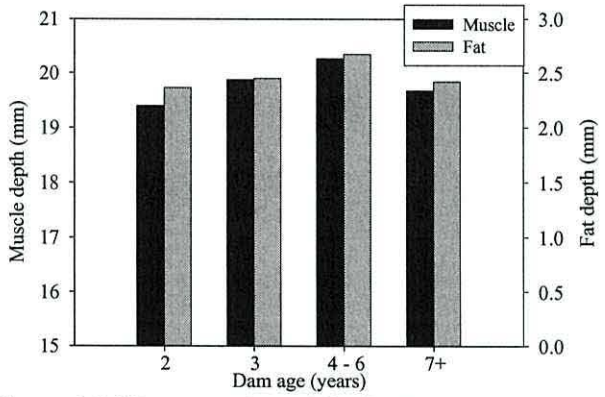


Figure 6.6 Mean muscle and fat depths versus dam age

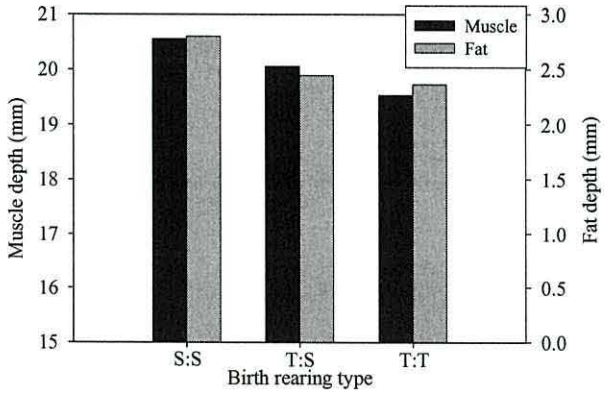


Figure 6.7 Mean muscle and fat depths of birth rearing types

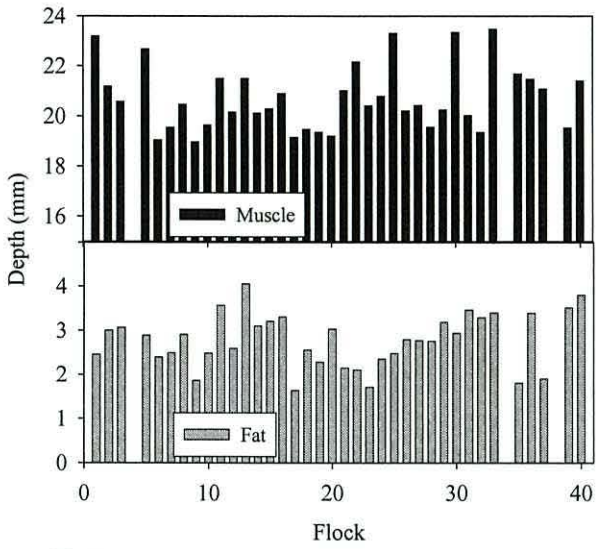


Figure 6.8 Mean muscle and fat depths for individual flocks

Estimates of variance components and genetic parameters for muscle and fat depths together with logL values for the six models are summarised in Tables 6.5 and 6.6. Direct maternal genetic covariance caused an improvement in logL value, but was non-significant. Model 5 appeared to be an appropriate model to use for muscle depth and Model 4 was adequate for fat depth. The parameter estimates for muscle depth of direct heritability, maternal heritability, maternal permanent environmental effect and maternal temporary environmental effect were 0.25, 0.02, 0.04, and 0.08, respectively. The estimates for fat depth of direct heritability, maternal heritability, and maternal temporary environmental effect were 0.22, 0.04, and 0.16, respectively. Both maternal permanent environmental effect and direct maternal genetic covariance were non-significant when included in models for fat depth. The phenotypic variances for muscle and fat depth were 4.63 mm and 0.64 mm, respectively.

Table 6.5 Models to estimate (co)variance components and genetic parameters for ultrasonic muscle depth of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	1.62	1.18	1.16	1.13	1.15	1.41
σ^2_m		0.28	0.10	0.10	0.08	0.23
σ^2_{am}						-0.26
σ^2_{pe}			0.27		0.20	0.22
σ^2_{ce}				0.16	0.36	0.36
σ^2_e	3.09	3.18	3.09	2.85	2.85	2.71
σ^2_p	4.71 ± 0.091	4.64 ± 0.087	4.63 ± 0.087	4.64 ± 0.086	4.63 ± 0.086	4.67 ± 0.093
h^2	0.343 ± 0.033	0.255 ± 0.038	0.251 ± 0.037	0.243 ± 0.037	0.248 ± 0.037	0.303 ± 0.052
m^2		0.060 ± 0.017	0.023 ± 0.019	0.022 ± 0.018	0.018 ± 0.018	0.049 ± 0.029
pe^2			0.059 ± 0.021		0.043 ± 0.021	0.048 ± 0.023
ce^2				0.085 ± 0.027	0.077 ± 0.027	0.077 ± 0.026
C_{AM}						-0.056 ± 0.033
r_{AM}						-0.462 ± 0.167
h^2_T	0.347	0.289	0.263	0.270	0.257	0.243
logL	-10234.3	-10226.5	-10222.6	-10227.3	-10217.8	-10224.1
diff	0	7.8 (S)	3.9 (S)	-4.7 (S)	4.8/9.5 (S/S)	-6.3 (S)

See Table 6.3 for the definition of abbreviations

Table 6.6. Models to estimate (co)variance components and genetic parameters for ultrasonic fat depth of Welsh Mountain lambs.

	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
σ^2_a	0.22	0.15	0.15	0.14	0.14	0.15
σ^2_m		0.04	0.03	0.03	0.03	0.03
σ^2_{am}						-0.01
σ^2_{pe}			0.01		>0.00	>0.00
σ^2_{ce}				0.10	0.10	0.11
σ^2_e	0.43	0.45	0.44	0.37	0.37	0.36
σ^2_p	0.65 ± 0.012	0.64 ± 0.012	0.64 ± 0.012	0.64 ± 0.012	0.64 ± 0.012	0.64 ± 0.012
h^2	0.341 ± 0.034	0.238 ± 0.039	0.237 ± 0.039	0.220 ± 0.038	0.220 ± 0.038	0.235 ± 0.047
m^2		0.062 ± 0.018	0.052 ± 0.022	0.042 ± 0.017	0.042 ± 0.017	0.050 ± 0.025
pe^2			0.016 ± 0.021		>0.000	>0.000
ce^2				0.164 ± 0.027	0.164 ± 0.027	0.164 ± 0.027
C_{AM}						-0.014 ± 0.027
r_{AM}						-0.134 ± 0.224
h^2_T	0.341	0.269	0.263	0.240	0.240	0.238
logL	-2525.63	-2517.05	-2516.77	-2503.14	-2503.14	-2503.14
diff	0	8.58 (S)	0.28 (N.S)	13.91 (S)	13.63/0 (S/N.S)	0 (N.S)

See Table 6.3 for the definition of abbreviations.

6.4 DISCUSSION

6.4.1 Chosen model

A model (Model 5) that included animal direct effect, additive maternal genetic effect, maternal permanent environmental effect and maternal temporary environmental effect was chosen to estimate components of variance and heritabilities for eight-week weight, scan weight, and muscle depth. For fat depth maternal permanent environmental effect was not significant so could be disregarded from the above model (Model 4).

6.4.1 Genetic parameters

The estimates of direct heritability (h^2) for the traits examined suggest that they are all moderately heritable, with values ranging from 0.18 to 0.25. Therefore selection the traits can proceed with some degree of confidence that genetic progress can be made. As anticipated the heritability for weight is less at eight weeks than at the time of scanning (mean 21 weeks).

The estimates for maternal heritability (m^2) were low, ranging from 0.02 to 0.06 for the four traits. There was a slight decline in the estimate of m^2 for scan weight compared with eight-week weight.

Permanent environmental effect had little influence on fat depth, but accounted for 4 to 7 % of the phenotypic variance for the other traits. The maternal permanent environmental effect for fat depth, although non-significant, could be included in models without causing a problem (see Chapter 5).

Maternal temporary environmental effect was particularly important for eight-week weight, accounting for 24 % to the phenotypic variance. This decreased for scan weight to 14 %, and for muscle depth and fat depth values were 8 % and 14 %, respectively.

It can be seen that it is important to include maternal effects in models when estimating heritability. Although maternal genetic effect was quite low for all

traits, it is clear that the total effect of the dam is quite substantial when maternal environmental effects are also incorporated. Total maternal effect (sum of genetic and environmental maternal effects) for eight-week weight, scan weight, muscle depth and fat depth accounted for 36 %, 26 %, 14 %, and 20 %, respectively, to the total phenotypic variance.

Including the direct-maternal genetic covariance in models either had no effect on the logL value or resulted in a non-significant improvement. For eight-week weight and scan weight covariances were 0.008 and 0.001, respectively, and the positive value of the covariance caused a decrease of both direct heritability and maternal heritability for those traits. However, for muscle and fat depths the values were negative, -0.06 and -0.01 respectively, and caused an increase in both direct heritability and maternal heritability.

6.4.3 Comparison of results with other studies

Comparing the results of the CAMDA data (Chapter 5, 10677 animals) with the result of analysis of the data from three group breeding schemes (this chapter, 24569 animals), similar findings were obtained. However, while the model that included animal, additive maternal genetic effects, maternal permanent environmental effects, and maternal temporary environmental effects as random effects seemed the most appropriate for all traits examined in the present chapter, simpler models were satisfactory for scan weight and ultrasonically-scanned traits recorded in the CAMDA dataset. For eight-week weight and scan weight, estimates of maternal heritability were higher, and those of maternal permanent environmental and maternal temporary environmental variances were lower, in the CAMDA analysis (Chapter 5).

A possible reason for differences may be the greater number of records available in the dataset considered in the current chapter. For instance, there were 10509 records for scan weight, which was over six times the number available for the CAMDA flock.

6.4.3.1 Direct heritability

Roden (1999) produced a selection index for Welsh Mountain flocks based on estimates made from data including data from CAMDA. The heritability estimates used by Roden (1999) for scan weight, muscle depth and fat depth were 0.19, 0.35, and 0.30 respectively. The heritability estimates for muscle and fat depths are higher than reported here, possibly because the traits were measured at an older age. Thorsteinsson and Eythorsdottir (1998) reported heritability estimates of 0.42 for both muscle and fat depth in Icelandic lambs, measured at 19-20 weeks. However, the heritability estimates of 0.40 reported by Saatci *et al.* (1998) were from older animals, with a mean age of 393 days. Heritability estimates differ depending on the model chosen. In Chapter 5, it was suggested that an animal model (Model 1) was adequate for scanned traits. If this model were applied to the data used in this chapter heritabilities for muscle and fat would be 0.34 and 0.34, respectively. These are closer to the heritabilities reported by Roden (1999) and used by Signet for its lean index.

Varying estimates of heritability have been obtained by using data of the CAMDA nucleus flock. Direct heritability for twelve-week weight was estimated previously as 0.16 (Ap Dewi *et al*, 2002), 0.21 (Saatci *et al*, 1999) 0.29 (Aslaminejad and Roden, 1997) and 0.33 (Pollott *et al*, 1994). A model including additive maternal genetic and maternal environmental effects produced the first two (lower values) whereas the third value was given by a model that did not include maternal environmental effects but did include a covariance of direct and maternal genetic effects. The covariance reported by Aslaminejad *et al.* (1997) was negative, and negative values tend to increase direct heritability and maternal heritability. Direct heritability of scan weight at a mean age of 436.9 days reported by Ap Dewi *et al.* (2002) was 0.29. Direct heritability estimates of eight-week weight and scan weight were 0.18 and 0.24 respectively, using CAMDA data from years 1976 to 2003 (Chapter 5), and almost identical values were obtained in the study described in this chapter. Although animal ages were older, Ap Dewi *et al.* (2002) reported comparable direct heritability estimates for muscle and fat depths with values of 0.22 and 0.24 respectively.

Because small datasets were used for earlier estimates of genetic parameters for the Welsh Mountain breed Roden (1999) also used estimates for other hill breeds. In the Scottish Blackface, estimates of direct heritability have been reported as 0.15 for eight-week weight (Bishop and Mackenzie, 2001), and 0.17 (Roden *et al*, 2003) and 0.22 (Conington *et al*, 2001) for weaning weight. In another Welsh breed, the Lleyn, heritability for eight-week weight was calculated as 0.16. Direct heritability estimates for muscle and fat depths in the Scottish Blackface reported by Roden *et al.* (2003) were 0.27 and 0.44 respectively, and as estimated by Conington *et al.* (2001) were 0.30 and 0.25 respectively. Both sets of authors reported higher estimates for muscle depth and fat depth. In particular, heritability for fat depth was considerably higher than the estimates obtained here for Welsh Mountain (Roden *et al*, 2003). Roden *et al.* (2003) suggested that the range of estimates shows that some populations have greater potential for genetic progress than others.

6.4.2.2 Maternal effects

The additive maternal genetic effect accounted for 6 %, 5 %, 2 % and 4 % to the phenotypic variance of eight-week weight, scan weight, muscle depth and fat depth, respectively. The value for eight-week weight was smaller than that reported from studies that used data solely from the CAMDA flock, which produced a value of 0.09 for both twelve-week weight (Saatci *et al*, 1999) and eight-week weight (Chapter 5). Aslaminejad *et al.* (1999) also produced estimates from CAMDA data and reported maternal heritability as 0.16 for 18-week weight, from a model with direct and additive maternal genetic effect. For weaning weight, Safari *et al.* (2005) reported pooled estimates from literature for maternal heritability and maternal temporary environmental effect of 0.10 and 0.14 respectively, for meat breeds. There are few estimates of maternal effects for scanned traits of the Welsh Mountain breed. Ap Dewi *et al.* (2002) did not include maternal effects, as animals were measured between 12 to 13 months; hence maternal effects would be negligible. In Chapter 5, the models that included maternal effects were not significantly better than others for muscle and fat depth, and only additive maternal genetic effect was significant for scan weight. However, in the study described in this chapter the effects appeared to

be significant for scan weight and ultrasonically-scanned traits, with the exception of maternal permanent environmental effect for fat depth. The larger dataset used in the analysis described in this chapter, in comparison to Chapter 5, may have facilitated the disentangling of maternal effects. Other authors have reported fairly low estimates for maternal heritabilty for ultrasonically-scanned muscle and fat depths, ranging from 0.04 to 0.11 and 0.01 to 0.07, respectively (Larsgard and Olesen, 1998; Maniatis and Pollott, 2002a; Nasholm, 2004). The results are similar to those of Hagger (1998) for early growth traits in Swiss lambs and Ap Dewi *et al.* (2002) for 12-week weight of Welsh Mountain lambs, who all found that maternal temporary environmental (litter) effects were considerably more important than maternal permanent environmental effects.

CHAPTER 7

Estimating Variance Components due to Direct and Maternal Effects on Eight-week weight, Scan weight, Ultrasonic muscle and Fat depths of Beulah Speckled Face Lambs

Plate 7.1 Beulah Speckled Face ewe at the Royal Welsh Show 2005

ABSTRACT

Six models were considered for univariate analysis, ranging from a simple animal model, just including animal as a random factor, to more complex models taking account of additive maternal genetic effect, maternal permanent environmental effect, maternal temporary environmental effect and the covariance between direct and maternal genetic effects. The chosen model used to estimate variance components and heritability estimates for eight-week weight, scan weight, ultrasonic muscle and fat depths, was one that contained all the above factors excluding the direct-maternal covariance. Direct heritability estimates (h^2) from univariate analysis for eight-week weight (EWW), scan weight (SW), muscle (MD) and fat depth (FD) were 0.09, 0.18, 0.19 and 0.20, respectively. Maternal heritability estimates (m^2) for EWW, SW, and MD were 0.07, 0.08, and 0.03, respectively. For FD maternal additive genetic effect was not significant. Estimates for maternal permanent environmental effects (pe^2) for EWW, SW, MD, and FD were 0.11, 0.08, 0.04, and 0.11, respectively. Estimates of maternal temporary environmental effects (ce^2) for EWW, SW, MD, and FD were 0.26, 0.16, 0.12, and 0.12, respectively.

7.1 INTRODUCTION

7.1.1 Beulah Speckled Face

The Beulah Speckled Face is a widespread hill and upland breed from Mid Wales; it is found in 1000 sheep flocks and has the fourth largest purebred population in the UK, accounting for 3.3 % of the national flock (Pollott, 2006). On the hills ewes tend to be purebred providing flock replacements, finished lambs, or store lambs for finishing on lowland farms (Eppynt Hill & Beulah Speckled Face Sheep Society, 2006). Thirty-six percent of ewes are mated pure, and the remainder are either crossed with a terminal sire for lamb meat production or mated to longwool sires to produce a prolific crossbred ewe for lowland lamb production (Hussain *et al*, 2006). The Beulah Speckled Face is popular as the hill component of the Welsh Mule and a sixth of the flocks containing the breed rear crossbreeds. The Beulah type Welsh Mule accounts for 0.4 % of the national flock (Pollott, 2006).

Origins of the breed are uncertain. It appears that the breed first roamed the hills of Mynydd Epynt, Llanafan, Abergwesyn and Llanwrtyd Wells, around the Powys village of Beulah, over 100 years ago (Eppynt Hill & Beulah Speckled Face Sheep Society, 2006). It was once thought the Beulah Speckled Face was the result of a cross between a Welsh Mountain ewe and a Kerry Hill ram; however, it is now considered more likely that the breed is based upon a Welsh Mountain ewe and Derbyshire Gritstone ram cross. The Epynt Hill and Beulah Speckle Face Sheep Society was first established in 1958 (Williams-Davies, 1981).

The Beulah Speckled Face is an intermediate sized breed, larger than the Welsh Mountain breed, and is recognized by its distinctive speckled face (Figure. 7.1). The face and legs are free from wool, ewes are hornless, as are most rams, and a long head with erect ears pointing forward is preferred. The fleece is white, varying from high quality to coarse-fibred (NSA, 2005). Beulah Speckled Face ewes are described as good mothers that provide lambs with a plentiful supply of milk. Average lambing percentage is around 160-175 % (NSA, 2005; Williams-

Davies, 1981), although up to 200 % is not uncommon for flocks of older ewes. Average weights for mature ewes and rams are 52 kg and 86 kg respectively. The Beulah Speckled Face is far more docile than the Welsh Mountain breed. Strains of the Beulah, the Welsh Hill Speckled Faces or Hardy Speckled Faces, are hardier and smaller than the Beulah, and are able to live in harsher environments.

7.2 METHODS

7.2.1 Source of animals and data

Currently there are nine members in the sire referencing scheme (see section 3.1.1.4). However, the number of members and the farms involved has varied during the time data were collected (see Table C.1 in Appendix). The dataset of the Beulah Sire Referencing Scheme was obtained from MLC in the form of a PEST file and a pedigree file. Information available and used were unique animal identification, dam identification, sire identification, litter code, date of birth, litter size born, litter size reared, dam age, adjusted eight-week weight, flock code, sex, scan age, scan weight, and ultrasonic muscle and fat depth.

7.2.2 Data editing

It was evident that some animals had been fostered or had been artificially reared, and these were removed from the dataset. Following the methods used in Chapter 4, measurements that were more than three standard deviations from the group mean and individuals with incomplete records were removed from the dataset. Prior to eliminations there were 15309 individuals in the dataset, which consequently decreased to 13498 (88% of original dataset).

7.2.3 Description of data after cleaning and editing

In the edited dataset there were 266 sires and 5063 dams. The number of offspring per sire ranged from one to 518. The number of offspring per dam ranged from one to 13, and averaged 2.67 lambs. The number of litters of an individual ewe ranged from one to eight, with a mean number of litters of 1.8.

Litter groups were composed of animals born to the same dam in the same year. There were 8967 litter groups and the number of lambs per litter group ranged from one to three.

Table 7.1 summarises the number of classes for each fixed effect. Fewest animals were recorded in 1994 (113 animals Table C.2, Appendix C). There was a substantial increase in the number of records available from 1997, with the highest number of records available in 2000 (1863, Table C.2, Appendix C). Records for both males and females were available, and one castrate was removed from the dataset. Birth-rearing types were created to describe litter size born and litter size reared. There were records for single born - triplet reared (one record) and twin born - triplet reared (four records), but these were eliminated as they represented very few animals of the dataset. Age of dam at the time the animal was born ranged from one to seven years. Dam ages four, five and six years had been grouped together, as had dam ages of seven years and greater, in the file obtained from MLC. There were 28 flocks and genetic links were determined from the number of sires used across flocks. Of a total of 266 sires, 26 were used on more than one flock. The number of flocks a single ram was used on ranged from 2 to 24, and thus all flocks shared a sire at least once (Table C.5, Appendix C).

Table 7.1 Summary of fixed effects

Fixed effect	Number of classes	Range/type
Year of Birth	20	1985 - 2004
Sex	2	Male, Female
Birth-rearing type	7	Single born: Single reared (S:S) Single born: Twin reared (S:T) * Twin born: Single reared (T:S) Twin born: Twin reared (T:T) Triplet born: Single reared (Tr:S) Triplet born: Twin reared (Tr:T) Triplet born: Triplet reared (Tr:Tr)
Dam age	5	1, 2, 3, 4-6, 7
Flock	28	1 - 28

* Includes only lambs of the genetic dam

The mean scan age was 150 days, and this was used as a covariate for analysis of the traits muscle depth and fat depth. It was not used for the eight-week weight

analysis. Descriptive statistics of traits, after data editing and cleaning, are presented in Table 7.2.

Table 7.2. Basic statistics for each trait and covariate

	Count	Mean	St. Dev.	Minimum	Maximum
Trait					
8-week weight (kg)	13498	16.84	3.591	5.8	28.3
Scan weight (kg)	10569	29.90	5.527	13.0	49.0
Muscle depth (mm)	9651	20.92	2.888	13.0	29.0
Fat depth (mm)	9652	2.28	1.06	0.03	5.80
Covariate					
Age at Scanning (days)	10569	149.6	11.74	112	189

In some studies, including a study of the Beulah Speckle Face breed (Hussain *et al*, 2006), ultrasonic fat depth has been transformed to improve normality (Moore *et al*, 2006; van Heelsum *et al*, 2001). Normality of the data for the four traits was assessed using Minitab 14. All traits showed significant ($P \leq 0.01$) deviations from normality using the Kolmogorov-Smirnof test. However, the traits presented fairly normal distributions when assessed visually, so data were not transformed (Figure C1, Appendix C).

7.2.4 The models

The fixed effects used to estimate components of variance were dam age and an effect which combined year of birth, sex, birth-rearing type and flock together, referred to as YSBF. Inclusion of YSBF into the model would include interactions to be accounted for in the analysis. Counts, mean values and standard deviations for fixed effects are shown in Appendix C Table C.2. The same models with random effects were used and selected as described in Section 5.3.3 and 5.3.3.1.

The full model (Model 6) is shown below

Equation 7. 1

$$Y_{ijklmno} = \mu + a_i + b_{jklm} + c_n + z_n + x_o + w_o + v_{ol} + u_{no} + e_{ijklmno}$$

where μ = the overall mean of eight-week weight, scan weight, muscle depth or fat depth; a_i = fixed effect of rearing dam age ($_i$ = 1-7); b_{ijkl} contemporary group of j^{th} sex (male/female) k^{th} birth-rearing type (=1-7) l^{th} year of birth (1985 to 2004) m^{th} flock (1-28); c_n = is age at scanning as a covariate (not needed for eight-week weight) of the animal n; z_n = random effect of animal n; x_o = the random maternal additive genetic effect of the o^{th} dam; w_o = the random

maternal permanent environmental effect of the o^{th} dam; v_{ol} = the random maternal temporary environmental effect of the o^{th} dam in the l^{th} year; u_{no} = the random direct-maternal interaction between the n^{th} animal and o^{th} dam; $e_{ijklmno}$ = random environmental effect.

The same six models that were used for the analysis of the Welsh Mountain data (see Section 6.2.3) were used here, together with a seventh model for fat depth only, which was similar to Model 5 but excluded additive maternal genetic effect. Model 7 was analysed because in models that including maternal permanent environmental effect the additive maternal genetic effect was fixed at a boundary, so the model was tested excluding the effect. Also Model 6 was not analysed because additive maternal genetic effect had been fixed at a boundary.

7.3 RESULTS

7.3.1 Eight-week weight

Descriptive statistics for fixed effects are shown in Tables C.2 to C.4 in Appendix C, and Figure 7.1 shows the mean weight at eight weeks for the fixed effects year of birth, birth rearing type, dam age and flock. Year of birth for the period 1985-2004 was used, with larger numbers of records available from 1997 onwards. The lowest mean weight of 12.22 kg was in 1993 and the heaviest mean weight of 20.49 kg was in 1992 (Table C.2, Figure 7.1). Comparison of mean weights showed that males were heavier than females by about 1.34 kg (Table C.3). Mean weights were lowest for offspring of seven-year old dams (16.58 kg) and heaviest for offspring of three-year-old dams (21.18 kg). Mean weight increased with dam age until three or four years, then decreased slightly for older dams (Table C.3, Figure 7.2). The trend was for mean weight to decrease with increasing litter size. Mean weights ranged from 14.46 kg (triplet born, triplet reared) to 18.76 kg (single born, single reared) (Table C.3, Figure 7.3). Mean eight-week weights of flocks ranged from 14.32 kg to 18.86 kg (Table C.4, Figure 7.4).

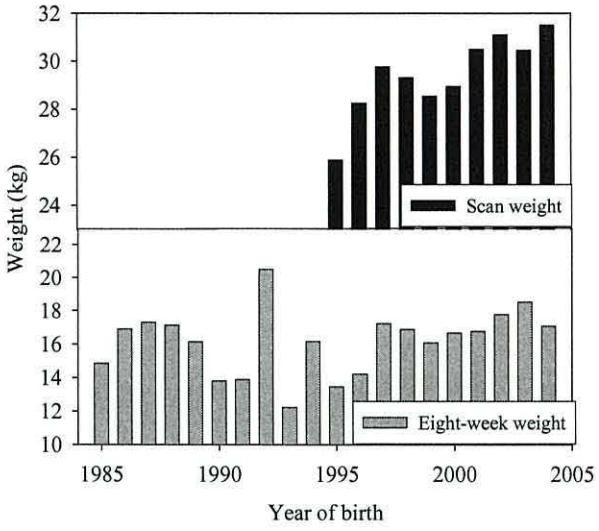


Figure 7.1 Mean eight-week weights and scan weights for the fixed effect year of birth.

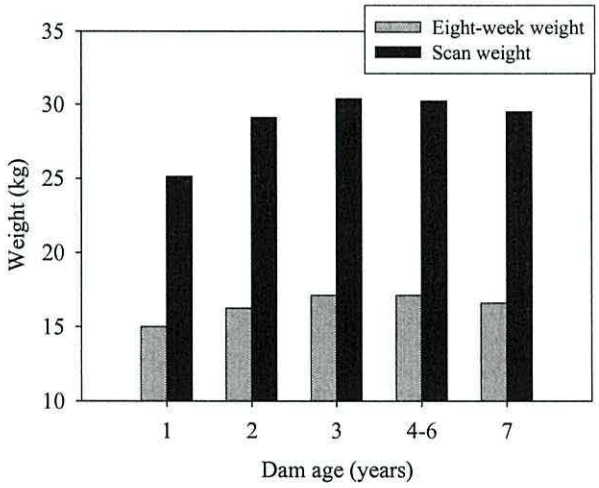


Figure 7.2 Mean eight-week weights and scan weights for the fixed effect of dam age.

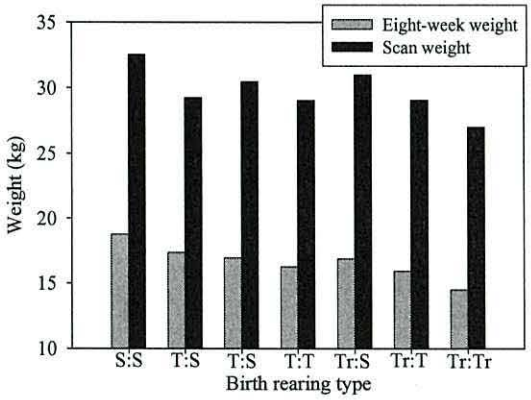


Figure 7.3 Mean eight-week weights and scan weights for the fixed effect of birth rearing type.

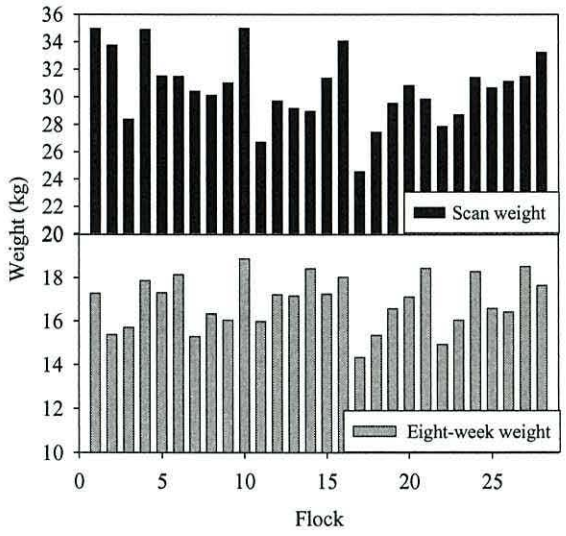


Figure 7.4 Mean eight-week weights and scan weights for the fixed effect of flock.

Estimates of variance components and genetic parameters for eight-week weight of Beulah Speckled Face lambs, together with log likelihood (logL) values for all models, are summarised in Table 7.3. Direct and maternal heritability estimates of the models ranged from 0.07 to 0.48 and 0.07 to 0.28 respectively.

Model 5 appeared to be the most appropriate model to use for analysing data for eight-week weight. With the exception of model 6, all models were significantly different from their neighbouring model. Model 5 produced estimates for direct and maternal heritability of 0.09 and 0.07 respectively. The phenotypic variance was 6.67 kg.

7.3.2 Scan week weight

Descriptive statistics for fixed effects are shown in Tables C2 to C4 in Appendix C, and Figure 7.2 shows the mean weights at scanning for the fixed effects year of birth, birth rearing type, dam age and flock. Year of birth for the period 1995-2004 was used, and there appeared to be a trend in increasing mean weight over this period. The lowest mean weight of 25.89 kg was in 1995 and the heaviest mean weight of 31.51 kg was in 2004 (Table C.2, Figure 7.1). Comparison of mean weights showed that males were heavier than females by about 3.13 kg (Table C.3). Mean weights were lowest in offspring of yearling dams (25.11 kg) and heaviest in offspring of three year-old dams (30.37 kg) (Table C.3, Figure 7.2). For birth-rearing types minimum and maximum mean weights were 26.98

kg and 32.53 kg, respectively. Lambs that were reared as singles achieved heavier weights, even when born as twins or triplets. Mean weights decreased with increasing litter size reared, increasing litter size born (Table C.3, Figure 7.3). Mean scan weight of flocks ranged from 24.5 kg to 34.96 kg, and the minimum and maximum values were recorded in the same flocks as minimum and maximum eight-week weight (Table C.4, Figure 7.4).

Estimates of variance components and genetic parameters for scan weight of Beulah Speckled Face lambs, together with logL values for all models, are summarised in Table 7.4. Direct and maternal heritability estimates of the models ranged from 0.17 to 0.47 and 0.08 to 0.21, respectively. Model 5 again appeared to be the most appropriate model. Model 5 produced estimates for direct and maternal heritability, permanent environmental effect, and maternal temporary environmental effect of 0.18, 0.08, 0.08 and 0.16, respectively. The phenotypic variance was 15.41 kg.

7.3.3 Ultrasonic muscle depth and fat depth

Descriptive statistics for fixed effects are shown in Tables C.2 to C.4 in Appendix C, and Figures 7.6 to 7.9 show the mean muscle and fat depths for the fixed effects year of birth, birth rearing type, dam age and flock. Year of birth for the period 1991-2004 was used. However, there were no records available for 1992 and 1993, and until 1995 the numbers of animals recorded were few (Table C.2). The lowest mean muscle depth of 17.45 mm was in 1995 and the largest mean muscle depth of 22.73 mm was in 2004. The lowest mean fat depth of 1.39 mm was in 1995 and the largest mean muscle depth of 3.02 mm was in 1991 (Table C, Figure 7.5). Mean muscle depths for males and females were 21.06 mm and 20.79 mm respectively. Mean fat depths for males and females were 2.14 mm and 2.41 mm respectively (Table C.3). The trend was for mean muscle and fat depths to increase with increasing dam age, which peaked at dam age three, then decreased slightly for older dam ages. Minimum and maximum mean muscle depths were 19.60 mm and 21.19 mm respectively. Minimum and maximum mean fat depths were 1.76 mm and 2.35 mm respectively (Table C.3, Figure 7.6). Of the seven birth-rearing types minimum and maximum mean

muscle depths were 20.13 mm and 21.82 mm respectively. Minimum and maximum mean fat depths were 1.83 mm and 2.68 mm, respectively. The trend observed in mean muscle depths and fat depths was similar to that of mean scan weight. Lambs that were reared as singles achieved higher muscle and fat depths (Table C.3, Figure 7.7). Mean muscle and fat depths of the flocks ranged from 19.40 mm to 23.59 mm, and 1.44 mm to 3.44 mm, respectively (Table C.4, Figure 7.8).

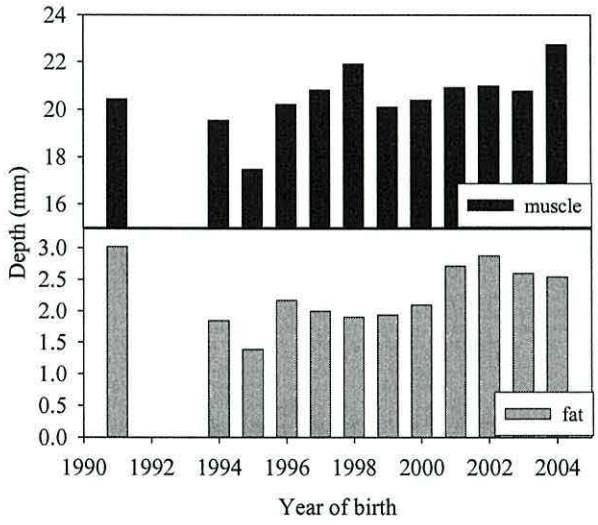


Figure 7.5 Mean muscle and fat depths for the fixed effect of year of birth

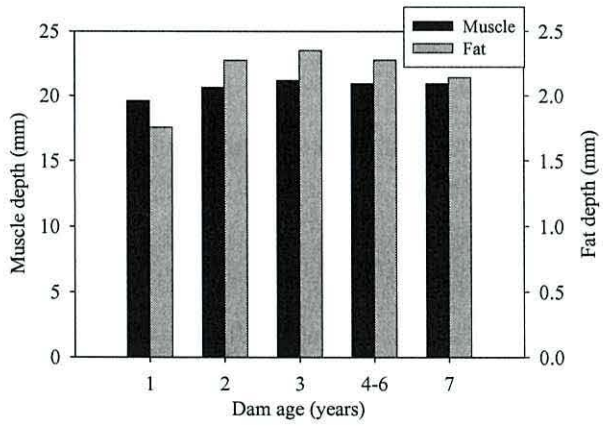


Figure 7.6 Mean muscle and fat depths for the fixed effect of dam age

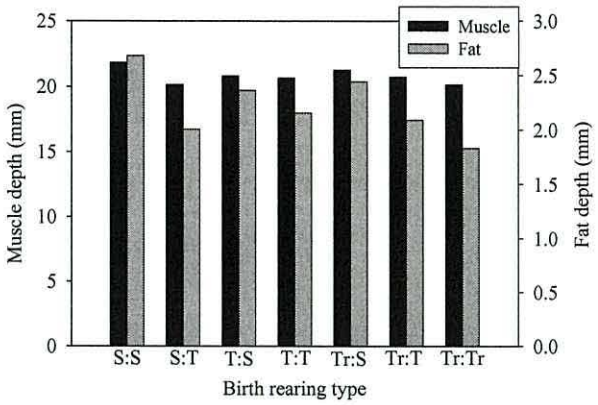


Figure 7.7 Mean muscle and fat depths for the fixed effect of birth rearing type.

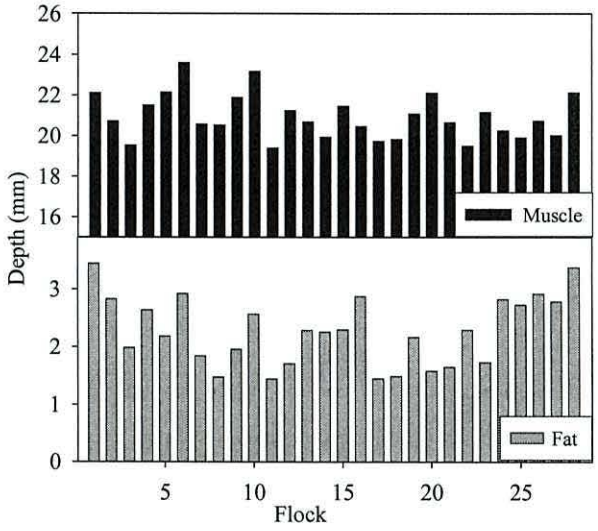


Figure 7.8 Mean muscle and fat depths for the fixed effect of flock.

Estimates of variance components and genetic parameters for muscle depth and fat depth of Beulah Speckled Face lambs, together with logL values for all models, are summarised in Tables 7.5 and 7.6. Direct heritability estimates of the models for muscle depth ranged from 0.20 to 0.34. Model 5 was found to be the most appropriate, and estimates of direct heritability, maternal heritability, maternal permanent environmental and maternal temporary environmental variances were 0.19, 0.03, 0.04, and 0.12, respectively.

In the analysis of fat depth the addition of maternal permanent environmental effect (Model 3) caused maternal additive genetic effect to be fixed at a boundary, as it was extremely low. Thus, Model 6, which included direct-maternal covariance was not evaluated. Instead, Model 7 was tested; this was Model 5 without the maternal additive genetic effect, and showed the effect was not

required in the model, but that it did not matter if it was included. Estimates from Models 5 and 7 gave the same results, and results for direct heritability, maternal permanent environmental and maternal temporary environmental variances were 0.20, 0.11, and 0.12, respectively.

Table 7.3 Models to estimate (co)variance components and genetic parameters for eight-week weight of Beulah Speckled face lamb.

	1	2	3	4	5	6
σ^2_a	3.45	0.67	0.81	0.50	0.57	0.70
σ^2_m		1.89	0.52	1.16	0.46	0.66
σ^2_{am}						-0.27
σ^2_{pe}			1.24		0.76	0.78
σ^2_{ce}				1.92	1.75	1.74
σ^2_e	3.73	4.32	4.13	3.16	3.13	3.06
σ^2_p	7.18 ± 0.11	6.88 ± 0.11	6.70 ± 0.10	6.74 ± 0.10	6.67± 0.10	6.68 ± 0.10
h^2	0.481 ± 0.02	0.097 ± 0.02	0.121 ± 0.02	0.074 ± 0.02	0.086 ± 0.02	0.105 ± 0.03
m^2		0.275 ± 0.01	0.078 ± 0.02	0.172 ± 0.02	0.069 ± 0.02	0.099 ± 0.03
pe^2			0.185 ± 0.02		0.114 ± 0.02	0.116 ± 0.02
ce^2				0.285 ± 0.02	0.263 ± 0.02	0.261± 0.02
C_{AM}						-0.040± 0.02
r_{AM}						-0.390 ± 0.17
h^2_T	0.481	0.234	0.160	0.160	0.120	0.207
logL	-18505.4	-18318	-18280.5	-18144	-18129.9	-18128.4
diff	0	187.4 (S)	37.5 (S)	174 (S)	150.6/14.1 (S)	1.5 (N.S.)

σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{am} direct-maternal genetic covariance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal temporary environmental variance; σ^2_e error variance; σ^2_p phenotypic variance; h^2 direct heritability; m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance; C_{AM} Genetic covariance between direct and maternal effects expressed as a proportion of the phenotypic variance; r_{AM} genetic correlation between direct and maternal effects; h^2_T total heritability; logL log likelihood ratio; diff difference between neighbouring models; Model 4 compared with 2, model 5 compared with 3 and 4. S = significant, N.S = non significant.

Table 7.4 Models to estimate (co)variance components and genetic parameters for scan weight of Beulah Speckled Face lambs.

	1	2	3	4	5	6
σ^2_a	7.68	2.65	2.94	2.58	2.73	3.08
σ^2_m		3.35	1.32	2.32	1.25	1.80
σ^2_{am}						-0.67
σ^2_{pe}			1.89		1.15	1.15
σ^2_{ce}				2.69	2.44	2.43
σ^2_e	8.62		9.28	7.90	7.83	7.65
σ^2_p	16.3 ± 0.30	15.63 ± 0.27	15.43 ± 0.27	15.49 ± 0.27	15.41± 0.27	15.44 ± 0.28
h^2	0.471 ± 0.027	0.170 ± 0.028	0.191 ± 0.031	0.166 ± 0.029	0.177 ± 0.031	0.200 ± 0.038
m^2		0.214 ± 0.016	0.086 ± 0.025	0.150 ± 0.017	0.081 ± 0.023	0.116 ± 0.036
pe^2			0.122 ± 0.023		0.075 ± 0.023	0.075 ± 0.024
ce^2				0.174 ± 0.018	0.159 ± 0.018	0.157 ± 0.018
C_{AM}						-0.044 ± 0.029
r_{AM}						-0.286 ± 0.148
h^2_T	0.471	0.277	0.233	0.241	0.218	0.192
logL	-18435.2	-18337.9	-18324.4	-18290.1	-18285.3	-18284.0
diff	0	97.3 (S)	13.5 (S)	47.8 (S)	39.1/4.8 (S)	1.3 (N.S.)

See Table 7.3 for abbreviation definitions

Table 7.5 Models to estimate (co)variance components and genetic parameters for muscle depth of Beulah Speckled Face lambs.

	1	2	3	4	5	6
σ^2_a	1.67	0.90	0.95	0.88	0.90	0.95
σ^2_m		0.48	0.15	0.28	0.14	0.17
σ^2_{am}						-0.05
σ^2_{pe}			0.37		0.19	0.19
σ^2_{ce}				0.65	0.59	0.59
σ^2_e	3.29	3.46	3.37	3.02	3.01	2.98
σ^2_p	4.96	4.85	4.83	4.83	4.83	4.83
h^2	0.336 ± 0.029	0.187 ± 0.032	0.197 ± 0.032	0.183 ± 0.032	0.186 ± 0.032	0.196 ± 0.039
m^2		0.100 ± 0.016	0.031 ± 0.020	0.058 ± 0.016	0.029 ± 0.020	0.036 ± 0.025
pe^2			0.076 ± 0.020		0.039 ± 0.021	0.040 ± 0.025
ce^2				0.135 ± 0.020	0.123 ± 0.021	0.123 ± 0.021
C_{AM}						-0.011 ± 0.023
r_{AM}						-0.132 ± 0.243
h^2_T	0.336	0.235	0.212	0.211	0.201	0.199
logL	-11791.9	-11770.2	-11763.7	-11747.4	-11745.8	-11745.7
diff	0	21.7 (S)	6.5 (S)	22.8 (S)	17.9/1.6 (S)	0.1 (N.S.)

See Table 7.3 for abbreviation definitions

Table 7.6 Models to estimate (co)variance components and genetic parameters for ultrasonic fat depth of Beulah Speckled Face lambs.

	1	2	3	4	5	7
σ^2_a	0.23	0.11	0.13	0.12	0.12	0.12
σ^2_m		0.07	0.00	0.04	0.00	
σ^2_{pe}			0.08		0.06	0.06
σ^2_{ce}				0.10	0.07	0.07
σ^2_e	0.39	0.41	0.38	0.34	0.34	0.34
σ^2_p	0.61	0.60	0.60	0.60	0.60	0.60
h^2	0.349 ± 0.029	0.188 ± 0.032	0.213 ± 0.032	0.197 ± 0.034	0.204 ± 0.032	0.204 ± 0.032
m^2		0.012 ± 0.017	0.000 ± 0.000	0.071 ± 0.017	0.000 ± 0.000	
pe^2			0.141 ± 0.015		0.108 ± 0.017	0.108 ± 0.017
ce^2				0.159 ± 0.021	0.119 ± 0.021	0.119 ± 0.021
h^2_T	0.349	0.250	0.213	0.232	0.204	0.204
logL	-2528.5	-2504.37	-2479.19	-2478.41	-2464.08	-2464.54
diff	0	24.13 (S)	25.18 (S)	25.96 (S)	15.11/14.33 (S)	-0.46 (N.S)

See Table 7.3 for abbreviation definitions; Model 7 compared with 5.

7.4 DISCUSSION

A model (Model 5) that included animal direct effect, additive maternal genetic effect, maternal permanent environmental effect and maternal temporary environmental effect was the most appropriate for estimating components of variance and heritability estimates for eight-week weight, scan weight, muscle depth, and fat depth.

7.4.1 Direct Heritability

Direct heritability of eight-week weight had the lowest value (0.09), whereas the traits examined at scanning can be described as moderately heritable, with heritabilities that ranged from 0.18 to 0.20. Therefore, the traits measured at scanning can be selected for with some degree of confidence that genetic progress can be made. As expected the results show that direct heritability increased from eight-week weight to time of scanning (mean age 21 weeks). This tendency is due to the lamb becoming more dependent on other food sources, and less reliant on the decreasing supply of milk from the dam.

7.4.2 Maternal heritability and maternal environmental effects

Estimates of maternal heritability were low, ranging from 0.03 to 0.08, and was not significant for fat depth. For eight-week weight and scan weight there was little difference between the estimates for maternal heritability. Maternal permanent environmental effect ranged from 4 to 11 % of the phenotypic variance for the traits. While maternal additive genetic effect was non-significant for fat depth, maternal permanent environmental effect was considerably higher (11 %) than for muscle depth (4 %). Maternal temporary environmental effect had quite a large effect, ranging from 12 to 26 % of the phenotypic variance, particularly for eight-week weight where it accounted for 26 % of the phenotypic variance. The maternal environmental effects are of greatest influence at a younger age.

When estimating heritability the importance of including maternal effects in an analysis are clear. The total effect of the dam is quite substantial. For eight-week weight, scan-weight, muscle depth, and fat depth the total contribution of dam effects to phenotypic variance were 44 %, 32 %, 19 %, and 23 %, respectively. The proportion due to maternal effects (m^2, pe^2, ce^2) declines with increasing age, particularly as a result of the reductions in maternal environmental effects (maternal permanent environmental effects and maternal temporary environmental effects). Without the inclusion of maternal effects direct heritability would be over-estimated.

7.4.2 Direct-maternal genetic covariance

Fitting the direct and maternal genetic covariance generally gave a logL value closer to zero, but the change was not significant for any of the traits. Consistent with the results of Hussain *et al.* (2006) the estimates of direct-maternal genetic correlation for eight-week weight, scan weight, and muscle depth were negative, and ranged from -0.13 to -0.39. The negative direct-maternal correlation caused both direct heritability and maternal heriability to increase slightly in Model 6. Negative values indicate the potential for an antagonistic relationship when breeding programs aim to improve genetic merit for both individual growth and

maternal performance. Negative correlations of this kind have been reported from several studies (Hagger, 1998; Jara *et al*, 1998; Wilson *et al*, 2005), and simulation studies have indicated that the antagonistic relationship has occurred in estimates due to poor data structure (Maniatis and Pollott, 2003). In this study poor data structure could arise because some flocks being part of the sire referencing scheme for a short time, resulting in insufficient data for some dams and their progeny.

Genetic parameters for the Beulah Speckled Face breed have also been reported by Hussain *et al.* (2006). Direct heritability estimates from this study are similar with the exception of eight-week weight, which was observed to have a much lower heritability in the present study (0.09 compared with 0.17). Unlike other researchers Hussain *et al.* (2006) did not encounter an increase in direct heritability with increasing age, from eight weeks to scanning, whereas in this study it was apparent. Results for maternal heritability were similar for eight-week weight; however, Hussain *et al.*'s (2006) estimates were higher for the scanning traits than in the present study. In this study additive maternal genetic effect did not appear to be significant for fat depth; however, the maternal heritability for $\log_{10}$ fat depth was 0.18 in Hussain *et al.*'s (2006) study, which also indicated that additive maternal genetic effects were particularly important in their contribution to phenotypic variance of traits measured at scanning. In the study reported here, however, the highest value was 0.08 for scan-weight. Hussain *et al.* (2006) commented that permanent environmental effects and maternal temporary environmental effects were fairly low for scan traits, ranging from 0.04 to 0.08, and permanent environmental effect was not significant for $\log_{10}$ fat depth. In this study permanent environmental effects were fairly low and ranged from 0.04 to 0.11 across all traits, but maternal temporary environmental effects tended to be higher and ranged from 0.12 to 0.26. In this study additive maternal genetic effect was not significant for fat depth; however, this could be due to the inability to partition variation between additive maternal genetic effect and permanent environmental effect. In the case where ewes only have records for one litter this problem is likely to arise.

It can be difficult to compare results when models used and the traits analysed by other studies are different. Safari *et al.* (2005) reported mean estimates of genetic parameters from a range of studies. Weaning weight and scan weight (21 weeks) are likely to be close to the same age, and the estimates reported by Safari *et al.* (2005) of direct heritability, maternal heritability, and maternal temporary environmental variance were 0.18, 0.10, and 0.14 respectively, similar to that of scan weight here (0.18, 0.08, 0.16). Safari *et al.* (2005) reported heritabilities for muscle depth and fat depths as 0.26 and 0.24, respectively, which were higher than found here (0.19 and 0.20 respectively). In agreement with Hussain *et al.* (2006) direct heritability estimates for the Beulah Speckled Face reported here seem to be at the lower end of the range than found in other UK breeds, such as the Welsh Mountain (Ap Dewi *et al*, 2002), Scottish Blackface (Conington *et al*, 2001), Bluefaced Leicester (van Heelsum *et al*, 1999) and Suffolk (Maniatis and Pollott, 2002b).

CHAPTER 8

Estimating Heritability of Maternal Traits in Welsh Mountain and Beulah Speckled Face Breeds

Plate 8.1 Welsh Mountain lamb on Y Garn

ABSTRACT

A model that included both additive direct genetic effect and permanent environmental effect of the animal was found to be the most appropriate for univariate analysis of litter size born (LSB), litter size reared (LSR), and litter weight (LW) for the Welsh Mountain dataset. In the Welsh Mountain breed direct heritability estimates (h^2) for LSB, LSR, and LW were 0.13, 0.09, and 0.11 respectively. Estimates for permanent environmental effects of the animal (pea^2) for LSB, LSR, and LW were 0.08, 0.07, and 0.08, respectively. Similar estimates were obtained from the Beulah Speckled Face breed and direct heritability estimates (h^2) for LSB, LSR, and LW were 0.13, 0.08, and 0.10 respectively. Permanent environmental effect was only significant for LW and was 0.10. The Welsh Mountain dataset included records for mature weight. The direct heritability estimate for mature weight was 0.52, using a model that included only direct additive genetic effect of the animal as a random effect.

8.1 INTRODUCTION

The Welsh Index takes into account two breeding goals. One goal is to improve maternal ability, and the other is to improve the lamb's own potential for growth

and carcass composition. Only females that give birth to lambs express maternal traits and maternal ability is an important attribute of hill ewes, as they need to survive, conceive, give birth, and raise lambs in generally harsh environmental conditions. Maternal ability is assessed through the performance of a ewe's lambs (see Plate 8.1). The maternal traits measured in order to achieve breeding goals are litter size, litter weight, and mature weight of the ewe.

8.1.1 Litter size born (LSB)

Litter size is defined as the total number of lambs born dead or alive when pregnancy reaches full term. Number of lambs born per ewe is often used as a selection criterion because it is easy to measure and report, and heritability estimates are generally higher than for other reproductive traits, such as fertility and lamb survival (Rao and Notter, 2000). The most important factor affecting profitability of a sheep enterprise, particularly for lamb meat production, is the prolificacy (Janssens *et al*, 2004), and is best measured by the number of lambs born within a specific interval. There is considerable variation between breeds in mean litter size, from one lamb to four lambs. An optimum rather than maximum number of lambs born is considered better for a breeding goal. The target mean litter size born depends upon the husbandry, feed resources available to the flock, and the season of lambing.

8.1.2 Litter size reared (LSR)

Litter size reared is the number of lambs successfully reared until weaning, and is influenced by the number of lambs born and the survival rate of lambs. Litter size reared is more important commercially than litter size born as it determines the financial return.

8.1.3 Litter weight (LW)

Ercanbrack and Knight (1998) considered total weight of lamb produced per breeding ewe as the most economically-important measure of a commercial sheep enterprise. Litter weight and individual lamb weight are not the same trait

unless single lambs are reared. Litter weight is the total weight of lambs in the litter and it is indicative of the mothering ability of the ewe. Eight-week weights are generally used. Heavier lambs indirectly identify ewes with better maternal characteristics such as higher milk supply and good maternal care. Ewes with larger litters would generally be expected to produce higher litter weights.

8.1.4 Mature weight (MW)

Mature size is generally measured as the liveweight of a ewe at first mating. The indirect gains from increasing the mature size of the ewe are heavier offspring, higher litter size, and heavier fleece weight (Conington *et al*, 2004). Also a benefit of larger ewes could possibly be a higher cull value. In hill sheep there may also be emphasis on increasing weights and growth rates of lambs, but an increase in mature size of the ewe would mean greater maintenance inputs. There would be costs associated with heavier ewes such as supplementary feed, additional fertilizer and extra land needed or, conversely, fewer ewes kept per hectare of land. Particularly in a harsh hill environment larger ewes may not be advantageous. Conington *et al.* (2004) found that the cost of increasing mature size outweighed the benefits. However, mature weight is likely to increase through index selection, because of the positive genetic correlation of mature weight with live weight at weaning (Conington *et al*, 2001).

The aim of the work described in this chapter was to obtain estimates of variance components and heritabilities, by use of an appropriate model, for the traits litter size at birth, litter size at rearing, litter weight, and mature size in Welsh Mountain and Beulah Speckled Face breeds.

8.2 METHOD

The data were obtained from two Welsh sheep breeds, the Welsh Mountain and the Beulah Speckled Face. The Welsh Mountain data came from the breeding groups CAMDA, CAMP, and Llysfasi, and the Beulah Speckled Face data came from the Beulah Sire Referencing Scheme. The same datasets were employed as were used in the work described in Chapters 6 and 7.

Litter size at birth and litter size reared ranged from one to two lambs in the Welsh Mountain dataset, and from one to three lambs in the Beulah scheme; on average the Beulah Speckled Face produced and reared more lambs. Mean litter sizes at birth and rearing were 1.45 lambs and 1.37 lambs respectively in the Welsh Mountain, and 1.68 lambs and 1.55 lambs respectively, in the Beulah Speckled Face. Table 8.1 shows that not all lambs survive to weaning, with lamb losses of 5.5 % in the Welsh Mountain and 7.7 % in the Beulah. Mean litter weight is slightly higher in the Beulah Speckled Face at 25.62 kg, compared to 24.91 kg for the Welsh Mountain breed. Mature weight records were only available from the Welsh Mountain breed, and the mean weight was 36.31 kg.

All 1975 records for mature weight were from the CAMDA flock and were from females only. Exact ages of the animals when the recording of mature weight was taken are not known. It was assumed that within a single year animals were weighed on the same date, and therefore the effect of date of birth was nested within year of birth. Ap Dewi *et al.* (2002) stated that ewe lambs were generally weighed at 12 to 13 months of age, after returning from an away-wintering grazing period.

Table 8.1 Number of observations, mean, standard deviation and minimum and maximum values of the traits litter size born, litter size reared and litter weight for Welsh Mountain and Beulah Speckled Face sheep, and of mature ewe weight for Welsh Mountain sheep.

Variable	Count	Mean	S.d.	Minimum	Maximum
Welsh Mountain					
Litter size birth (LSB)	18029	1.45	0.497	1	2
Litter size reared (LSR)	18029	1.37	0.484	1	2
Litter weight (kg)	18029	24.91	9.734	5	60.5
Mature weight (kg)	1975	36.31	4.18	24.0	55.0
Beulah Speckled Face					
Litter size birth (LSB)	8872	1.68	0.56	1	3
Litter size reared (LSR)	8872	1.55	0.52	1	3
Litter weight (kg)	8872	25.62	8.80	5.8	76.4

Birth year, dam age, sex, birth rearing type, flock and interactions between these, with the exception of dam age, were treated as fixed effects, based upon commonly accepted procedures of other authors (Ap Dewi *et al*, 2002; Saatci, 1998). The significance of univariate analyses were carried out for each trait to determine the significance of fixed and random effects, so to choose an appropriate model to obtain values for genetic parameters.

The effects considered are listed below.

Dam age is the age of the dam at the time when an animal is born, and was included for litter size born, litter size reared, litter weight and mature weight.

Year of Birth is the year that the ewe gives birth and was included in models used for litter size and litter weight. In the case of mature weight year of birth is the year the animal was born.

Flock was included in models used for litter size born, litter size reared and litter weight. It was not used for models to analyse mature weight as only one flock had records of this type.

Birth rearing type was included in models used for mature weight. There were three classes, namely single born – single reared, twin born – single reared, and twin born – twin reared.

Sex was only included in models used for litter weight, and was a code constructed from sex of lamb and birth rearing type. For the Welsh Mountain there were five codes, namely single male, single female, twins both male, twins both females, and twins with one male and one female. For the Beulah Speckled Face there were eight codes, and the additional codes were for triplet groups: two males and one female; two females and one male; and three females. None of the triplet groups had three males.

Litter size born, litter size reared and litter weight are traits that can be repeatable, as a ewe may have more than one litter. Therefore, in the model for analysing these traits the random permanent environmental effect of the animal was included.

The full model for litter weight was

Equation 8. 1

$$Y_{ijklm} = \mu + a_i + b_j + c_k + d_l + y_m + z_m + e_{ijklm}$$

where μ = the overall mean litter weight; a_i = fixed effect of dam age; b_j = fixed effect of year; c_k = fixed effect of sex of lambs in litter; d_l = fixed effect of flock; y_m = the random direct additive genetic effect of animal m; z_m = the random permanent environmental effect of the animal; e_{ijklm} = random environmental effect.

The models for litter size born used the same fixed effects as the model for litter weight, with the exclusion of c_k (sex of lambs in litter). Two models were used for litter size born, litter size reared and litter weight. The first model (1) included only the direct additive genetic effect of animal as a random effect. The second model (2) included both the direct additive genetic effect and the permanent environmental effect of animal as random effects.

Some studies have mentioned the persistence of maternal effects in mature animals (Meyer, 1992), so the models studied for weight and ultrasonically-scanned traits in chapters 5, 6, and 7, with additive maternal genetic effect, maternal permanent maternal effect and maternal temporary environmental effect, were tested in addition to additive direct genetic effect to find whether maternal effects were significant for mature ewe weight.

The full model for mature weight was

Equation 8. 2

$$Y_{ijklm} = \mu + a_i + b_j + c_k + d_{j/l} + w_m + x_n + y_n + z_n + e_{ijklm}$$

where μ = overall mean of mature weight; a_i = fixed effect of dam age; b_j = fixed effect of year; c_k = fixed effect of birth rearing type; $d_{j/l}$ = fixed effect of age nested within year; w_m = the random direct additive genetic effect of animal m; x_n = the random maternal additive genetic effect of the n^{th} dam; y_n = the random maternal permanent environmental effect of the n^{th} dam; z_{nj} = the random maternal temporary environmental effect of the n^{th} dam in the j^{th} year; e_{ijklmn} = random environmental effect.

8.3 RESULTS

The fixed effects found to be significant for the traits litter size born, litter size reared, litter weight, and mature weight for both breeds are shown in Table 8.2.

Table 8.2. Fixed effects included in each chosen univariate model.

	Welsh Mountain				Beulah		
Fixed Effects	**LSB**	**LSR**	**LW**	**MW**	**LSB**	**LSR**	**LW**
Dam age	✓	✓	✓	✓	✓	✓	✓
Year of birth	✓	✓	✓	✓	✓	✓	✓
Flock	✓	✓	✓		✓	✓	✓
Sex			✓				✓
Birth rearing type				✓			
Year of birth / date of birth				✓			
Year * flock	✓	✓	✓		✓	✓	✓
Year * sex			✓				
Flock * sex			✓				
Year * flock * sex			✓				

8.3.1 Welsh Mountain analysis

Estimates of variance components and genetic parameters for litter size born (LSB), litter size reared (LSR), and litter weight (LW) for the two models are summarized in Table 8.3. For the univariate analysis of litter size born, litter size reared, and litter weight it was found that the most appropriate model included direct additive genetic effect and permanent environmental effect of the animal as random effects. When the permanent environmental effect was not included in the models the direct additive genetic effect was over-estimated. Direct heritability estimates (h^2) for litter size born, litter size reared and litter weight were 0.13, 0.09, and 0.11 respectively. Estimates for permanent environmental effects of the animal (pea^2) for litter size born, litter size reared and litter weight were 0.08, 0.07, and 0.08, respectively. Phenotypic variances for litter size born, litter size reared and litter weight were 0.23, 0.21, and 11.25 kg, respectively.

Estimates of variance components and genetic parameters for mature weight for the models 1-5, examining the importance of maternal effects, are summarized in Table 8.4. For the univariate analysis of mature weight (MW) it was found that the most appropriate model included only direct additive genetic effect as a random effect. It was noticed there were maternal effects, but the addition of these did not significantly improve the model. When both maternal genetic effect and maternal temporary environmental effect were included in the model, they contributed 3 % and 7 %, respectively to the phenotypic variance, although it should be noted that standard errors were high. The direct heritability of mature weight was high at 0.52. The phenotypic variance was 11.68 kg.

Table 8.3 Univariate analysis of litter size born, litter size reared, and litter weight for the Welsh Mountain breed.

Models	Litter size born (1)	Litter size born (2)	Litter size reared (1)	Litter size reared (2)	Litter weight (1)	Litter weight (2)
σ^2_a	0.04	0.03	0.03	0.02	1.83	1.23
σ^2_{pea}		0.02		0.02		0.85
σ^2_e	0.18	0.18	0.18	0.18	9.42	9.10
σ^2_p	0.228 (0.003)	0.226 (0.003)	0.213 (0.002)	0.212 (0.002)	11.25 (0.127)	11.18 (0.125)
h^2	0.193 (0.011)	0.129 (0.014)	0.140 (0.010)	0.085 (0.012)	0.162 (0.010)	0.110 (0.012)
pea^2		0.082 (0.014)		0.072 (0.013)		0.076 (0.013)
LogL	4574.86	**4594.18 (S)**	4983.97	**5001.42 (S)**	-30190.4	**-30170.9 (S)**

σ^2_a direct additive effect; σ^2_{pea} permanent environmental variance of the animal; σ^2_e error variance; σ^2_p phenotypic variance; h^2 direct heritability; pea^2 permanent environmental variance of the animal expressed as a proportion of phenotypic variance; Logl log likelihood ratio; **S** model 2 is significantly better than model 1; bold print shows chosen model.

Table 8.4 Univariate analysis of mature weight for the Welsh Mountain breed

	Model 1	Model 2	Model 3	Model 4	Model 5
σ^2_a	6.13	5.81	5.78	6.00	5.78
σ^2_m		0.35	0.26		0.26
σ^2_{pe}					0.00
σ^2_{ce}			0.86	1.00	0.86
σ^2_e	5.55	5.50	4.74	4.65	4.74
σ^2_p	11.68 (0.453)	11.66 (0.451)	11.64 (0.406)	11.65 (0.404)	11.64 (0.406)
h^2	0.523 (0.047)	0.498 (0.053)	0.497 (0.054)	0.515 (0.049)	0.497 (0.054)
m^2		0.030 (0.026)	0.022 (0.026)		0.022 (0.026)
pe^2					0.00
ce^2			0.074 (0.057)	0.085 (0.055)	0.074
logL	**-3315.28**	-3314.47 (NS)	-3313.54 (NS)	-3313.99 (NS)	-3313.54 (NS)

σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal temporary environmental variance; σ^2_e error variance; σ^2_p phenotypic variance; h^2 direct heritability; m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance; logL log likelihood ratio; N.S not significant different; bold print shows chosen model.

8.3.2 Beulah Speckled Face

Estimates of variance components and genetic parameters for litter size born, litter size reared, and litter weight for the two models are summarized in Table 8.5. For the univariate analysis of litter size born and litter size reared the most appropriate model included only direct additive genetic effect as a random effect. For both litter size born and litter size reared logL values were positive. There was a more positive logL value when permanent environmental effect of the animal was included, but it was not significant. For litter weight it was found that the most appropriate model included both direct additive genetic effect and permanent environmental effect of the animal as random effects, because the logL value was closer to zero (or more positive). Direct heritability estimates (h^2) for litter size born, litter size reared, and litter weight were 0.13, 0.08, and 0.10 respectively. The estimate for permanent environmental effect of the animal (pea^2) for litter weight was 0.10. Phenotypic variances for litter size born, litter size reared, and litter weight were 0.28, 0.25, and 11.11 kg, respectively.

Table 8.5 Univariate analysis of litter size born, litter size reared, and litter weight for the Beulah Speckled Face breed.

Models	Litter size born (1)	Litter size born (2)	Litter size reared (1)	Litter size reared (1)	Litter weight (1)	Litter weight (2)
σ^2_a	0.04	0.03	0.02	0.01	2.56	1.37
σ^2_{pea}		0.01		0.01		1.39
σ^2_e	0.24	0.24	0.23	0.23	11.44	11.11
σ^2_p	0.282 (0.004)	0.281 (0.004)	0.250 (0.004)	0.250 (0.004)	14.00 (0.230)	13.870 (0.226)
h^2	0.130 (0.014)	0.108 (0.020)	0.075 (0.012)	0.057 (0.016)	0.183 (0.016)	0.099 (0.023)
pea^2		0.030 (0.021)		0.029 (0.019)		0.100 (0.025)
LogL	**997.143**	988.214 (NS)	**1454.80**	1456.06 (NS)	-15461.6	**-15453.7** (S)

σ^2_a direct additive effect; σ^2_{pea} permanent environmental variance of the animal; σ^2_e error variance; σ^2_p phenotypic variance; h^2 direct heritability; pea^2 permanent environmental variance of the animal expressed as a proportion of phenotypic variance; Logl log likelihood ratio; **S** model 2 is significantly better than model 1; bold print shows chosen model; NS model 2 is not significantly different to model 1.

8.4 Discussion

8.4.1 Chosen models

The estimates of direct heritability in the two breeds were quite similar. For litter size born it was 0.13 in both breeds, for litter size reared it ranged from 0.08 to 0.09, and litter weight it ranged from 0.10 to 0.11, in the chosen models. In the Beulah Speckled Face permanent environmental effect of the animal was not significant for either litter size trait, even though the value of logL improved slightly when it was added to the model. When the effect was included in the model direct heritability decreased slightly and the permanent environmental effect contributed 3 % of the phenotypic variance. The effect was significant for litter weight, contributing 10 % to the phenotypic variance, which equaled the direct heritability. In the Welsh Mountain breed, permanent environmental effect was significant for litter size born, litter size reared and litter weight, and their contributions to phenotypic variances were 0.08, 0.07, and 0.11, respectively, which were close to but a little less than their direct heritabilities. All of the three traits have low heritability as reported by other authors, and similar to the values given by other studies. The review of Safari *et al.* (2005) reported mean

heriabilities for litter size born, litter size reared, and litter weight of 0.10, 0.07, and 0.13, respectively.

Litter size is expressed in discrete numbers (1, 2, 3, or 4), and thus statistical analysis can be complicated. In this study litter size was treated in the same way as the continuous traits and analysed using a linear model with variance components obtained by REML methods, in an approach similar to that used in many other studies (Ap Dewi *et al*, 2002; Bromley *et al*, 2000; Hagger, 2000). However, it has been suggested that non-linear methods based on the threshold model should be used to account for the categorical nature of the traits and the non-normal distribution of phenotypes (Altarriba *et al*, 1998; Gianola, 1982). Using this approach (Altarriba *et al*, 1998; SanCristobal-Gaudy *et al*, 2001; Vitezica *et al*, 2006) heritabilities of litter traits were higher than when using a linear model (Altarriba *et al*, 1998; Kadarmideen *et al*, 2000). However, Kadarmideen *et al.* (2000) found that standard errors were higher when using the threshold model, implying that selection accuracy could be lower. Although threshold models are regarded as theoretically superior for ordinal data, Kadarmideen *et al.* (2000) reported that current computational time and demands were overwhelming; perhaps this could be improved in the future. Hagger (2000; 2002) reviewing results of both linear and non-linear models, considered the advantage, if there was any, of the non-linear model to be very small.

8.4.2 Litter size born

Reported heritabilities for litter size born range from 0.06 to 0.07 for Suffolk and 0.09 to 0.13 for Texel breeds (Janssens *et al*, 2004), 0.09 for Rambouillet, Columbia, Suffolk, and Polpay (Hanford *et al*, 2002; Hanford *et al*, 2005; Rao and Notter, 2000), 0.11 for Targhee (Rao and Notter, 2000), and 0.10 for Composite (Al-Shorepy and Notter, 1996) and French breeds Ovin Ile de France, Blanc du Massif Central and Mouton Vendeen sheep (Baelden *et al*, 2005). Ap Dewi *et al.* (2002) obtained an estimate of 0.15 for litter size in the Welsh Mountain.

8.4.3 Litter size reared

The heritability for litter size at rearing is generally smaller than that for litter size at birth (Hanford *et al*, 2002; Hanford *et al*, 2005). A similar heritability estimate of 0.07 for litter size reared was obtained for the Scottish Blackface, another hill breed (Conington *et al*, 2001)

8.4.4 Litter weight

Bromley *et al.* (2001) reported estimates for Polpay, Rambouillet, and Targhee breeds of 0.10, 0.11, and 0.08 respectively, for litter weight, similar to the values obtained here. Conington *et al.* (2001) obtained a similar estimate of 0.10 from Scottish Blackface. The estimates obtained here were much lower than the 0.20 estimated by Ap Dewi *et al.* (2002) for the same breed, using data from the CAMDA flock. Litter weight is a complex composite trait (Bromley *et al*, 2001) and its low heritability is not unexpected due to its linkages with fertility, prolificacy, lamb growth, lamb survival to weaning, and ewe health from breeding to weaning (Ercanbrack and Knight, 1998). Environmental effects are considerable as shown by the large residual variances (Tables 8.3 and 8.5). However, although the heritability was fairly low, phenotypic variances in the Beulah, and Welsh Mountain breeds were 13.87 kg, and 11.18 kg, respectively, and thus response to selection could be significant.

8.4.5 Mature Weight

The direct heritability estimate for the Welsh Mountain was moderate, with a value of 0.52. A model with only direct additive genetic effect of the animal was used. Maternal effects appeared to be present but their inclusion did not improve the model significantly. When maternal additive genetic effect and maternal temporary environmental effect were both included the residual and direct additive genetic variance reduced slightly and the maternal effects accounted for 0.02 and 0.07 respectively of the phenotypic variance. Ap Dewi *et al.* (2002) estimated mature weight on the same flock but did not include maternal effects in their model. The moderate heritability and the phenotypic variance (11.68 kg)

suggest that selection upon the trait could be made if it was desired and would be successful. The direct heritability obtained was close to values reported by other authors, such as 0.48 in Rambouillet at 18 months (Lee *et al*, 2000), 0.47 in Scottish Blackface (Conington *et al*, 2001) and 0.49 in the same flock of Welsh Mountain (Ap Dewi *et al*, 2002).

8.4.6 The implications of selecting for litter traits

Litter size and litter weight have quite low heritability, but the phenotypic variances show that there could be scope for genetic improvement. Litter size is generally one of the main selection objectives in breeding schemes for meat breeds. It is ineffective if litter size born is increased but ewes are incapable of rearing more lambs. It is wasteful if ewes are carrying higher litter sizes throughout pregnancy, with the corresponding need for extra nutrition, if lambs do not then survive afterwards. Increased litter size may result in lower birth weights, with greater risk of mortality. Lee *et al.* (2000) suggested that increased litter size would also lead to increased mature size. For the Welsh Mountain in particular, which generally survives in harsh environments, increasing litter size may not be appropriate. Ewes would require more energy for maintenance for their own survival and lactation. It would be better to put emphasis on litter size reared or litter weight, so that ewes are selected that have the ability to rear successfully the lambs they have given birth to, in the environment that they inhabit.

Evaluation of Bivariate Models to Analyse Weight and Ultrasonic Scanning Traits for Welsh Mountain and Beulah Speckled Face Breeds

ABSTRACT

Bivariate analysis was performed on growth, ultrasonic-scanning traits, and litter traits for both Welsh Mountain and Beulah Speckled Face breeds. These traits were eight-week weight (EWW), scan-weight (SW), ultrasonic muscle depth (MD), ultrasonic fat depth (FD), mature weight (MW), litter size born (LSB), litter size reared (LSR), and litter weight (LW). All genetic correlations between weight and ultrasonic traits were positive. Genetic correlations among weight traits were high in both breeds. Genetic correlations between growth and ultrasonic traits with litter traits were all positive with the exception of the correlation between LSR and FD in the Beulah Speckled Face breed, which had a low negative value of -0.01. LSB was strongly correlated with LSR but both were negatively or weakly positively correlated with LW. Phenotypic correlations were higher than genetic correlations for all trait combinations except for weight trait combinations in the Welsh Mountain and the combination of LSB with LSR in both breeds. Several models were examined and it was observed that selection of the most appropriate model in univariate analysis was important because in subsequent bivariate analysis genetic and phenotypic correlations can vary radically as a result of model choice. Reliable genetic and phenotypic covariances are necessary for construction of selection indexes.

9.1 INTRODUCTION

Analyses using bivariate models are particularly important in the process of constructing a selection index. Some traits are not entirely independent of each other and traits are referred to as being 'correlated' if the change in one trait causes simultaneous change in another. Correlations between traits are expressed

statistically by the correlation coefficient, which can take any value between –1.0 and 1.0. Falconer and Mackay (1996) define a correlation as the ratio of the appropriate covariance to the product of the two standard deviations. The closer the correlation coefficient is to zero, the weaker the relationship is between two traits. Bivariate models enable correlations between traits to be identified. In terms of selection it is vitally important to know if improvement of one trait might simultaneously cause changes in other traits.

Phenotypic correlation is the directly observed association between two traits, and is determined from measurements of the two traits in individuals of a population. Phenotypic correlations can be partitioned into two types of correlation between traits, genetic and environmental (Falconer and Mackay, 1996). The genetic correlation is the correlation between breeding values, and can be used to estimate how the selection of parents for one trait would cause the change in a second trait in the progeny. The basis is genetic correlation is mainly pleiotropy, when a single gene affects two or more traits, so that as segregation occurs at a gene locus it results in variation in the characters it affects. The degree of correlation due to pleiotropy expresses the extent to which two characters are influenced by the same genes. Genetic correlations can be positive, where an increase in one trait would also mean an increase in another trait, or negative, where an increase in one results in the reduction of another. Environmental correlations occur when two traits are influenced by the same differences of environmental conditions, and similarly can be positive or negative.

The phenotypic correlation is largely determined by the genetic correlation if both traits have high heritabilities, whereas if both heritabilities were low then the environmental correlation would be the main determinant. Hence, the magnitude or sign of the phenotypic correlation may not necessarily be a reflection of the genetic correlation. Large differences in magnitude, and sign, of genetic and environmental correlations would indicate that these sources of variation affect traits through different physiological mechanisms.
The phenotypic correlation (r_P) between two traits is calculated as

Equation 9. 1

$$r_P = \frac{\text{cov}_P}{\sigma_{PX}\sigma_{PY}}$$

where cov_P is the phenotypic covariance between two traits; σ_{PX} is the phenotypic variance of trait X; σ_{PY} is the phenotypic variance of trait Y.

The genetic correlation (r_G) between two traits is calculated as

Equation 9. 2

$$r_G = \frac{\text{cov}_{XY}}{\sqrt{(\text{var}_X\ \text{var}_Y)}}$$

where cov_{XY} is the direct additive genetic covariance between the two traits X and Y; var_X direct additive genetic variance of trait X; var_Y is the direct additive genetic variance of trait Y.

Safari *et al.* (2005) reviewed correlations between wool, growth, carcass, and reproductive traits, and observed that for many traits there was wide variation in genetic correlation results among different studies. They suggested that more estimates of genetic correlations were needed and maternal effects should be included in models.

9.2 METHODS

9.2.1 Bivariate analysis

Bivariate analyses were carried out for both Welsh Mountain and Beulah Speckled Face breeds for all pair-wise combinations between growth traits, ultrasonically-scanned traits and litter traits. Starting values of variance components were obtained from the most appropriate models in the corresponding univariate analyses of each trait (Chapter 6, 7 and 8, tabulated in Tables E.1 and E.2 in Appendix E). The random factors, fixed effects and covariates were the same as those used in the univariate analysis for each trait (see Table 9.1 for random effects).

All bivariate analyses included the direct additive effect for both traits and the covariance between additive effects. If one or both of the traits had maternal genetic effect in the model used for univariate analysis, then the bivariate analysis of individual and different traits included the covariance between additive maternal genetic effect and the direct additive genetic effect. If both

models used for univariate analysis of traits contained any one of permanent environmental effect of the animal, additive maternal genetic, maternal permanent environmental or maternal temporary environmental effects the covariance of the separate effects was also included. The residual (error) variances of each trait were included, together with an error covariance for all trait combinations except those for LSB, LSR and LW with growth and ultrasonically-scanned traits. The error covariance for these exceptions was fixed at zero since the litter traits could have had repeated records, whereas the growth and ultrasonically-scanned traits were single records, mainly from lambs. The number of observations for each trait and the number of animals with records for each pair-wise combination are shown in Tables 9.2 and 9.3.

Table 9.1 Random factors used in bivariate analysis of each trait for Welsh Mountain and Beulah Speckled Face breeds

	Welsh Mountain						Beulah Speckled Face					
	σ^2_a	σ^2_m	σ^2_{pe}	σ^2_{ce}	σ^2_{pea}	σ^2_e	σ^2_a	σ^2_m	σ^2_{pe}	σ^2_{ce}	σ^2_{pea}	σ^2_e
EWW	✓	✓	✓	✓		✓	✓	✓	✓	✓		✓
SW	✓	✓	✓	✓		✓	✓	✓	✓	✓		✓
MD	✓	✓	✓	✓		✓	✓	✓	✓	✓		✓
FD	✓	✓		✓		✓	✓		✓	✓		✓
MW	✓					✓						
LSB	✓				✓	✓	✓					✓
LSR	✓				✓	✓	✓					✓
LW	✓				✓	✓	✓				✓	✓

EWW eight week weight; SW scan weight; MD muscle depth; FD fat depth; MW mature weight; LSB litter size born; LSR litter size reared; LW litter weight; σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal temporary environmental variance; σ^2_{pea} permanent environmental variance of the animal; σ^2_e error variance.

For the Welsh Mountain mature weight was only included in bivariate analyses with eight-week weight and litter traits, as there were no animals with mature weight records that also had records for scan weight and ultrasonically-scanned traits. Ap Dewi *et al.* (2002) reported results for these combinations from the dataset of the CAMDA flock, but different animals had been used in their study.

Table 9.2 The number of observations by trait (in bold print on the diagonal) and the number of animals with records for both traits (below the diagonal) from the Beulah Speckled Face dataset.

	EWW	SW	MD	FD	LSB	LSR	LW
EWW	**13498**						
SW	10569	**10569**					
MD	9651	9651	**9651**				
FD	9652	9652	9651	**9652**			
LSB	1782	1455	1390	1390	**8872**		
LSR	1782	1455	1390	1390	5063†	**8872**	
LW	1782	1455	1390	1390	5063†	5063†	**8872**

† Number of animals. These traits have repeated records. Actual number of recorded litters for all litter traits was 8872 (in bold). Refer back to Table 9.1 for abbreviations.

Table 9.3 The number of observations by trait (in bold print on the diagonal) and the number of animals with records for both traits (below the diagonal) from Welsh Mountain dataset.

	EWW	SW	MD	FD	LSB	LSR	LW	MW
EWW	**24569**							
SW	10509	**10509**						
MD	8389	8389	**8389**					
FD	8369	8369	8368	**8369**				
LSB	3475	1049	1014	1014	**18029**			
LSR	3475	1049	1014	1014	9883†	**18029**		
LW	3475	1049	1014	1014	9883†	9883†	**18029**	
MW	1975	0	0	0	1875	1875	1875	**1975**

† Number of animals. These traits have repeated records. Actual number of recorded litters for all litter traits was 18029 (in bold).

ASReml was first run with the covariances between traits set at zero and all other components fixed. The values obtained for the covariances from the first run were then entered into the model for a second run, and for this run all components were unconstrained. If convergence was reached in the second run, phenotypic variances, heritabilities and correlations were obtained. If convergence failed in the second run, the model was run again employing the !Continue qualifier (Gilmour *et al*, 2002). In cases where convergence was not reached after a third run the values from the third run were reported with a note to treat them with caution. In instances where many parameters were fixed at a boundary after the second run, a third run was done with the covariances fixed, and the values from this third run were reported.

9.2.2 Evaluation of bivariate models

As explained above (section 9.2.1), starting values for variance components were taken from the models chosen as the most appropriate for each trait in the univariate analyses. Starting values from other univariate models were also analysed in bivariate analyses so to examine the effect on genetic and phenotypic models if they had been chosen for univariate analysis. There are many possible model combinations, but in order to keep the study to a manageable size, only within-model combinations were used.

e.g. Model 1 EWW and Model 1 SW

Model 2 EWW and Model 2 SW

Model 3 EWW and Model 3 SW

Model 4 EWW and Model 4 SW

Model 5 EWW and Model 5 SW
but not Model 1 EWW and Model 2 SW
or Model 2 EWW and Model 3 SW
or Model 3 EWW and Model 4 SW.
These analyses were used with all combinations between EWW, SW, MD, and FD.

9.3 RESULTS

9.3.1 Welsh Mountain

Correlations between weight, ultrasonically-scanned and litter traits are shown in Table 9.4 and (co)variances are shown in Tables E.3, E.4 and E.5.

9.3.1.1 Weight and ultrasonically-scanned traits

The genetic and phenotypic correlations between all traits were positive. EWW and SW had the strongest genetic correlation, followed by EWW and MW, SW and MD, EWW and MD, SW and FD, EWW and FD, and lastly MD and FD, with values of 0.95, 0.90, 0.37, 0.30, 0.19, 0.17 and 0,18, respectively. The genetic correlations between EWW and SW and between EWW and MW were higher than phenotypic correlations. However, the remaining four trait combinations had higher phenotypic correlations than genetic correlations. Maternal genetic correlations were variable, ranging from 0.12 to 0.92. Maternal permanent environmental correlations were fixed at a boundary in all cases. Maternal temporary environmental correlations were all high, ranging from 0.63 to 0.83. Residual correlations ranged from 0.25 to 0.64, whilst phenotypic correlations ranged from 0.36 to 0.77. In all bivariate analyses of growth and ultrasonically-scanned traits the direct-maternal correlation was small and non-significant (Appendix, Table E.3). The covariance between additive maternal genetic effect and direct additive genetic effect for the same trait had negative values for SW, MD, and FD. The covariance between maternal genetic effect of SW and direct additive genetic effect of EWW also had a negative value (Appendix, Table E.3).

9.3.1.2 Litter traits

As would be expected all correlations for LSB and LSR were high. Correlations between LW and both LSB and LSR were low and negative, with values of -0.10 and –0.04, respectively, and the covariances were both non-significant (Appendix, Table E.4).

9.3.1.3 Litter traits with weight and ultrasonically-scanned traits

The correlations with EWW, SW, MD and FD were similar for LSB and LSR; however, all genetic correlations were slightly higher for LSR. All correlations were positive and ranged from 0.13 to 0.47 with LSB, and 0.20 to 0.47 with LSR. In the analyses for LW and other growth and ultrasonically-scanned traits it was difficult to reach convergence without parameters being fixed at a boundary. Values should therefore be treated with caution. Genetic correlations between LW and EWW, SW and MD ranged from 0.77 to 1.00. Genetic correlations between litter traits and MW were positive and high, ranging from 0.47 to 0.78.

Table 9.4 Parameter estimates of Welsh Mountain for growth, ultrasonically-scanned, and litter traits estimated from bivariate analysis.

Traits	G	PEA	M	PE	CE	E	P
EWW	0.949		0.922	0.990†	0.827	0.637	0.769
SW	(0.020)		(0.063)	(0.00)	(0.030)	(0.016)	(0.014)
EWW	0.295		0.219	0.990†	0.703	0.374	0.439
MD	(0.117)		(0.265)	(0.00)	(0.083)	(0.034)	(0.019)
EWW	0.165		0.880		0.775	0.250	0.377
FD	(0.133)		(0.193)		(0.077)	(0.036)	(0.018)
EWW	0.900					0.426	0.491
MW	(0.038)					(0.036)	(0.017)
SW	0.370		0.123	0.990†	0.724	0.549	0.564
MD	(0.110)		(0.380)	(0.00)	(0.099)	(0.032)	(0.022)
SW	0.189					0.481	0.466
FD	(0.00)					(0.023)	(0.008)
MD	0.164		0.349		0.629	0.334	0.361
FD	(0.136)		(0.292)		(0.131)	(0.034)	(0.023)
LSB	0.993	0.995				0.815	0.846
LSR	(0.009)	(0.019)				(0.003)	(0.002)
LSB	-0.100[ns]	-0.185				-0.338	-0.299
LW	(0.083)	(0.118)				(0.010)	(0.009)
LSR	-0.039[ns]	0.134				-0.166	-0.133
LW	(0.004)	(0.017)				(0.002)	(0.001)
LSB	0.411						
EWW	(0.065)						
LSB	0.459						
SW	(0.096)						
LSB	0.212						
MD	(0.104)						
LSB	0.125						
FD	(0.106)						
LSR	0.429						
EWW	(0.075)						
LSR	0.467						
SW	(0.111)						
LSR	0.233						
MD	(0.121)						
LSR	0.203						
FD	(0.125)						
LW	0.990†						
EWW	(0.000)						
LW	0.995						
SW[cf]	(0.049)						
LW	0.773						
MD[cf]	(0.050)						
LW	0.860						
FD	(0.052)						
LSB	0.481						
MW	(0.062)						
LSR	0.467						
MW	(0.073)						
LW	0.780						
MW	(0.057)						

G genetic correlation; PEA permanent environmental correlation (animal); M additive maternal genetic correlation; PE maternal permanent environmental correlation; CE maternal temporary environmental correlation; E residual error correlation; P phenotypic correlation; † parameter fixed at boundary; [ns] parameter not significant; [nc] analysis did not converge; [cf] covariance fixed. Refer to Table 9.1 for trait abbreviations.

9.3.2 Beulah Speckled Face

Correlations between weight, ultrasonically-scanned traits and litter traits are shown in Table 9.5 and (co)variances are shown in Tables E.6, E.7 and E.8.

9.3.2.1 Weight and ultrasonically-scanned traits

The genetic and phenotypic correlations between all traits were positive relationships. EWW and SW had the strongest genetic correlation, followed by SW and FD, SW and MD, EWW and FD, MD and FD, and lastly EWW and MD, with values of 0.56, 0.45, 0.40, 0.22, 0.20, and 0.15, respectively. For all trait combinations phenotypic correlations were greater than genetic correlations. Maternal genetic, maternal permanent, and maternal temporary environmental correlations were generally high. Some permanent environmental correlations appeared to be extremely high (e.g. 0.99) because they had been fixed at a boundary. Residual correlations ranged from 0.28 to 0.67. Phenotypic correlations ranged from 0.36 to 0.71.

9.3.1.1 Litter traits

The genetic correlation between LSB and LSR was high with a value of 0.94, as expected. Both LSB and LSR were poorly correlated with LW, with genetic correlations of –0.07 and –0.002, respectively. LSR and LW did not converge unless covariances were fixed. Residual and phenotypic correlations were also negative.

9.3.1.2 Litter traits with weight and ultrasonically-scanned traits

Correlations between LSB and EWW, SW, MD, and FD were all positive and ranged from 0.02 to 0.42. Correlations between LSR and the same traits were similar to the correlations for LSB, except for the correlation with FD, which was negative, although small (-0.01). Estimates of genetic correlations between LW and EWW, SW, MD, and FD were positive and high, with values of 0.98, 0.88, 0.79 and 0.74.

Table 9.5 Correlations for Beulah Speckled Face between weight, ultrasonically-scanned and litter traits estimated from bivariate analysis.

Traits	G	M	PE	CE	R	P
EWW	0.564	0.861	0.990†	0.694	0.668	0.711
SW	(0.108)	(0.067)	(0.000)	(0.031)	(0.018)	(0.020)
EWW	0.150	0.722	0.990†	0.614	0.428	0.453
MD	(0.164)	(0.157)	(0.000)	(0.052)	(0.025)	(0.019)
EWW	0.223		0.766	0.534	0.279	0.358
FD	(0.145)		(0.088)	(0.069)	(0.028)	(0.014)
SW	0.397	0.805	0.990†	0.910	0.598	0.610
MD	(0.115)	(0.111)	(0.00)	(0.048)	(0.022)	(0.022)
SW	0.449		0.913	0.725	0.461	0.517
FD	(0.102)		(0.092)	(0.069)	(0.026)	(0.013)
MD	0.200		0.826	0.841	0.397	0.449
FD	(0.126)		(0.143)	(0.089)	(0.027)	(0.013)
LSB	0.937				0.728	0.746
LSR	(0.028)				(0.006)	(0.005)
LSB	-0.066^{ns}				-0.282	-0.258
LW	(0.096)				(0.014)	(0.013)
LSR	0.002^{ns}				-0.227	-0.208
LW^{nc}	(0.120)				(0.016)	(0.015)
LSB	0.417					
EWW	(0.113)					
LSB	0.361					
SW	(0.100)					
LSB	0.110					
MD	(0.102)					
LSB	0.020^{ns}					
FD	(0.099)					
LSR	0.451					
EWW	(0.131)					
LSR	0.327					
SW	(0.124)					
LSR	0.171					
MD	(0.125)					
LSR	-0.010^{ns}					
FD	(0.122)					
LW	0.976					
EWW	(0.071)					
LW	0.883					
SW	(0.064)					
LW	0.793					
MD	(0.069)					
LW	0.742					
FD	(0.066)					

See table 9.4 for definition of abbreviations

9.3.3 Evaluation of models used in bivariate analysis

Results of the analysis are illustrated by the Beulah Speckled Face breed and shown in Tables E.9 to E.14 in Appendix E. In the analysis of EWW with SW the genetic correlation was very similar for all five models (0.54 – 0.59). However, with the addition of extra random effects (one added each time from

Model 1 to 5) the environmental and phenotypic correlation increased greatly from Model 1 to Model 2, but was quite stable afterwards. In the analysis of EWW with MD the genetic correlation was fairly high for Model 1 (0.54) but decreased for subsequent models (to 0.15 for Model 5), whereas the environmental and phenotypic correlations remained roughly contact. The trend was similar for EWW with FD and for SW with MD, where the genetic correlations decreased from 0.47 to 0.22 and from 0.68 to 0.40 respectively. In the analysis of SW with FD the genetic correlation decreased from 0.57 to 0.44, and the environmental correlation also decreased slightly. In the analysis of MD with FD the genetic correlations were variable amongst models ranging from 0.08 (Model 4) to 0.52 (Model 1), whilst environmental and phenotypic correlations remained more or less constant.

9.4 DISCUSSION

The bivariate analysis produced phenotypic variances and direct heritability estimates that were virtually identical to those obtained in the univariate analyses of the traits.

9.4.1 Weight and ultrasonically-scanned traits

All the correlations were positive for growth and ultrasonically-scanned traits, which mean that an increase in one trait will lead to the increase in the other trait. In both Welsh Mountain and Beulah Speckled Face breeds the strongest genetic correlations were between the weight traits EWW and SW (0.95 and 0.56 respectively). This was to be expected as they are similar traits, and are measured at times that are fairly close together (approximately 12 weeks apart). In the Welsh Mountain the genetic correlation between EWW and MW was also high (0.90), but was less than that between EWW and SW because the interval between the measurements was much greater apart. Safari *et al.* (2005) observed that weights of adjacent age classes were the most strongly correlated and that correlations increased with age from birth to adult. The maternal additive genetic, maternal temporary environmental and residual correlations were all high between EWW and SW, which indicate that similar environmental effects

affect both traits. The maternal permanent environmental effect was often fixed at a boundary during analysis. The genetic correlations between weight traits (EWW, SW) and ultrasonically-scanned traits (MD, FD) were moderate. The results were as expected; the correlations were higher between SW with ultrasonically-scanned traits than between EWW because SW was measured at the same time as the ultrasonically-scanned traits.

9.4.1.1 Comparison of breeds

In the Welsh Mountain the phenotypic correlations between EWW and SW and between EWW and MW were lower than the genetic correlations, which is consistent with reports in the review of Safari *et al.* (2005). However, in the Beulah the phenotypic correlation between EWW and SW was higher than the genetic correlation. The genetic correlation between EWW and SW was much greater in the Welsh Mountain than the Beulah Speckled Face (0.95 compared with 0.56). The correlation for the Beulah Speckled Face was close to that obtained by Ap Dewi *et al.* (2002) in the Welsh Mountain even though scan age was different. The genetic correlations for SW and MD were similar in both breeds; however the genetic correlation between SW and FD was much greater in the Beulah Speckled Face than the Welsh Mountain (0.45 compared with 0.19). The genetic correlation between EWW and MD was greater in the Welsh Mountain than the Beulah Speckled Face (0.30 compared with 0.15). For all combinations of weight and ultrasonically-scanned traits the phenotypic correlations were higher than the genetic correlations. In both breeds the genetic correlation between MD and FD was lower than both traits with SW, and ranged from 0.16 to 0.20.

9.4.1.2 Comparison with other studies

The study of Ap Dewi *et al.* (2002) of the CAMDA Welsh Mountain flock gave rather different results for genetic correlations from those presented here (see Table 9.6). The genetic correlations between EWW and FD in the current study were positive (0.17 for Welsh Mountain and 0.22 for Beulah schemes), whereas Ap Dewi *et al.* (2002) reported a negative correlation (-0.11). The genetic

correlations between SW and both MD and FD were higher in Ap Dewi *et al.*'s (2002) study, particularly for SW and FD. In the study of Ap Dewi *et al.* (2002) animals were scanned later in life than in the current study. Since direct heritability estimates tend to increase with age, genetic correlations would be expected to be higher. The genetic correlation between MD and FD was not significant in Ap Dewi *et al.*'s (2002) study, and low (0.16) in the current study.

Table 9.6. Comparison of genetic correlation estimates of the present study and previous studies of the same breed.

	Welsh Mountain		Beulah Speckled Face	
Traits	Present study	Ap Dewi *et al.* (2002)	Present study	Hussain *et al.* (2006)
EWW / MW	0.90	0.82		
EWW / SW	0.95	0.54	0.56	0.59
MW / SW		0.93		
EWW / MD	0.37	0.13	0.15	0.23
EWW / FD	0.17	-0.11	0.22	0.09†
MW / MD		0.25		
MW / FD		0.02		
SW / MD	0.37	0.46	0.40	0.51
SW / FD	0.19	0.67	0.45	0.44†
MD / FD	0.16	0.05	0.20	0.33†
LSB / LW	-0.12	-0.05	-0.05	
LSB / EWW	0.41	0.36	0.42	
LSB / SW	0.46	0.29	0.36	
LSB / MD	0.21	0.35	0.11	
LSB / FD	0.13	<-0.01	0.02	
LSB / MW	0.48	0.56		
LW / EWW	0.99	0.10	0.98	
LW / SW	1.00	0.58	0.88	
LW / MD	0.77	0.28	0.79	
LW / FD	0.73	0.20	0.74	
LW / MW	0.78	0.76		

Study of Ap Dewi *et al.* used twelve-week weight rather than eight-week weight.
† log FD was used by Hussain *et al.* (2006)

The correlations between weight and ultrasonically-scanned traits for the Beulah Speckled Face were fairly similar to those obtained by Hussain *et al.* (2006) (Table 9.6). The correlations in the current study tended to be lower than those reported by Hussain *et al.* (2006), with the exception of the correlation between EWW and FD, and between SW and FD.

Safari *et al.* (2005) reported mean genetic correlations between live weight and both MD and FD; these were 0.34, 0.36 and 0.33 respectively. However, the

ranges for these genetic correlations were -0.44 to 0.84, -0.23 to 0.73 and -0.28 to 0.76 respectively indicating large variation between studies.

9.4.2 Litter traits

LSB and LSR were strongly correlated genetically, environmentally, and phenotypically in both breeds, as expected. Both LSB and LSR were negatively correlated with LW. A similar negative correlation was reported by Ap Dewi *et al.* (2002). Correlations between LW and both LSB and LSR have been found to be strongly positive in many other studies (Bromley *et al*, 2001; Hanford *et al*, 2001; Safari *et al*, 2005). However, these correlations found in the current study were low and the covariances were not significant in the model. Hanford *et al.* (2001) reported high positive genetic correlations between LW and both LSB and LSR (with values of 0.72 and 0.95 respectively) in Rambouillet sheep. Bromley *et al.* (2001) reported the genetic correlations between LW with LSB to range from 0.42 to 0.65, and between LW and LSR to range from 0.80 to 0.99, in a study of four sheep breeds. Vanimisetti *et al.* (2005) reported genetic correlations between LW and LSB and LSR as 0.42 and 0.94, respectively, in Katahin sheep. The review of Safari *et al.* (2005) gave weighted means of genetic correlations between LW and LSB and between LW and LSR of 0.60 and 0.80, respectively. However, the 95% confidence intervals of the means were large, from 0.00 to 0.89 for the correlation between LW and LSB and from -0.43 to 0.99 for the correlation between LW and LSR. The results of the present study are different because litter size is included as an effect (in the combined effect of litter size and sex) for total litter weight.

Since litter size is incorporated into the model of litter weight, then litter weight is effectively a measure of the ewe's ability to produce lambs (a combination of birth weight and rearing ability) independent of any genes affecting litter size. In other words, as an EBV, ewes are compared as if they had all produced the same number of lambs. A negative phenotypic correlation between litter weight and litter size is expected as a higher litter size is associated with lambs with poorer individual litter weights, explained by lower birth weight and less milk per lamb. Single lambs tend to have higher birth weights, have a better headstart and are

less vulnerable than twins or triplets. In the Welsh Mountain breed, the poor environmental conditions in which it lives limits the number of lambs a ewe can successfully rear, and in some cases perhaps two lambs might be too many, especially for first time mothers. Conington *et al.* (2004) found, that in hill ewes surviving in extensive conditions, an increase in the number of lambs after a certain point resulted in a decrease in revenue.

However, the weakly negative genetic correlation between litter size and litter weight is more difficult to interpret and would imply that genes affecting prolificacy are associated negatively with genes affecting litter weight. The genetic correlation between LSR and LW though was positive in the Beulah breed.

Michels *et al.* (2000) argued that natural selection favoured smaller litters from small breeds, such as the Welsh Mountain. The Beulah is larger, more prolific and tends to live in more favourable conditions. It should be noted that triplets had been left in the Beulah dataset. It is understandable that in some cases ewes giving birth to triplets could have a negative impact on total lamb weight. Further work could include repeating the analysis after the removal of triplet lambs, and also to produce estimates from different parities.

9.4.3 Litter traits with weight and ultrasonically-scanned traits

All correlations between litter traits with weight and ultrasonically-scanned traits were positive, with the exception of the correlation between LSR and FD. These results indicate that animals with heavier eight-week weight, scan weight or mature weight, and greater muscle and fat depths, should go on to produce larger litter sizes and increased total weight of lambs weaned. It is expected that weight traits measured later in life would be more highly correlated with litter traits than weight traits measured earlier in life. This was found to be the case with the Welsh Mountain breed in which correlations with litter size born increased from eight-week weight to mature weight (0.41 for EWW, 0.46 for SW, 0.48 for MW). This trend was not as clear with the Beulah Speckled Face (0.42 for EWW, 0.36

for SW) but this could be because there were far fewer records of dams with scan weight records in the dataset. Genetic correlations between weight traits and LSR tended to be slightly higher than those between weight traits and LSB. Some of the correlations involving LW should be treated with caution due to problems with convergence and the fact that some parameters were fixed at a boundary. However, there were no problems with convergence in the analysis of LW and MW, which gave a genetic correlation of 0.78. This is very close to the value reported by Ap Dewi *et al.* (2002) of 0.76.

9.4.4 Evaluation of Models

A range of bivariate models, were used to correspond with the models in the used univariate analyses (Chapters 6 and 7). It appears that choice of model can have a major effect on estimates of genetic and phenotypic correlations. For instance, in the bivariate analysis of EWW and MD, Model 1 (σ^2_a only) and Model 5 (σ^2_a, σ^2_m, σ^2_{pe}, and σ^2_{ce}) produced genetic correlations of 0.57 and 0.15 respectively. Choice of inappropriate models may lead to genetic gains that are lower than expected. For instance, if the breeding goal was to increase both eight-week weight and muscle depth both Model 1 and Model 5 would suggest that if EWW was selected for, then MD would also increase. However, the increase in MD would be expected to be much greater using Model 1 than model 5 because the genetic correlation between the two traits is stronger.

CHAPTER 10

Exploration of Cytoplasmic Inheritance as a Maternal Effect in Welsh Mountain Sheep

ABSTRACT

Two models were used to investigate the influences of cytoplasmic effects on weight and ultrasonically-scanned traits in Welsh Mountain Sheep. There were no cytoplasmic effects for the traits eight-week weight (EWW) and muscle depth (MD). Cytoplasmic effects contributed 1 – 2 % of phenotypic variance for the traits scan-weight (SW) and fat depth (FD), but the effect was generally non-significant. It was observed that as the number of animals per maternal line increased, the magnitude of cytoplasmic effects also increased for SW and FD. Models used to estimate genetic parameters do not necessarily require maternal line to be included as an effect.

10.1 INTRODUCTION

In eukaryotic organisms the mitochondria, double-membraned organelles found in most cells, have several roles in cell physiology; they are responsible for the majority of energy metabolism through ATP production, maintenance of redox potential, production of heat and free radicals, storage of calcium, and modulation of calcium signals (Frey and Mannella, 2000). Mitochondria possess their own DNA, mitochondrial DNA (mtDNA), within the mitochondrial matrix. The mtDNA is a closed, circular, double-stranded DNA molecule that is about 16,500 base pairs long, and contains 37 genes. Of the 37 genes, 24 code for the translational machinery of the mtDNA (22 transfer RNA genes and two ribosomal genes), and 13 genes code for subunits of the electron transport chain (William *et al*, 2004).

Mounolou and Lacroute (2005) reviewed the discoveries that were made in the 1950s and 1960s of mitochondria. In the 1950s it was found that mitochondria

had their own DNA, and it was unexpectedly observed that the transmission of mitochondrial characters did not abide by Mendelian rules but followed a pattern of 'cytoplasmic inheritance.' Wagner (1972) discussed the importance of mitochondria in animal breeding, pointing out that they could be responsible for genetic variation in cytoplasmic effects as they contained maternally inherited DNA. In mammals, mtDNA is only inherited from the mother because sperm-derived mitochondria are degraded during embryogenesis (Hayashida *et al*, 2005). Males receive cytoplasmic material from their dams, but cannot transmit it to their offspring. Hence, apart from mutations, animals of a maternal line should have identical mtDNA, and theoretically the component of variance due to mtDNA could be estimated (Roughsedge *et al*, 2000).

The influence of variation in mtDNA on traits of livestock species has been examined in several studies. Effects on production traits, particularly in dairy cattle have been reported by Albuquerque *et al.* (1998), Bell *et al.* (1985), Boettcher, *et al.* (1996a; 1996b), Huizinga *et al.* (1986) and Sutarno *et al.* (2002), although conclusions about whether cytoplasmic effects are important differ between authors. In dairy cattle, extensive mtDNA diversity has been reported, and has been associated with variation in milk-yielding traits (Bell *et al*, 1985; Freeman, 1990; Huizinga *et al*, 1986; Schutz *et al*, 1994). Huizinga *et al.* (1986) reported that 10 % of the phenotypic variation in weight of milk fat plus protein (kg), and 13 % of the phenotypic variation in milk returns were due to cytoplasmic effects. Bell *et al.* (1985) reported cytoplasmic effects accounting for 2.0 %, 1.8 %, 1.8 %, and 3.5%, of the total variation of milk yield, milk fat yield, fat-corrected milk yield, and milk fat %.

In the determination of the importance of cytoplasmic effects different methods have been utilised by researchers. Earlier methods, for instance those of Bell *et al.* (1985), Huizinga *et al.* (1986) and Tess *et al.* (1987), some of which resulted in reports of significant cytoplasmic effects, were later challenged (Kennedy, 1986; Tess and Robison, 1990). Researchers have included maternal lineage in models to account for cytoplasmic effects, both as fixed (Schutz *et al*, 1992) and random effects, and Boettcher *et al.* (1996b) and Freeman (1990) give reasons why it can be considered as both. When included as a random effect maternal

lineage had a lesser effect (Boettcher *et al*, 1996b). Kennedy (1986) and Tess and Robison (1990) both concluded that an animal model should be used, otherwise direct additive genetic effects not accounted for would cause the exaggeration of cytoplasmic effects. Tess and Robison (1990) repeated a previous study, using an animal model, and found that cytoplasmic effects were no longer significant. Generally it is now accepted that the effect should be random, and should be included in an animal model with direct additive genetic effect, additive maternal genetic effects, and environmental maternal effects also included where necessary. Several studies that have employed the animal model with maternal additive genetic effect, permanent environmental effect and cytoplasmic effect as random components, have concluded that cytoplasmic effects are negligible (Northcutt *et al*, 1991; Rohrer *et al*, 1994; Tess and MacNeil, 1994).

Mannen *et al.* (1998; 2003) found significant cytoplasmic effects contributing to two carcass traits, longissmus muscle area and beef marbling score, in Japanese Black cattle. Sutarno *et al.* (2002) reported a significant association between calving rate and mitochondrial polymorhisms in purebred Hereford and Composite multibreed beef cattle.

There have been fewer studies of the association between mtDNA polymorphisms with phenotypic variation in sheep, but it has been suggested that they could exist. Maniatis and Pollot (2002b) found no evidence of cytoplasmic effects, when included in a full animal model, for eight week weight, scanning weight or ultrasonic measurements of muscle and fat depth in Suffolk lambs. Similarly, in Columbia (Hanford *et al*, 2003), Targee (Van Vleck *et al*, 2002), Rambouillet (Snowder *et al*, 2004) and Polpay (Van Vleck *et al*, 2005) breeds, cytoplasmic effects appeared to be unimportant for the traits birth weight, weaning weight, fleece weight and the number of lambs born. Hence, these authors considered that it was not necessary to include in genetic evaluation models.

The implications of cytoplasmic genetic effects affecting performance are that some maternal lines might be particularly valued, due to the inheritance of

cytoplasmic elements from the dam only (Tess and Robison, 1990). Schutz *et al.* (1994) suggested that a sire's estimated breeding value, based upon pedigree, might be biased if the dam's contribution is not adjusted for mitochondrial effects. Current breeding evaluations do not include the effect of cytoplasmic inheritance through the maternal line. The aim of this study was to estimate the contribution of the maternal lines to weight and ultrasonically-scanned traits of the Welsh Mountain breed.

10.2 METHODS

10.2.1 Description of data

Data from the CAMDA, CAMP, and Llysfasi Welsh Mountain groups, described in Chapters 3 and 6, were analysed to study the effect of cytoplasmic inheritance. The traits considered were eight-week weight (EWW), scan-weight (SW), ultrasonic muscle depth (MD), and ultrasonic fat depth (FD). Animals were assigned to maternal lines by identifying foundation females (dams that had no records of their own dams). Each foundation female was assumed to be unrelated to the other foundation dams. Foundation females were regarded as a cytoplasmic source and given individual codes. All descendants were given the same code of the foundation female, as these animals were assumed to have the same mtDNA genotype within the line (i.e. it was assumed no mutation of mtDNA had taken place).

In total there were records for 24569 animals of 452 sires and 9883 dams from years 1985 to 2004. All had records for EWW, but there were fewer records for SW, MD, and FD (Table 10.1). In the pedigree file there were 12 generations and the oldest dam was born in 1969. It was observed that some lines had very few animals, for instance lines consisting of a foundation dam with only one descendant. These lines with few animals might be expected to bias an analysis to determine the importance of cytoplasmic effects. Therefore four subsets of the full dataset, with minima of 5, 10, 15, and 20 animals per maternal line, were analysed. Increasing the cut-off point for the minimum number of animals allowed in each line caused a reduction in the size of the dataset (Table 10.1).

Table 10.1 Numbers of records, sires, dams, maternal lines and animals/maternal line for eight-week weight (EWW), scan weight (SW), muscle depth (MD) and fat depth (FD) of Welsh Mountain sheep. Values shown are for the full dataset and for subsets containing maternal lines with at least five, ten, 15 and 20 animals/line.

	Trait	No. of records	No. of Sires	No. of Dams	No. of maternal lines	Average no. of animals/line	Mean	Standard deviation
EWW	All	24569	452	9883	5302	4.63	18.277	4.532
(kg)	5+	16586	380	4989	655	25.32	19.614	4.271
	10+	14801	315	4403	377	39.26	20.004	4.077
	15+	13580	308	4001	273	49.74	20.160	4.029
	20+	12689	307	3721	219	57.94	20.304	3.978
SW	All	10509	241	5724	3932	2.67	26.779	5.695
(kg)	5+	5179	169	2185	527	9.83	26.544	5.451
	10+	3625	105	1550	226	16.04	27.061	5.390
	15+	3625	105	1550	226	16.04	27.061	5.390
	20+	3210	105	1379	187	17.17	27.330	5.277
MD	All	8389	235	4872	3352	2.50	20.005	2.878
(mm)	5+	4269	167	1961	518	8.24	19.748	2.935
	10+	3407	111	1584	298	11.43	19.837	2.988
	15+	2847	105	1341	219	11.36	19.890	3.000
	20+	2437	105	1172	180	13.54	19.990	2.964
FD	All	8369	235	4859	3339	2.51	2.559	1.132
(mm)	5+	4267	167	1960	517	8.25	2.553	1.118
	10+	3407	111	1584	298	11.43	2.572	1.134
	15+	2847	105	1341	219	11.36	2.587	1.142
	20+	2437	105	1172	180	13.54	2.612	1.139

A fifth subset was constructed to examine the effect of number of generations on the outcome of the analysis. This subset included all animals that had records of their dams, and great-dams (i.e. there were records for at least three generations) (Table 10.2).

Table 10.2 Numbers of records, sires, dams, maternal lines and animals/maternal line for eight-week weight (EWW), scan weight (SW), muscle depth (MD) and fat depth (FD) of Welsh Mountain sheep for the subsets containing maternal lines with at least three generations.

Trait	No. of records	No. of Sires	No. of Dams	No. of maternal lines	Average no. of animals/line	Mean	Standard deviation
EWW (kg)	16100	347	5066	930	4.63	19.76	4.220
SW (kg)	4784	138	2150	625	25.32	26.34	5.426
MD (mm)	3881	136	1870	559	39.26	19.74	2.950
FD (mm)	3881	136	1870	559	49.74	2.51	1.119

10.2.2 Data analysis and models used

The five datasets were analysed with ASReml (Gilmour *et al*, 2002) using a univariate model. Two models were used. The fixed effects used in both models

were dam age, year of birth, sex, birth rearing type and flock. The first model included direct genetic effect, maternal additive genetic effect, maternal permanent environmental effect, and maternal temporary environmental effect as random effects, all were previously shown to be significant random effects (Chapter 6). The second model also included maternal line as a random effect, as shown below.

$$Y_{ijklmno} = \mu + a_i + b_{jklm} + c_n + z_n + x_o + w_o + v_{ol} + u_o + e_{ijklmno}$$

where μ = is the overall mean of eight-week weight, scan-weight, muscle depth or fat depth; a_i = fixed effect of rearing dam age (i = 2-7); b_{jklm} contemporary group of j^{th} sex (male/female), k^{th} birth rearing type (=1-3), l^{th} year of birth (1985 to 2004), and m^{th} flock (1-40); c_n = age at scanning as a covariate of the animal n (not needed for eight-week weight); z_n = random effect of animal n; x_o = the random maternal additive genetic effect of the o^{th} dam; w_o = the random maternal permanent environmental effect of the o^{th} dam; v_{ol} = the random maternal temporary environmental effect of the o^{th} dam in the l^{th} year; u_o = cytoplasmic genetic effect of the o^{th} dam; $e_{ijklmno}$ = random environmental effect.

10.3 RESULTS

Genetic parameter estimates for eight-week weight (EWW), scan weight (SW) and ultrasonically-measured traits muscle depth (MD) and fat depth (FD) with the *log* likelihood (logL) ratio values to compare models that excluded or included cytoplasmic effects are presented in Tables 10.3, 10.4, 10.5, 10.6 and 10.7.

10.3.1 Eight-week weight

The inclusion of cytoplasmic inheritance as a random effect in the model made no difference whatsoever to the logL values (Table 10.3). Comparison of datasets shows that the effect of increasing the number of animals per maternal line (or decreasing the total number of animals in the dataset) tended to cause direct heritability and maternal heritability to increase, maternal permanent environmental variance to decrease, and maternal temporary environmental variance to remain fairly constant. Direct heritability, maternal heritability, maternal permanent environmental variance and maternal temporary

environmental variance ranged from 0.18 to 0.20, 0.06 to 0.08, 0.06 to 0.05, and 0.22 to 0.24 respectively. Phenotypic variance increased with the number of animals / maternal line and ranged from 6.6 to 7.5 kg (Table 10.3).

10.3.2 Scan-weight (SW)

For all the subsets of data, the inclusion of cytoplasmic effects resulted in logL values moving closer to zero (Table 10.4). There was a significant difference in logL value between the two models for the dataset containing all animals. In the other datasets, the differences between models were not significant. The inclusion of cytoplasmic effects caused direct heritability and maternal heritability to decrease, and maternal permanent environmental variance to increase; maternal common environmental variance remained unchanged in all datasets. Residual variance tended to increase and phenotypic variance to decrease with the inclusion of the effect. Phenotypic variance ranged from 11.41 to 11.94 kg without the effect, and 11.39 to 11.92 kg with the effect. Direct heritability, maternal heritability, maternal permanent environmental variance and maternal temporary environmental variance ranged from 0.20 to 0.25, 0.05 to 0.08, and 0.07 to 0.09, respectively for models without the effect. With cytoplasmic effect direct heritability, maternal heritability and maternal permanent environmental variance ranged from 0.20 to 0.24, 0.04 to 0.06, and 0.07 to 0.09 respectively. Values of maternal temporary environmental variance were the same for both models and for the different datasets ranged from 0.11 to 0.14. Cytoplasmic variance ranged from 0.01 to 0.02 and increased as the cut-off point for the number of animals per maternal line increased (or with decreasing size of the dataset) (Table 10.4).

10.3.3 Muscle depth (MD)

As for EWW, the inclusion of cytoplasmic effects made no difference to the results (Table 10.5). The values obtained from the two models for each dataset were identical. In each analysis the cytoplasmic effect was fixed at a boundary, because its contribution to phenotypic variance was so small. When the number of animals per maternal line increased (resulting in decreasing dataset size) direct heritability decreased, maternal heritability increased, and maternal permanent

environmental variance tended to increase. Direct heritability, maternal heritability, maternal permanent environmental variance and maternal temporary environmental variance ranged from 0.18 to 0.24, 0.02 to 0.06, 0.01 to 0.05, and 0.07 to 0.11 respectively. Phenotypic variance ranged from 4.62 to 4.80 mm.

10.3.4 Fat depth (FD)

As for SW, differences were observed in the values obtained for the different models. The logL values moved closer to zero with the addition of cytoplasmic effects, but none of the differences were significant. When the effect was included direct heritability and maternal heritability tended to decrease, and maternal permanent environmental and maternal temporary environmental variance remained the same or increased slightly. Residual variance either remained unchanged or increased slightly. Direct heritability, maternal heritability, maternal temporary environmental and maternal common environmental variance ranged from 0.16 to 0.24, 0.04 to 0.07, 0.00 to 0.01 and 0.13 to 0.20 respectively for models without the effect. With cytoplasmic effect direct heritability, maternal heritability and maternal common environmental variance ranged from 0.14 to 0.22, 0.03 to 0.05, 0.00 to 0.01 and 0.13 to 0.20 respectively. The phenotypic variance varied from 0.61 to 0.67 mm without the effect, and from 0.64 to 0.66 mm with the effect included. Cytoplasmic variance ranged from 0.01 to 0.02 and increased as the cut-off point for the number of animals per maternal line increased (or with the decreasing size of the dataset) (Table 10.6).

10.3.5 Dataset containing at least three generations

Results were similar to those for the other datasets (Table 10.7). Maternal line had no effect on eight-week weight or muscle depth. Maternal line did have an effect on scan weight and fat depth, contributing approximately 2 % of phenotypic variance, but the effect was not significant. The addition of maternal line to the model caused direct heritability and maternal heritability to decrease, and maternal permanent environmental variance to increase slightly; and maternal temporary environmental variance remained virtually the same (Table 10.7).

Table 10. 3 Variance components and genetic parameters for eight-week weight with models that exclude (Model 1) or include (Model 2) cytoplasmic effects for the full dataset and for subsets containing maternal lines with at least five, ten, 15 and 20 animals/line.

	Increasing no. of offspring/maternal line, decreasing no. of animals in dataset →									
	1+		5+		10+		15+		20+	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
σ^2_a	1.21	1.21	1.30	1.30	1.44	1.44	1.47	1.47	1.48	1.48
σ^2_m	0.36	0.36	0.57	0.57	0.60	0.60	0.62	0.62	0.62	0.62
σ^2_{pe}	0.41	0.41	0.39	0.39	0.36	0.36	0.36	0.36	0.34	0.34
σ^2_{ce}	1.57	1.57	1.59	1.59	1.62	1.62	1.63	1.63	1.69	1.69
σ^2_{cy}	-	0.00	-	0.00	-	0.00	-	0.00	-	0.00
σ^2_e	3.01	3.01	3.34	3.34	3.34	3.34	3.33	3.33	3.33	3.33
σ^2_p	6.556 ± 0.073	6.556 ± 0.073	7.196 ± 0.101	7.196 ± 0.101	7.374 ± 0.111	7.374 ± 0.111	7.402 ± 0.116	7.402 ± 0.116	7.466 ± 0.121	7.466 ± 0.121
h^2	0.184 ± 0.018	0.184 ± 0.018	0.181 ± 0.021	0.181 ± 0.021	0.196 ± 0.023	0.196 ± 0.023	0.198 ± 0.024	0.198 ± 0.024	0.198 ± 0.024	0.198 ± 0.024
m^2	0.055 ± 0.011	0.055 ± 0.011	0.079 ± 0.014	0.079 ± 0.014	0.082 ± 0.015	0.082 ± 0.015	0.084 ± 0.016	0.084 ± 0.016	0.084 ± 0.016	0.084 ± 0.016
pe^2	0.063 ± 0.011	0.063 ± 0.011	0.054 ± 0.012	0.054 ± 0.012	0.049 ± 0.012	0.049 ± 0.012	0.048 ± 0.013	0.048 ± 0.013	0.046 ± 0.013	0.046 ± 0.013
ce^2	0.239 ± 0.012	0.239 ± 0.012	0.221 ± 0.013	0.221 ± 0.013	0.220 ± 0.014	0.220 ± 0.014	0.220 ± 0.014	0.220 ± 0.014	0.227 ± 0.015	0.227 ± 0.015
cy^2	-	0.00	-	0.00	-	0.00	-	0.00	-	0.00
logL	-33839	-33839	-23465.6	-23465.6	-21177.3	-21177.3	-7024.30	-7024.30	-18206.4	-18206.4

σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal temporary environmental variance; σ^2_{cy} *cytoplasmic genetic variance;* σ^2_e error variance; σ^2_p phenotypic variance; h^2 direct heritability; m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance; cy^2 cytoplasmic genetic variance expressed as a proportion of phenotypic variance; logL log likelihood..

Table 10. 4 Variance components and genetic parameters for scan weight with models that exclude (Model 1) or include (Model 2) cytoplasmic effects for the full dataset and for subsets containing maternal lines with at least five, ten, 15 and 20 animals/line.

	Increasing no. of offspring/maternal line, decreasing no. of animals in dataset →									
	All		5+		10+		15+		20+	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
σ^2_a	2.87	2.77	2.32	2.24	2.65	2.55	2.79	2.70	2.80	2.78
σ^2_m	0.55	0.43	0.70	0.54	0.84	0.67	0.89	0.70	0.73	0.47
σ^2_{pe}	0.84	0.84	0.99	1.01	0.91	0.94	0.88	0.92	0.80	0.86
σ^2_{ce}	1.58	1.57	1.24	1.24	1.27	1.26	1.38	1.38	1.35	1.35
σ^2_{cy}	-	0.16	-	0.17	-	0.17	-	0.19	-	0.22
σ^2_e	5.69	5.72	6.15	6.19	6.08	6.12	6.00	6.03	6.20	6.20
σ^2_p	11.51 ± 0.203	11.49 ± 0.202	11.41 ± 0.277	11.39 ± 0.275	11.73 ± 0.321	11.71 ± 0.319	11.94 ± 0.351	11.92 ± 0.349	11.88 ± 0.366	11.88 ± 0.366
h^2	0.250 ± 0.037	0.241 ± 0.038	0.204 ± 0.045	0.197 ± 0.043	0.225 ± 0.051	0.218 ± 0.050	0.233 ± 0.054	0.227 ± 0.053	0.236 ± 0.059	0.234 ± 0.058
m^2	0.048 ± 0.022	0.037 ± 0.022	0.062 ± 0.026	0.048 ± 0.026	0.072 ± 0.030	0.057 ± 0.030	0.075 ± 0.032	0.059 ± 0.032	0.061 ± 0.035	0.040 ± 0.033
pe^2	0.073 ± 0.023	0.074 ± 0.022	0.087 ± 0.026	0.089 ± 0.025	0.077 ± 0.28	0.080 ± 0.027	0.074 ± 0.030	0.077 ± 0.029	0.068 ± 0.032	0.072 ± 0.031
ce^2	0.137 ± 0.022	0.137 ± 0.022	0.109 ± 0.027	0.109 ± 0.027	0.108 ± 0.030	0.108 ± 0.029	0.116 ± 0.031	0.116 ± 0.031	0.114 ± 0.034	0.114 ± 0.034
cy^2	-	0.014 ± 0.010	-	0.015 ± 0.011	-	0.015 ± 0.012	-	0.016 ± 0.012	-	0.019 ± 0.013
logL	-17227	**-17217.3**	-8435.95	-8434.88	-6981.3	-6980.4	-6068.7	-6067.8	-5373.5	-5372.2

See Table 10.3 for definition of abbreviations. Value in bold shows that Model 2 is significantly different to Model 1.

Table 10. 5 Variance components and genetic parameters for muscle depth with models that exclude (Model 1) or include (Model 2) cytoplasmic effects for the full dataset and for subsets containing maternal lines with at least five, ten, 15 and 20 animals/line.

	Increasing no. of offspring/maternal line, decreasing no. of animals in dataset →									
	all		5+		10+		15+		20+	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
σ^2_a	1.12	1.12	1.10	1.10	1.03	1.03	0.93	0.93	0.83	0.83
σ^2_m	0.10	0.10	0.10	0.10	0.16	0.16	0.25	0.25	0.26	0.26
σ^2_{pe}	0.16	0.16	0.21	0.21	0.17	0.17	0.07	0.07	0.05	0.05
σ^2_{ce}	0.39	0.39	0.36	0.36	0.34	0.34	0.48	0.48	0.51	0.51
σ^2_{cy}	-	0.00 B	-	0.00 B	-	0.00 B	-	0.00 B	-	0.00
σ^2_e	2.85	2.85	2.88	2.88	3.04	3.04	3.07	3.07	3.03	3.03
σ^2_p	4.62 ± 0.086	4.62 ± 0.086	4.65 ± 0.121	4.65 ± 0.121	4.751 ± 0.135	4.751 ± 0.135	4.80 ± 0.146	4.80 ± 0.146	4.68 ± 0.151	4.68 ± 0.151
h^2	0.243 ± 0.037	0.243 ± 0.037	0.238 ± 0.045	0.238 ± 0.045	0.217 ± 0.048	0.217 ± 0.048	0.195 ± 0.049	0.195 ± 0.049	0.176 ± 0.051	0.176 ± 0.051
m^2	0.022 ± 0.018	0.022 ± 0.018	0.021 ± 0.021	0.021 ± 0.021	0.034 ± 0.025	0.034 ± 0.025	0.051 ± 0.028	0.051 ± 0.028	0.055 ± 0.031	0.055 ± 0.031
pe^2	0.034 ± 0.022	0.034 ± 0.022	0.045 ± 0.025	0.045 ± 0.025	0.036 ± 0.027	0.036 ± 0.027	0.015 ± 0.029	0.015 ± 0.029	0.012 ± 0.032	0.012 ± 0.032
ce^2	0.085 ± 0.027	0.085 ± 0.027	0.077 ± 0.033	0.077 ± 0.033	0.071 ± 0.037	0.071 ± 0.037	0.100 ± 0.041	0.100 ± 0.041	0.110 ± 0.046	0.110 ± 0.046
cy^2	-	0.00	-	0.00	-	0.00	-	0.00 B	-	0.00 B
logL	-10217.8	-10217.8	-5185.7	-5185.7	-4252.3	-4252.3	-3576.19	-3576.19	-3035.35	-3035.35

See Table 10.3 for definition of abbreviations. B = parameter was fixed at a boundary during analysis.

Table 10. 6 Variance components and genetic parameters for fat depth with models that exclude (Model 1) or include (Model 2) cytoplasmic effects for the full dataset and for subsets containing maternal lines with at least five, ten, 15 and 20 animals/line.

	Increasing no. of offspring/maternal line, decreasing no. of animals in dataset →									
	All		5+		10+		15+		20+	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
σ^2_a	0.14	0.13	0.15	0.14	0.16	0.15	0.14	0.12	0.10	0.09
σ^2_m	0.03	0.02	0.03	0.02	0.02	0.02	0.04	0.03	0.04	0.03
σ^2_{pe}	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
σ^2_{ce}	0.10	0.10	0.08	0.08	0.13	0.14	0.11	0.11	0.11	0.11
σ^2_{cy}	-	0.01	-	0.01	-	0.01	-	0.01	-	0.01
σ^2_e	0.37	0.38	0.38	0.38	0.35	0.35	0.37	0.38	0.40	0.40
σ^2_p	0.61 ± 0.120	0.64 ± 0.012	0.65 ± 0.017	0.64 ± 0.017	0.67 ± 0.019	0.66 ± 0.019	0.66 ± 0.020	0.65 ± 0.020	0.66 ± 0.021	0.66 ± 0.021
h^2	0.213 ± 0.038	0.202 ± 0.037	0.235 ± 0.047	0.220 ± 0.046	0.240 ± 0.052	0.222 ± 0.051	0.209 ± 0.055	0.188 ± 0.052	0.158 ± 0.055	0.140 ± 0.051
m^2	0.045 ± 0.017	0.035 ± 0.018	0.042 ± 0.024	0.029 ± 0.023	0.037 ± 0.025	0.025 ± 0.024	0.057 ± 0.025	0.039 ± 0.028	0.065 ± 0.027	0.045 ± 0.027
pe^2	0.00	0.00	0.006 ± 0.024	0.008 ± 0.023	0.006 ± 0.026	0.007 ± 0.025	0.00	0.003 ± 0.028	0.00	0.00
ce^2	0.157 ± 0.027	0.158 ± 0.027	0.129 ± 0.038	0.131 ± 0.038	0.200 ± 0.042	0.203 ± 0.042	0.165 ± 0.045	0.170 ± 0.047	0.168 ± 0.051	0.175 ± 0.051
cy^2	-	0.013 ± 0.011	-	0.015 ± 0.011	-	0.016 ± 0.012	-	0.020 ± 0.013	-	0.022 ± 0.014
logL	-2462.84	-2461.87	-1204.77	-1203.72	-1002.68	-1001.61	-835.31	-833.86	-740.81	-739.2

See Table 10.3 for definition of abbreviations.

Table 10. 7 Variance components and genetic parameters for eight-week weight, scan weight, muscle depth and fat depth with models that exclude (Model 1) or include (Model 2) cytoplasmic effects using a dataset containing at least three generations.

	EWW		SW		MD		FD	
	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2	Model 1	Model 2
σ^2_a	1.61	1.61	2.40	2.30	1.17	1.17	0.13	0.12
σ^2_m	0.56	0.56	0.81	0.59	0.11	0.11	0.03	0.02
σ^2_{pe}	0.40	0.40	0.93	0.96	0.17	0.17	0.00	0.00
σ^2_{ce}	1.64	1.64	1.35	1.36	0.35	0.35	0.12	0.13
σ^2_{cy}	-	0.00	-	0.23	-	0.00	-	0.01
σ^2_e	3.15	3.15	5.98	6.03	2.98	2.98	0.35	0.36
σ^2_p	7.360 (0.109)	7.360 (0.109)	11.49 (0.290)	11.46 (0.288)	4.786 (0.130)	4.786 (0.130)	0.643 (0.017)	0.640 (0.017)
h^2	0.219 (0.024)	0.219 (0.024)	0.209 (0.047)	0.201 (0.046)	0.245 (0.049)	0.245 (0.049)	0.209 (0.049)	0.194 (0.047)
m^2	0.077 (0.014)	0.077 (0.014)	0.071 (0.029)	0.051 (0.028)	0.023 (0.023)	0.023 (0.023)	0.048 (0.026)	0.035 (0.024)
pe^2	0.055 (0.012)	0.055 (0.012)	0.081 (0.027)	0.084 (0.026)	0.036 (0.026)	0.036 (0.026)	0.002 (0.026)	0.003 (0.025)
ce^2	0.222 (0.013)	0.222 (0.013)	0.118 (0.028)	0.118 (0.028)	0.074 (0.036)	0.074 (0.036)	0.195 (0.040)	0.196 (0.040)
cy^2	-	0.00	-	0.020 (0.012)	-	0.00	-	0.018 (0.012)
logL	-22902.7	-22902.7	-7892.79	-7891.09	-4814.84	-4814.84	-1076.00	-1074.57

See Table 10.3 for definition of abbreviations.

10.4 Discussion

There were no significant differences in Log likelihood (logL) values between models that did and did not include cytoplasmic effects and variance components were virtually the same in both models for eight-week weight and muscle depth. LogL values for scan weight and fat depth improved slightly with the inclusion of cytoplasmic effects, but in only one dataset (for scan weight) was the difference significant. For both scan weight and fat depth cytoplasmic effects accounted for approximately 1-2 % of the phenotypic variation. The phenotypic variances and residual errors remained approximately the same in both models, which meant that, for scan weight and fat depth, the inclusion of cytoplasmic effects caused slight decreases in direct heritability and maternal heritability.

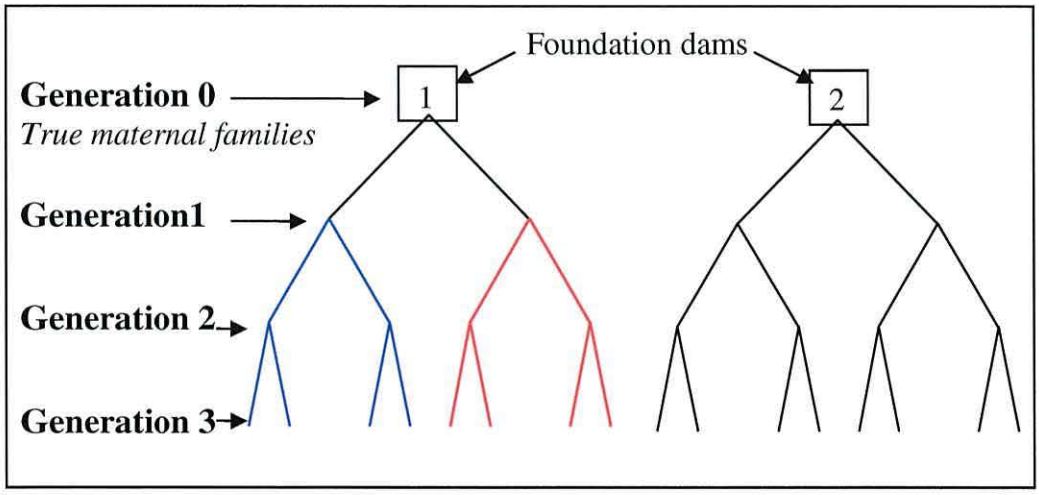


Figure 10.1 Illustration of maternal lines. Source Roughsedge *et al.* (2001)

It was observed that some maternal lines in the dataset had very few animals. Inclusion of such lines in an analysis may cause maternal lineage variance to be confounded with the direct additive genetic effect. Maternal lines with few animals could result from a lack of pedigree information. In the study of Roughsedge *et al.* (2000) of dairy cows, the authors commented that some cows could not be traced back to a distant cytoplasmic origin, and might be of the same maternal lineage as others in the dataset. If there is insufficient information, maternal subfamilies can be assigned to different maternal lines, although they may in fact belong to one true family. Roughsedge *et al.* (2001) concluded from a simulation study that incomplete maternal pedigree information, resulting in

animals being assigned to different lineages when they actually belong to the same one, can cause a downward bias in estimates of cytoplasmic effect. As illustrated in Figure 10.1, if the pedigree is not traced far enough back because of a lack of information, a single maternal line maybe represented by more lines; for instance if pedigree was known only from generation 1 two maternal lines would be recorded even though they come from the same animal in generation 0.

Some authors have commented that analyses on small datasets from a limited number of populations may reduce the ability of tests to find significant differences between maternal lines (Mannen *et al*, 1998; Mezzadra *et al*, 2005; Schnitzenlehner and Essl, 1999; Schutz *et al*, 1994). Mezzadra *et al.* (2005) examined the influence of cytoplasmic inheritance by a method of assigning maternal lines, in addition to analysing the direct association between mitochondrial DNA polymorpisms and productive traits. It was found that in 23 supposed maternal lineages there were only five different mitochondrial genotypes, and it was suggested that the failure to detect a cytoplasmic effect could be a reflection of some maternal lines having the same genotype. Eledath and Hines (1996) studied Holstein cattle and found ten different mitochondrial genotypes in 16 maternal lines. In the study described in this chapter the data came from three Welsh Mountain breeding groups, in which there might be a greater chance of finding variation among maternal lines than in a closed flock. However, as in other studies, there is always the possibility that animals assigned to different lines could be subfamilies sharing a common mitochondrial genome.

Roughsedge *et al.* (2000) found no significant differences among maternal lineages for yield traits in dairy cattle. However, when maternal lineages were restricted to those with five or more records, maternal lineage contributed 4.4 % of phenotypic variance for persistency of milk production. Boettcher *et al.* (1996b) also suggested that more accurate estimates of maternal lineage effects would be obtained with more animals per maternal line. In this study it was observed for both scan weight and fat depth that the contribution made by maternal line to phenotypic variance increased as maternal lines were restricted to those with higher numbers of animals. For scan weight the contribution due to cytoplasmic effect was 1.4 % of phenotypic variance in the dataset with all

animals, and increased to 1.9 % when the dataset was restricted to maternal lines with 20 or more animals per line. Similarly, for fat depth the contribution to phenotypic variance increased from 1.3 % to 2.2 % when the same datasets were compared.

Previous studies have indicated that if a trait is highly energy dependent, the component of variation due to maternal lineage is more likely to be identified, and to be significant, as the ability of mitochondria to provide ATP is challenged (Brown *et al*, 1988). In dairy cattle several authors have found that maternal lineage has a significant effect on content of milk fat (Bell *et al*, 1985; Boettcher *et al*, 1996b; Freeman, 1990; Schutz *et al*, 1992). Boettcher *et al.* (1996b) found maternal lineage to be associated with fat percentage and to contribute 2.7 % to the phenotypic variance of this trait and of the energy concentration in milk. Boettcher *et al.* (1996b) explained the strong effect on fat content of maternal lineage by the fact that fats are the energy-densest component of milk and that nearly all energy derived from food is converted to ATP in the mitochondria. Schutz *et al.* (1992) reported that maternal lineage influenced fat concentration, energy concentration, and to a lesser extent fat yield in milk. Bell *et al.*(1985) reported 3.5 % of the variation in milk fat percentage in the first lactation was due to maternal lineage. These studies seem to suggest that fat content of milk varies with maternal line; however, some authors have obtained the opposite results. Kennedy (1986) suggested that in models that do not include direct additive genetic effect, cytoplasmic effects took its place, and appeared large because of the high heritability of fat content. In this study maternal line did not have a significant effect on ultrasonic fat depth, but it accounted for 1-2 % of the phenotypic variance in this trait, perhaps for the reasons mentioned (i.e. the high energy content of fat).

Methods based on detecting mitochondrial DNA polymorphisms are probably more accurate than those based on assigning individuals to maternal lines, given the inaccuracies that arise in determining maternal pedigree. It should be noted, however that the same mitochondrial genotype can occur in different families. It was also pointed out by Schnitzenlehner and Essl (1999) that treating animals as members of a maternal line to have the same mitochondrial genome becomes

more unreliable with increasing numbers of generations, as the probability of mutation increases with increasing distance from the foundation dam.

Studies that have examined mitochondrial DNA polymorphism have also found that some are associated with certain traits. Mannen *et al.* (2003) studied the association between variation of transcribed mtDNA and variation in carcass traits in beef cattle. Substitutions were found within particular regions of mtDNA. Substitutions in the mtDNA sequence could alter the function of the mitochondrial ribosome and the rate of mitochondrial synthesis, and it was suggested that one polymorphism was associated with meat quality traits, longissimus muscle area and beef marbling score. Schnitzenlehner and Essl (1999) found that cytoplasmic effects were non-significant for dairy traits, but significant for fitness traits in cattle. Nevertheless, even if associations between mitochondrial polymorphisms and economically important traits exist, Sutarno *et al.* (2002) commented that mitochondrial markers were less valuable than nuclear ones in marker-assisted selection because they are maternally inherited, and because selection intensities in females are much less than in males.

The results of this study showed that cytoplasmic effects were generally not significant for the four traits examined. No effects at all were observed for eight-week weight, and muscle depth, but about 1-2 % of the variance for scan weight and fat depth was associated with cytoplasmic effects.

It would have been interesting to have carried out further analyses on datasets with restrictions on the number of generations. A dataset restricted to four generations was attempted but convergence failed in ASReml.

CHAPTER 11

Analysis of Scrapie Genotype data to estimate Gene Frequencies and the consequences of selecting for Resistance to Scrapie

ABSTRACT

Four alleles (AHQ, ARQ, ARR, and VRQ) and genotypes covering all five NSP risk groups were present in the CAMDA flock. Overall, the most common allele was ARR (35.2 %), and VRQ was the least common (5.4 %). The commonest genotypes were ARR/ARQ (23.7 %) and ARR/AHQ (23.1 %). The most resistant genotype, ARR/ARR, and the most susceptible genotype, VRQ/VRQ, were found in 10.2 %, and 0.3%, respectively, of the population tested. The associations of PrP genotypes with weight and ultrasonically-scanned traits were investigated in three analyses, the first using genotypes, the second using risk categories, and the third using copy number of alleles. Univariate analysis was carried out for each trait using an animal model with maternal effects where appropriate, and PrP was included as a fixed effect. There was little evidence of association between PrP genotypes and the four traits studied. In the analysis using risk groups the only significant difference was between Group I and Group II genotypes for muscle depth. The mean muscle depth for Group I (ARR homozygous) was greater than for Group II (ARR heterozygous); thus, selection of ARR homozygous should not have a detrimental effect on muscle depth.

11.1 INTRODUCTION

The profile of scrapie has risen in recent years, with increasing public awareness that it is a disease that resembles BSE (Bovine Spongiform Encephalopathy) in cattle and CJD (Creutzfeldt Jakob Disease) in man. Eradication of scrapie is part of an EU control programme, to protect against the theoretical risk that BSE is present in sheep and goat populations, masked as scrapie. The clinical signs of

experimentally-induced BSE in sheep are not distinguishable from those of scrapie, and it is possible that sheep were exposed to the same contaminated feed in the early 1980s that gave rise to BSE in cattle (Schreuder and Somerville, 2003). Naturally-occurring BSE has not been identified in sheep, but BSE was confirmed in a French goat in 2005 (Anon, 2005). There has been major government intervention to bring scrapie under control by a combination of selecting more resistant stock and closer surveillance of sheep and goat populations.

Under a contingency plan prepared by DEFRA, the worst case scenario would be the disposal of the entire UK sheep flock if BSE were to be identified in sheep (DNV Consulting, 2001). In July 2001 the National Scrapie Plan (NSP) was launched in the UK following recommendations of the Spongiform Encephalopathy Advisory Committee (SEAC). The aims of the various schemes included in the NSP were to increase genetic resistance to scrapie, thereby reducing incidence of disease due to TSE's (Transmissible Spongiform Encephalopathies) and the theoretical risk of BSE in the national sheep flock. The scheme categorises the genotypes that confer resistance/susceptibility to scrapie into five groups (Dawson *et al*, 1998; Warner, 2003). Group I has the highest resistance and Group IV and V are the most susceptible. The five groups not only reflect potential resistance/susceptibility, but also the potential for breeding animals to transfer alleles for resistance/susceptibility to their offspring. The NSP plan encourages the removal of the alleles conferring greatest susceptibility from the ram population, which will have the gradual effect of flocks becoming more resistant.

Studies have identified three major amino acid codons in the sheep prion protein (PrP) gene at positions 136, 154 and 171 where polymorphisms confer increased or decreased susceptibility to scrapie. The polymorphisms are associated with differing incubation periods, symptoms and pathology of scrapie. At least five alleles of the PrP gene have been identified in sheep, the codes for the major ones being ARR, ARQ, AHQ, ARH and VRQ. Breed differences are apparent in the frequencies of PrP alleles. In the UK the simplest situation occurs in breeds that only have two PrP alleles, for example the Cotswold, Hampshire Down, Soay, Suffolk and Vendeen breeds. The Suffolk breed has three common genotypes,

whereas in the Shetland, Cheviot, Swaledale there are many more. Breeding resistance in the Suffolk, is simply achieved by the selection of ARR homozygous rams. In the Cheviot, there is a wider choice of resistant types. However, because current schemes are focusing on the national flock rather than individual breeds, the ARR/ARR genotype is of primary interest in any breed and selection is mainly for this genotype. The selection of the ARR genotype and the introduction of the ARR allele to infected flocks is understood not only to reduce the incidence of the disease by increasing the proportion of less susceptible animals, but also prevents the environmental spread of infection by the placental route from infected ewes (Andréoletti *et al*, 2002).

However, there have been concerns that rapid breeding for resistance of scrapie may not always be appropriate, particularly in breeds where there are low frequencies of resistant alleles or in breeds that are rare and have a smaller population to select resistant animals from (Gmur *et al*, 2004). The Rare Breeds Genotype Survey showed that some breeds, such as the Leicester Longwool, Lincoln Longwool, Norfolk Horn, Ryeland and Wensleydale, already had high frequencies of the desirable ARR allele with percentages of 90.7, 86.4, 86.8, 89.2 and 90.6, respectively. However, breeds such as the Boreray, Castlemilk Moorit, North Ronaldsay and Soay were found to have very low frequencies of the ARR allele with percentages of 2.4, 3.1, 0.8 and 1.5 respectively, though they also had high frequencies of the ARQ allele (Rare Breeds Survival Trust, undated). The Texel breed, commonly used as a terminal sire, is disadvantaged by having a low frequency of ARR homozygous rams.

The disadvantages of selecting for just one genotype (ARR/ARR), it has been argued, is that it could lead to an unhealthy homogeneity (Elson *et al*, 1999), and caution has been advised even though the ARR/ARR genotype appears more resistant to TSE's in general (Kao *et al*, 2003). Although, the disease might be eliminated by breeding, the infectious agent would not, and it is possible that strains of scrapie could appear that might attack these genetically-uniform animals in the future (Slate, 2005). In addition, resistant types might still carry disease without showing obvious symptoms (Woolhouse *et al*, 2001), although there has been no evidence of this to date (Houston *et al*, 2003). It has been suggested that further research is required to evaluate the possible consequences

of selecting for resistance in large populations (Elson *et al*, 1999). Bossers *et al.* (2000) suggested that selection for several PrP variants associated with resistance would be a safer strategy and would contribute to a more genetically diverse sheep population. It is possible that scrapie-resistant sheep may lack other traits that breeders value, such as meat or wool quality; therefore it is important to keep selection for resistance when there is low scrapie risk in perspective (Dawson *et al*, 1998).

Links between scrapie resistance and economically-important production traits are being studied in many breeds. A focus on scrapie genotype alone may prove risky if resistant alleles are antagonistic to other economically important traits, or if they are sufficiently rare that selection for them increases inbreeding and reduces genetic variability. The concern of some breeders about the loss of genetic variation following intense selection for scrapie resistant genotypes limited uptake of the National Scrapie Plan. Breeders were concerned that they might lose high-performing animals if they were not resistant types. In addition, selecting only animals of resistant types lowers the selection differential and may slow the rate of genetic progress.

Natural selection is expected to reduce the frequency of alleles causing defective or susceptible conditions, yet scrapie in the UK still persists after 250 years (Woolhouse *et al*, 2001). Its persistence could be partly explained by the long incubation period of the disease together with its difficult inactivation, which could prolong its presence in the environment (Johnson *et al*, 2006; Thorgeirsdottir *et al*, 1999). Within-flock mortality associated with the PrP genotype can be high, which leads to strong selection against susceptible genotypes. Sheep may still have the opportunity to breed, but their life expectancy is shorter and they therefore contribute fewer offspring to the next generation. Lower frequencies of alleles for susceptibility have been reported in Cheviot and Suffolk flocks in the UK than in sheep in Australia, which is scrapie free, and this is possibly due to natural selection (Woolhouse *et al*, 2001).

Alleles for susceptibility may have a selective advantage in the absence of scrapie, if they are positively associated to traits that are favoured by breeders (i.e. if there is linkage disequilibrium between the relevant loci). In Brown Swiss cows it was found that the defective Weaver allele increased over time because it

was linked to the chromosome segment that affected milk yield (Hoeschele and Meinert, 1990). However, current research provides little evidence that PrP polymorphisms have phenotypic effects on, or linkage associations with, any other traits apart from scrapie resistance.

There have been no associations found between the PrP genotype and dairy production traits in Lacaune, Basco-Bearnaise or Manech French dairy breeds (Barillet *et al*, 2002) or East Friesian Milk sheep (De Vries *et al*, 2005). Roden *et al.* (2001) found that there was no evidence to suggest a relationship between PrP genotype and performance traits included in the Lean Index used in selection of the Suffolk breed. In Texel sheep results of Brandsma *et al.* (2004) indicated that selection of ARR/ARR genotypes had a small positive effect on litter size, but a small negative effect on 135-day weight, and considered that this was why the susceptible VRQ and ARQ alleles remained in the population. In German Texel, Suffolk, and German white-headed mutton sheep there was little evidence of any adverse link between PrP genotype, particularly ARR homozygous, with performance and reproductive traits (De Vries *et al*, 2004a; De Vries *et al*, 2004b). The few significant associations in the above studies were thought to be due to the small number of genotyped animals and the confounding of PrP genotypes with particular environmental conditions. De Vries *et al.* (2004a) found that daily live-weight gain and back muscle depth of the German black-headed sheep breed, were better in animals without an ARR allele than in those with an ARR allele; however, this result was again based upon few animals. Isler *et al.* (2006) studied associations between PrP haplotype and 25 growth, carcass, and meat quality traits. In the Romanov breed the ARR haplotype was associated with longer carcasses, narrow rumps, and less marbling than ARQ and VRQ haplotypes. The association between PrP genotype and estimated breeding values for prolificacy was studied in Rasa Aragonesa sheep and it appeared that most PrP genotypes did not have an effect on prolificacy (Ponz *et al*, 2006). The only significant association was for the VRQ/VRQ genotype, for which a lower estimated breeding value was observed. It was concluded that selecting against the genotype would not cause a negative effect on prolificacy. Ewe and lamb traits in Columbia, Hampshire, Rambouillet, Suffolk breeds and a western white-faced commercial flock were studied to determine associations between traits and the arginine allele (R) at codon 171 (Alexander *et al*, 2005). It was observed that

ewe or lamb genotype did not affect prolificacy, total birth weight, weight of lamb weaned (ewe traits), birth weight or weaned weight (lamb traits) in the first three breeds. Suffolk ewes without the R allele gave birth to more multiple lambs than ewes heterozygous for the allele, and produced lambs with lower individual weaned weights (but a higher total weaned weight). Ewes without the R allele and heterozygotes also produced more lambs in the commercial flock than homozygous R ewes, but there were no differences between genotypes in the total weight of lambs weaned. Vitezica *et al.* (2006) found no associations between PrP genotypes and fertility, litter size, ovulation rate, birth weight and average daily gain in the INRA 401 breed.

An assumption of the National Scrapie Plan is that the resistant genotype is, and will remain, resistant to scrapie. Some studies have shown that ARR homozygous animals can not be totally regarded as genetically resistant to TSE infection (Ikeda *et al*, 1995). It has been shown that animals with the genotype with highest resistance display clinical symptoms when infected with BSE by intracerebral inoculation (Houston *et al*, 2003; SEAC, 2003) and orally (Andréoletti *et al*, 2006). Through intensified surveillance of scrapie in the European Union and improvements in techniques a number of 'atypical' scrapie cases have been identified showing unusual histopathological and PrPSc molecular features (Benestad *et al*, 2003). Such cases have been found to occur in more resistant genotypes, i.e. homozygous AHQ and heterozygous or homozygous ARR sheep (Buschmann *et al*, 2004; De Bosschere *et al*, 2005; Everest *et al*, 2006; Le Dur *et al*, 2005; Onnasch *et al*, 2004; Orge *et al*, 2004). The VRQ allele which makes its carriers highly susceptible to conventional scrapie, appeared to confer resistance to atypical scrapie forms found in Norway, referred to as the Nor98 strain (Benestad *et al*, 2003; Moum *et al*, 2005). Benestad *et al.* (2003) found that within flocks with single atypical scrapie cases flock-mates with the VRQ and ARQ alleles were not affected. However, animals with the AHQ allele, generally thought to confer some resistance to conventional scrapie, were found to be affected (Benestad *et al*, 2003; Luhken *et al*, 2004). The eradication programmes in Europe would be an acceleration of directional selection, but it has been suggested that the PRNP gene has evolved by balancing selection, which could be the reason why many genotypes exist (Slate, 2005).

Therefore, the effectiveness of wide-scale genotyping and current breeding programmes have become questionable.

There is considerable variation between breeds, in the proportions of animals in NSP groups 1, 2 and 3. On average there are proportionately more animals found in group 3 in certain hill breeds such as Welsh Mountain and Scottish Blackface (Warner, 2003). Testing of over 107,000 animals, over the years 2001 to 2004, of the Welsh Mountain showed that the percentages of animals in group 1 and 2, group 3, and group 4 and 5 risk categories were 57.3, 31.8, and 10.8, respectively (DEFRA, 2004). Through selection of breeding animals with resistant genotypes the proportions of animals in higher risk categories have decreased. In a study of the CAMDA flock there were four allelic variants present, namely AHQ, ARQ, ARR, and VRQ, and the percentages of these alleles were 34.7 %, 31.9 %, 20.7 %, and 12.7 %, respectively (Lonyong, 2003; Lonyong *et al*, 2004). All ten of the possible genotypes from four alleles were found in the flock. The aim of the study described in this chapter is to build on the work of Lonyong (2003) by determining the frequency of genotypes in the CAMDA flock and testing whether there is an association between PrP genotype and weight and ultrasonically-scanned traits.

11.2 METHODS

Data were obtained from the CAMDA flock. Scrapie testing was carried out in years 2001 to 2004 inclusive under various schemes (such as the Ram Genotyping scheme and Welsh Ewe Genotyping Scheme (WEGS)) of the National Scrapie Plan (NSP), on breeding animals and lambs that would potentially be used for breeding. Blood was collected into EDTA tubes and sent to a laboratory for genotyping. Each animal tested had a bolus inserted with a NSP electronic identification number. Two datasets were used. Data for weight and carcass traits were obtained from the MLC, and genotype data were obtained from CAMDA. However, not all animals with genotype records were identified in the MLC records, and therefore not all data were used in the study.

The analyses used a dataset with 11595 animals; however there were only 971 animals with genotype records. Genotyped animals consisted of 116 male and

855 female animals. Genotyped animals were born in years 1997 to 2004. Genotyped animals in years with few records were excluded because effects of year and genotype might be confounded. Non-genotyped animals were not used in the comparisons in the association study. The traits examined were eight-week weight (EWW), scan-weight (SW), muscle depth (MD), and fat depth (FD) and the numbers of records from genotyped animals were 971, 656, 625, and 626, respectively.

There are three main PRNP codons (136, 154, and 171) responsible for determining scrapie susceptibility. The PrP genotyping involves extracting DNA from the white blood cells, as described by Elsen *et al.* (1999). Codons 136, 154, and 171 were examined for the polymorphisms listed below: -

codon 136 alanine (A) / valine (V)

codon 154 arginine (R) / histidine (H)

codon 171 arginine (R) / glutamine (Q) / histidine (H)

Table 11.1 Risk groups of the National Scrapie Plan

Genotype	Group	Degree of resistance/susceptibility
ARR/ARR	1	Genetically most resistant to scrapie
ARR/AHQ, ARR/ARH, **ARR/ARQ**	2	Genetically resistant to scrapie, but will need careful selection when used for further breeding.
AHQ/AHQ, AHQ/ARH, **AHQ/ARQ**, ARH/ARH, ARH/ARQ, **ARQ/ARQ**, **ARR/VRQ**	3	Genetically have little resistance to scrapie and will need careful selection when used for further breeding.
	4	Genetically susceptible to scrapie and should not be used for breeding unless in a controlled breeding programme approved by the NSPAC.
AHQ/VRQ, ARH/VRQ, **ARQ/VRQ**, **VRQ/VRQ**	5	Highly susceptible and should not be used for breeding.

Genotypes present in the CAMDA flock are printed in bold

The genotype proportions were calculated for the flock and genotypes were allocated to risk categories (Table 11.1) for the further analyses.

11.2.1 PrP genotypes and their association with growth and carcass traits

To study the association of PrP genotypes with other traits three types of analysis were performed using differing classifications of PrP genotype.

Analysis 1. Although ten genotypes were found in the CAMDA flock, records for the VRQ/VRQ were deleted because there were few animals in the group.

Thus nine classes (genotypes) were used in the analysis and descriptive statistics are shown in Table 11.2.

Table 11.2 Analysis 1: Number of animals, means and standard deviations for nine genotypes found in the CAMDA flock for eight-week weight (EWW), scan weight (SW), muscle depth (MD) and fat depth (FD).

	EWW (kg)		SW (kg)		MD (mm)		FD (mm)	
Genotype	Count	Mean (S.D)	Count	Mean (S.D)	Count	Mean (S.D)	Count	Mean (S.D)
ARR/ARR	101	22.71 (2.994)	80	29.76 (3.893)	78	23.23 (2.706)	78	2.79 (0.927)
ARR/AHQ	227	21.97 (3.093)	169	28.68 (4.237)	160	21.69 (3.342)	160	2.67 (0.992)
ARR/ARQ	235	22.05 (3.058)	175	29.07 (3.891)	167	21.90 (3.023)	167	2.83 (1.035)
AHQ/AHQ	61	21.74 (3.325)	35	29.49 (4.517)	31	21.03 (2.689)	31	3.15 (0.874)
AHQ/ARQ	166	22.64 (2.821)	109	28.51 (3.563)	104	20.30 (3.087)	105	2.90 (1.039)
ARQ/ARQ	87	22.32 (3.196)	44	29.65 (4.372)	43	21.37 (2.928)	43	3.08 (1.058)
ARR/VRQ	32	21.06 (3.273)	18	28.22 (3.805)	17	20.24 (3.817)	17	3.03 (1.035)
AHQ/VRQ	24	20.30 (3.057)	10	28.05 (4.070)	10	18.80 (2.348)	10	3.60 (0.775)
ARQ/VRQ	35	22.49 (1.966)	13	29.69 (1.888)	12	20.42 (3.059)	12	3.23 (0.999)

Analysis 2. The ten genotypes were put into four categories based upon the NSP risk groups (Table 11.1). Due to the weaknesses of data structure (there were few observations for some genotypes) risk categories 4 and 5 of the NSP were combined. The four groups were: 1) ARR homozygous (NSP group 1); 2) ARR heterozygous with either AHQ or ARQ (NSP group 2); 3) AHQ homozygous, ARQ homozygous, or AHQ/ARQ (NSP group 3); 4) VRQ heterozygous with ARR (NSP group 4), AHQ, or ARQ and VRQ homozygous (NSP group 5). Descriptive statistics for each genotype category are shown in Table 11.3.

Table 11.3 Analysis 2: Number of animals, means and standard deviations for risk groups (1 to 4) for eight-week weight (EWW), scan weight (SW), muscle depth (MD) and fat depth (FD).

	EWW (kg)		SW (kg)		MD (mm)		FD (mm)	
Risk Group	Count	Mean (S.D)	Count	Mean (S.D)	Count	Mean (S.D)	Count	Mean (S.D)
1	101	22.71 (2.994)	80	29.76 (3.893)	78	23.23 (2.706)	78	2.79 (0.927)
2	462	22.01 (3.072)	344	28.88 (4.064)	327	21.80 (3.180)	327	2.75 (1.016)
3	314	21.85 (3.034)	188	28.96 (3.965)	178	20.69 (3.005)	179	2.99 (1.017)
4	94	21.47 (2.892)	44	28.85 (3.455)	42	19.76 (3.230)	42	3.25 (0.959)

Analysis 3. Four analyses were carried out for each of the four traits. Animals were categorised into classes depending on whether they carried 2, 1, or 0 copies of an allele, as shown below. For the analysis of the VRQ allele, there were just two groups because there were few VRQ homozygous animals (the three VRQ homozygous animals were grouped with the VRQ heterozygous animals). The four classes were: -

1) ARR allele: ARR/ARR, ARR/XXX, XXX/XXX

2) AHQ allele: AHQ/AHQ, AHQ/XXX, XXX/XXX

3) ARQ allele: ARQ/ARQ, ARQ/XXX, XXX/XXX

4) VRQ allele: VRQ containing, XXX/XXX

where XXX represents alleles other than the one specified. Descriptive statistics for each genotype category are shown in Table 11.4.

Table 11.4 Analysis 3: Number of animals, means and standard deviations for classes categorised on whether there are 2, 1 or 0 copies of alleles ARR, AHQ, ARQ and VRQ for eight-week weight (EWW), scan weight (SW), muscle depth (MD) and fat depth (FD).

		Trait							
		EWW (kg)		SW (kg)		MD (kg)		FD (kg)	
Allele	No.	Count	Mean (S.d)	Count	Mean (S.d)	Count	Mean (S.d)	Count	Mean (S.d)
ARR	2	101	22.71 (2.994)	80	29.76 (3.893)	78	23.23 (2.706)	78	2.79 (0.927)
	1	494	21.95 (3.091)	362	28.85 (4.049)	344	21.72 (3.226)	344	2.76 (1.017)
	0	376	21.82 (2.976)	214	29.00 (3.874)	203	20.53 (3.002)	204	3.04 (1.010)
AHQ	2	61	21.74 (3.325)	35	29.49 (4.517)	31	21.03 (2.689)	31	3.15 (0.874)
	1	417	21.74 (3.004)	288	28.60 (3.978)	274	21.06 (3.306)	275	2.79 (1.019)
	0	493	22.21 (3.032)	333	29.31 (3.897)	320	21.97 (3.099)	320	2.88 (1.012)
ARQ	2	87	22.32 (3.196)	44	29.65 (4.372)	43	21.37 (2.928)	43	3.08 (1.058)
	1	436	21.93 (2.901)	297	28.89 (3.712)	283	21.25 (3.137)	284	2.87 (1.035)
	0	448	21.96 (3.151)	315	29.03 (4.164)	299	21.81 (3.283)	299	2.81 (0.978)
VRQ	1	94	21.47 (2.898)	44	28.85 (3.455)	42	19.76 (3.230)	42	3.25 (0.959)
	0	877	22.03 (3.057)	612	29.02 (4.015)	583	21.65 (3.164)	584	2.83 (1.009)

Models were initially tested for all traits to determine the effects to be included. Eight-week weight was analysed using a (full) model that included direct additive genetic effect, maternal additive genetic effect, maternal permanent

environmental effect, and maternal temporary environmental effect as random effects. Scan weight included the first three of the random effects as the model for eight-week weight, but did not include maternal temporary environmental effect. Muscle depth and fat depth were analysed with only direct additive genetic effect as a random effect. PrP genotype was included as a fixed effect in addition to age of dam, year of birth, sex, birth rearing type and, for eight-week weight only, the two-way and three-way interactions between the latter three effects.

The full model (i.e. the one used for eight-week weight) was

Equation 11. 1

$$Y_{ijklmn\,\mathrm{Pr}\,P} = \mu + a_i + b_j + c_k + d_l + bc_{jk} + bd_{jl} + cd_{kl} + bcd_{jkl} + f_m + G_{\mathrm{Pr}\,P} + z_m + x_n + w_n + v_{nj} + e_{ijklmn\,\mathrm{Pr}\,P}$$

where μ = the overall mean of eight-week weight, scan weight, muscle depth or fat depth; a_i = fixed effect of rearing dam age (i = 4); b_j = fixed effect year of birth (j = 1996 to 2004); c_k = fixed effect of sex (k = male/female); d_l = fixed effect of birth rearing type (l = 3); bc_{jk} = interaction between j^{th} year of birth and k^{th} sex; bd_{jl} = interaction between j^{th} year of birth and l^{th} birth rearing type; cd_{kl} = interaction between k^{th} sex and l^{th} birth-rearing type; bcd_{jkl} = interaction between j^{th} year, k^{th} sex and l^{th} birth-rearing type; $G_{\mathrm{Pr}\,P}$ = fixed effect of genotype group (Analysis 1, 2, and 3 PrP = 9, 4, and 3, respectively); f_m = age at scanning as a covariate (not needed for eight-week weight) of the animal m; z_m = random effect of animal m; x_n = random maternal additive genetic effect of the n^{th} dam; w_n = the random maternal permanent environmental effect of the n^{th} dam; v_{nj} = the random maternal temporary environmental effect of the n^{th} dam in the j^{th} year; $e_{ijklmn\,\mathrm{Pr}\,P}$ = random environmental effect.

The analyses were run using ASReml (Gilmour *et al*, 2002) for all four traits. Convergence of logL was reached for each analysis and t-tests were carried out to determine the significance of differences between all possible pairwise comparisons of PrP genotype groups. The critical probability was $P \leq 0.05$, and Bonferroni corrections were also applied to Analyses 2 and 3. They were calculated as 0.0125 ($P<0.05/4$) for Analysis 2 (genotype risk groups) and 0.0166 ($P<0.05/3$) for Analysis 3 (allele analysis).

11.3 RESULTS

11.3.1 Estimation of gene and allele frequencies

All ten of the possible genotypes from four alleles (namely AHQ, ARQ, ARR, and VRQ) were observed. The ARR allele was most common (35.8 %), followed by ARQ (31.4 %), AHQ (27.8 %), and VRQ (5.0 %) as shown in Figure 11.1

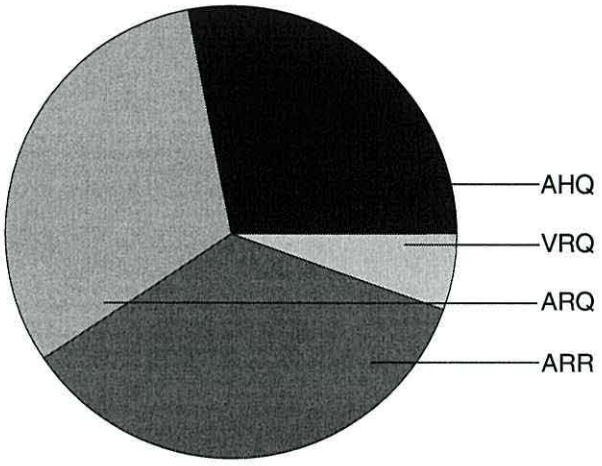


Figure 11.1 Overall proportion of alleles ARR, ARQ, AHQ and VRQ found in the CAMDA flock

Overall, the most common genotype was ARR/ARQ (24.2 %), followed by ARR/AHQ (23.4 %), AHQ/ARQ (17.1 %), ARR/ARR (10.4 %), ARQ/ARQ (9.0 %), AHQ/AHQ (6.3 %). The less common genotypes contained the VRQ allele and were ARQ/VRQ (3.6 %), ARR/VRQ (3.3 %), AHQ/VRQ (2.5 %), and VRQ/VRQ (0.3 %) (See Figure 11.2).

There has been a change in allele proportions since selection started in 2001 for resistant genotypes (Table 11.5). The ARR allele increased from 24.4 % in 2001 to 48.6 % in 2004, whereas the other alleles decreased. Similarly, the most resistant genotypes those containing the ARR allele (NSP groups 1 & 2) increased in frequency and the most susceptible those containing the VRQ allele (NSP groups 4&5) decreased in frequency in the same years (Table 11.5).

Table 11. 5 Percentage of alleles and genotypes present during years 2001 to 2004 in the CAMDA flock.

	Alleles (%)				NSP genotype groups (%)		
Year of birth	ARR	AHQ	ARQ	VRQ	1&2	3	4&5
2001	24.4	36.4	30.0	9.2	40.85	42.25	16.89
2002	43.8	29.2	26.4	0.7	73.62	25	1.39
2003	48.0	19.1	32.6	0.3	73.83	25.51	0.67
2004	48.6	25.3	24.0	2.0	79.64	16.28	4.06

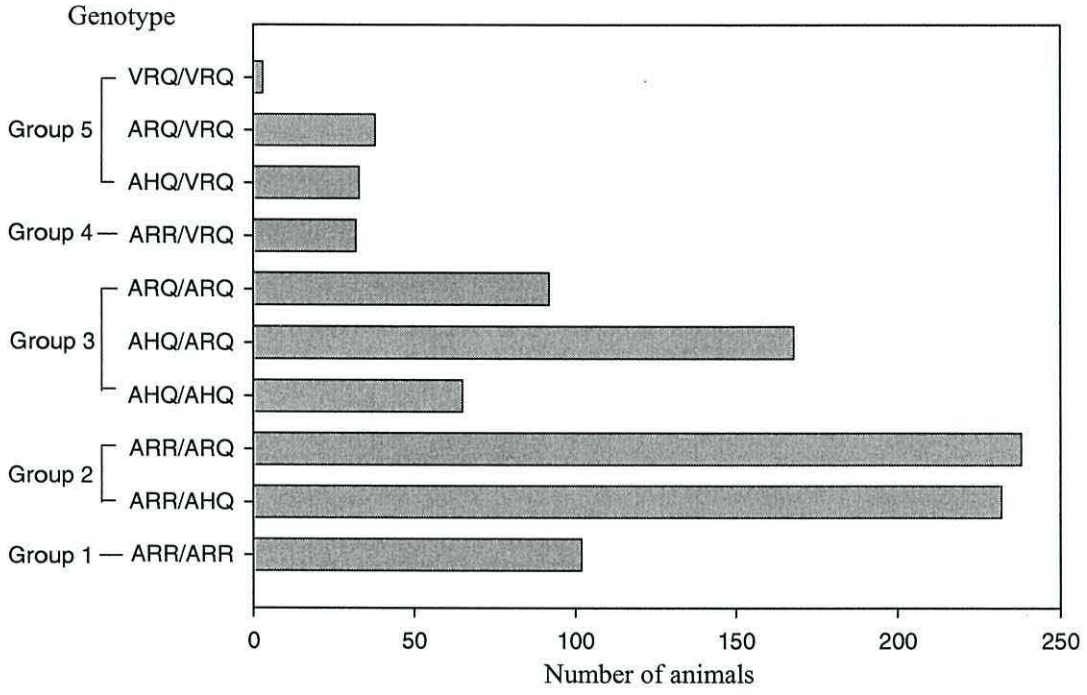


Figure 11.2 Overall number of animals in each genotype group

11.3.2 PrP genotypes and their association with growth and carcass traits

Analysis 1. t-values obtained from Analysis 1 are shown in Tables 11.6 and 11.7. There were no significant differences between genotypes in EWW or FD. However, some pairwise comparisons were significant for traits SW and MD. For SW there were significant differences between AHQ homozygotes and all genotypes containing the ARR allele. There were also significant differences between ARQ/VRQ with all other genotypes except AHQ/AHQ and AHQ/VRQ. For MD there were significant differences between ARQ/VRQ and all other genotypes except AHQ/AHQ, ARR homozygotes and both ARR/ARQ and ARR/VRQ, AHQ homozygotes and both ARR/AHQ and ARR/VRQ, and ARQ

homozygotes and ARR/ARQ. It should be noted that there were relatively few animals of the AHQ/AHQ and VRQ-containing genotypes.

Table 11. 6 Analysis 1: t values from comparisons between genotypes for eight-week weight (below the diagonal), and scan weight (above the diagonal).

Genotype	ARR/ ARR	ARR/ AHQ	ARR/ ARQ	AHQ/ AHQ	AHQ/ ARQ	ARQ/ ARQ	ARR/ VRQ	AHQ/ VRQ	ARQ/ VRQ
ARR/ARR		0.05	0.30	**2.33**	0.99	0.71	0.46	0.47	**2.84**
ARR/AHQ	0.71		0.10	**2.48**	1.00	0.62	0.61	0.39	**2.86**
ARR/ARQ	0.06	0.97		**2.36**	0.92	0.58	0.66	0.36	**2.86**
AHQ/AHQ	1.09	0.68	1.29		1.73	1.50	**2.09**	0.93	1.18
AHQ/ARQ	0.53	0.15	0.75	0.76		0.09	1.08	0.01	**2.44**
ARQ/ARQ	0.12	0.52	0.20	0.97	0.39		0.92	0.05	**2.34**
ARR/VRQ	0.93	1.46	0.97	1.70	1.35	1.01		0.71	**2.71**
AHQ/VRQ	0.66	1.11	0.67	1.40	1.02	0.73	0.16		1.73
ARQ/VRQ	1.05	0.68	1.19	0.13	0.76	0.96	1.64	1.38	

values significant at $P \leq 0.05$ are in bold

Table 11.7 Analysis 1: t values from comparisons between genotypes for muscle depth (below the diagonal), and fat depth (above the diagonal).

Genotype	ARR/ ARR	ARR/ AHQ	ARR/ ARQ	AHQ/ AHQ	AHQ/ ARQ	ARQ/ ARQ	ARR/ VRQ	AHQ/ VRQ	ARQ/ VRQ
ARR/ARR		1.19	0.91	0.17	1.02	0.42	0.19	-1.07	-0.33
ARR/AHQ	0.59		-0.37	-0.66	-0.04	-0.46	-0.47	-1.64	-0.89
ARR/ARQ	**2.05**	-0.55		-0.44	0.29	-0.24	-0.30	-1.51	-0.76
AHQ/AHQ	-0.38	**-2.20**	-1.85		0.62	0.19	0.04	-1.13	-0.42
AHQ/ARQ	1.76	-0.51	-0.03	1.82		-0.43	-0.44	-1.62	-0.88
ARQ/ARQ	1.74	-0.35	**-2.14**	1.52	-0.12		-0.12	-1.28	-0.59
ARR/VRQ	**2.01**	0.76	1.01	**2.07**	0.99	0.97		-1.06	-0.41
AHQ/VRQ	0.82	-0.21	-0.02	1.01	-0.01	0.05	-0.66		0.61
ARQ/VRQ	**-2.09**	**-3.32**	**-3.15**	-1.71	**-3.12**	**-2.86**	**-3.21**	**-2.26**	

values significant at $P \leq 0.05$ are in bold

Analysis 2. Trait data for all risk groups appeared to be normally distributed (Figures F.1 to F.4 in Appendix). Group 2 had the greatest number of animals and Group 4 had the fewest. The descriptive statistics for weight and carcass traits of the different genotypes in Table 11.3 show that the highest mean values for eight-week weight, scan weight, and muscle depth were in Group 1 (most resistant genotype, ARR/ARR), and lowest mean values were in Group 4 (most susceptible, VRQ-containing genotypes). Group 4 had the highest mean value for fat depth and the lowest mean values were observed in Groups 1 and 2. The results of t-tests for differences between the genotype groups for weight and carcass traits are shown in Table 11.8 and Table 11.9 below. With the exception of one result, it was observed that there were no significant differences between

the four risk groups. The significant difference was found between Group 1 and 2 for muscle depth.

Table 11.8 t-values from comparisons between genotype risk groups for eight-week weight (below the diagonal) and scan weight (above the diagonal) with degrees of freedom in parentheses.

	1		2		3		4	
1			1.23 (422)	NS	0.79 (266)	NS	0.17 (122)	NS
2	1.00 (561)	NS			0.41 (430)	NS	1.13 (386)	NS
3	0.50 (413)	NS	0.61 (774)	NS			0.89 (230)	NS
4	0.13 (193)	NS	1.09 (554)	NS	0.69 (406)	NS		

Table 11. 9 t-values from comparisons between genotype risk groups for muscle depth (below the diagonal) and fat depth (above the diagonal) with degrees of freedom in parentheses.

	1		2		3		4	
1			1.19 (403)	NS	1.38 (255)	NS	0.17 (118)	NS
2	**2.33** (403)	**S***			0.52 (504)	NS	1.09 (367)	NS
3	1.67 (254)	NS	0.59 (503)	NS			1.38 (219)	NS
4	0.89 (118)	NS	0.67 (367)	NS	0.33 (218)	NS		

S* Significant at both $P \leq 0.05$ and $P \leq 0.016$ (Bonferroni correction)

Analysis 3. There were no significant differences in traits EWW and FD between allele categories (Table 11.10).

Table 11.10 t-values from comparisons between genetic groups of Analysis 3

		EWW		SW		MD		FD	
Allele	Copies of allele	T value (df)		T value (df)		T value (df)		T value	
ARR	2 vs 1	0.22 (593)	NS	0.22 (460)	NS	**2.65 (420)**	**S***	1.00 (420)	NS
	2 vs 0	0.66 (477)	NS	1.78 (292)	NS	1.50 (279)	NS	0.85 (280)	NS
	1 vs 0	0.77 (870)	NS	**2.49 (574)**	**S***	1.26 (545)	NS	0.03 (546)	NS
AHQ	2 vs 1	0.86 (476)	NS	**2.29 (321)**	**S**	**2.13 (303)**	**S**	0.57 (304)	NS
	2 vs 0	1.27 (552)	NS	**2.29 (366)**	**S**	1.42 (349)	NS	0.20 (349)	NS
	1 vs 0	0.89 (908)	NS	0.13 (619)	NS	1.46 (592)	NS	0.78 (593)	NS
ARQ	2 vs 1	0.18 (521)	NS	0.02 (339)	NS	0.20 (324)	NS	0.19 (325)	NS
	2 vs 0	0.24 (533)	NS	0.21 (357)	NS	0.38 (340)	NS	0.15 (340)	NS
	1 vs 0	0.11 (882)	NS	0.38 (610)	NS	0.37 (592)	NS	0.68 (593)	NS
VRQ	1 vs 0	0.60 (969)	NS	1.18 (654)	NS	0.65 (623)	NS	0.94 (624)	NS

NS Not significant at $P \leq 0.05$ or $P \leq 0.016$ (Bonferroni correction)
S* Significant at both $P \leq 0.05$ and $P \leq 0.016$ (Bonferroni correction)
S Significant only when $P \leq 0.05$

For SW there were significant differences between ARR/XXX and XXX/XXX, between AHQ/AHQ and AHQ/XXX, and between AHQ/AHQ and XXX/XXX. However, the latter two comparisons were not significant when Bonferroni corrections were used. For MD there was a significant difference between ARR/ARR and ARR/XXX and between AHQ/AHQ and AHQ/XXX, but again the latter comparison was not significant with use of Bonferroni correction (Table 11.10).

11.4 Discussion

11.4.1 PrP allele / genotype frequencies

As previously found by Lonyong *et al.* (2004) four alleles were present in the CAMDA flock, namely AHQ, ARQ, ARR and VRQ, and these gave rise to ten genotypes covering all the five risk categories designated by the NSP. The allele frequencies were similar to that found by Roden *et al.* (2006) in the Welsh Mountain breed, using a sample size of over 96,000 animals tested during 2001 to 2003, and by Eglin *et al.* (2005). The ARH allele was reported in both studies (Eglin *et al*, 2005) but was only present in 0.1 % of the sample, thus indicating its rarity in the Welsh Mountain breed.

Eglin *et al.* (2005) reported considerable variation in the distribution of NSP risk groups within and between sectors of the sheep industry. It has been reported that hill breeds tend to have a lower proportion of NSP group 1 genotypes, and a greater proportion of group 3 genotypes, than to non-hill breeds. In the CAMDA flock the proportions in NSP groups 1, 2, and 3 were 10.4 %, 47.6 %, and 32.3 %. The proportion in NSP group 1 was lower than the average across hill breeds of 22.9 % (Eglin *et al*, 2005). The proportion of animals in NSP group 2 was within the range observed by Eglin *et al.* (2005) and above the average frequency of 40.6 % across all 38 breeds studied. Hill breeds generally have high frequencies of ARQ and AHQ alleles, and hence have many animals in NSP groups 3 and 2. Proportions in NSP groups 4 and 5 were low, with values of 3.3 % and 6.4 % respectively; and in general NSP group 5 tends to have a proportion of less than 10 % in most breeds (Eglin *et al*, 2005).

After the first genotyping in 2001, the CAMDA group carried out selective breeding and culling in an attempt to improve the genetic resistance of the flock to scrapie. Thus, it was expected that within the following years there would be an increase in the allele conferring most resistance (ARR) and a decrease in the allele that confers least resistance (VRQ). Lonyong (2003) examined the impact of selecting resistant rams to upgrade the flock and the number of generations it would take for a flock to become fully resistant, and found that the initial PrP genotype frequencies were a determining factor. Results from lambs born in years 2001 to 2004 show that initially the frequencies of resistant genotypes were fairly low (40.9 % of animals were in NSP groups 1 and 2). However, in the years following, the frequencies of these genotypes increased considerably and comparisons with NSP results of Welsh Mountain ram lambs perhaps show the CAMDA flock to have frequencies of resistant genotypes higher than average, and frequencies of susceptible genotypes (NSP groups 4 and 5) lower than average.

It has been well documented that there are significant differences among breeds in the genotypes that are susceptible to scrapie, depending upon which alleles are present. Studies have indicated that in breeds that carry the VRQ allele, such as the Welsh Mountain, Cheviot, Swaledale, and Shetland, scrapie occurs mostly in genotypes VRQ/VRQ and ARQ/VRQ, and rarely in AHQ/VRQ and ARR/VRQ genotypes (Dawson *et al*, 1998).

Overall the ARR allele was the most common allele, probably as a result of recent selection in the CAMDA flock. The ARR allele confers resistance. No scrapie cases have been reported in the UK in animals homozygous for ARR and the presence of the allele reduces the likelihood of scrapie when paired with other alleles (Baylis *et al*, 2004; Tongue *et al*, 2004).

The ARQ allele was the next most frequent allele, and has been reported as the most common in the UK. There have been suggestions that the ARQ allele could be ancestral as all other alleles differ from ARQ by just a single nucleotide substitution (Eglin *et al*, 2005; Elson *et al*, 1999). It has also been recorded in every sheep breed to date, with high frequencies in old breeds, such as Soays and

Icelandics. In the Suffolk, which lack the VRQ allele, the ARQ/ARQ genotype is associated with high risk of scrapie, whereas it is fairly resistant in the Cheviot, which has a larger range of genotypes (Dawson *et al*, 1998). Generally ARQ homozygotes are believed to be highly susceptible and the number of reported scrapie cases with the genotype has been similar to the number for VRQ homozygotes (Baylis *et al*, 2004). Susceptibility is reduced when ARQ is paired with ARR. Overall ARR/ARQ was the most common genotype in the CAMDA flock (24 %), as well as being reported as the most common in the UK. A small proportion (< 4 %) had the ARQ/VRQ genotype which is thought to be highly susceptible, accounting for over 50 % of the reported cases in the UK (Baylis *et al*, 2004).

The AHQ allele was also quite frequent in the CAMDA flock, and was reported as relatively abundant in hill breeds by Eglin *et al.* (2005). Animals carrying the AHQ allele have been described as at low risk in breeds where disease is linked to VRQ, but not in breeds where disease is found in ARQ/ARQ (Bossers *et al*, 2000; Dawson *et al*, 1998; Elson *et al*, 1999). AHQ is thought to confer partial resistance or to prolong the incubation period when paired with VRQ, but AHQ homozygotes are still thought to be at moderate to high risk of scrapie (Baylis *et al*, 2004), though the risk associated with AHQ is lower than that for ARQ (O'Doherty *et al*, 2002). The AHQ allele was observed mostly in the ARR/AHQ genotype, which would be expected to be quite resistant if exposed.

Genotypes with the VRQ allele are thought to have the greatest scrapie risk and were the least common in the CAMDA flock (< 10 %). ARQ/VRQ, ARH/VRQ and VRQ/VRQ are associated with greatest scrapie risk. ARR/VRQ is more resistant (Baylis *et al*, 2004), but is not recommended for breeding as it has the potential to produce risk group 5 progeny which are then at greater risk of disease if exposed to it (Dawson *et al*, 1998).

11.4.2 Association with other traits

Tranulis (2002) suggested that, given the large number of different PrP genotypes in many sheep breeds, a major association between PrP and selected

traits would be improbable. Results from this study indicate little evidence that there is any association between PrP genotype and the four traits analysed, and selection for the ARR allele did not appear to be detrimental to these traits.

In the analysis of genotypes, AHQ homozygotes had a significantly higher mean scan-weight than ARR homozygotes and heterozygous genotypes. The AHQ allele is regarded as conferring fairly high resistance; therefore, selection of genotypes carrying the allele should not be detrimental. However, ARQ/VRQ, probably the most susceptible of the genotypes analysed, had a significantly higher mean scan weight than six of the other eight genotypes. This may indicate that selecting against VRQ may decrease SW. However, there were few animals in some genotype classes, which may lead to weaknesses in data structure, so it might be sensible to treat some of the results obtained in the analysis with caution.

The descriptive statistics for risk groups prior to ASReml analysis (Table 11.3) showed that the trait means of EWW, SW, and MD were highest for Group 1 (most resistant) and lowest for Group 4 (most susceptible). However, for FD the highest mean was for Group 4, and the lowest means were for Groups 1 and 2. Similarly, the descriptive statistics for the four alleles (Table 11.4) shows that trait means of EWW, SW, and MD were highest for ARR homozygotes (most resistant) and of FD was highest for non-ARR genotypes. From these results it could be concluded that the ARR allele is in fact advantageous. However, further analysis in ASReml gave mean estimates that differed from those obtained originally (see Tables F.5 and F.6, in Appendix F) and rankings of risk groups or allele categories changed in some cases. This may indicate that the model used did not truly reflect the actual data. However, the original descriptive statistics do not account for other fixed and random effects and the model used should have disentangled any effects that are due to PrP genotype.

The use of the Bonferroni correction, which reduces the likelihood that values will be described as significant could be of questionable value in these analyses. Other authors have chosen to use Bonferroni correction in similar types of analyses (De Vries, 2004; Man *et al*, 2006; Sawalha *et al*, 2006; Vitezica *et al*,

2005). In this study the alpha level was set at 0.05, and the Bonferroni correction applied to those analyses (Analysis 2 and 3) where the number of groups being compared was small. In the use of Bonferroni correction the alpha level is adjusted downward to avoid spurious positives, reducing the chance of making a type one error by incorrectly declaring a difference, to account for the number of comparisons being performed. However, the drawback is that the chance of making a type two error increases, that no difference is declared, while there is a difference. In the genotype risk group analysis there was a significant difference at $P \leq 0.05$ between Group 1 and Group 2 for muscle depth but it was not significant when Bonferroni correction was applied. Group 1 was significantly better in the trait than Group 2, and thus selecting the more resistant genotype would not be damaging to the breeding objective of increased lean meat. As expected, a similar association was observed in the allele analysis for the ARR allele; however, the difference in MD between genotypes with one and two copies of the allele was also significant when Bonferroni correction applied. There were significant differences at $P \leq 0.05$ between AHQ/AHQ and AHQ/XXX for SW and MD and between AHQ/AHQ and XXX/XXX for SW; however, none of these differences were significant when the Bonferroni correction was applied. It should be noted that the frequency of AHQ/AHQ was fairly low.

11.4.3 Implications

It can be seen that the resistance of the CAMDA flock to scrapie is gradually increasing by selecting appropriate breeding animals. The sale of resistant rams should prove to be profitable for CAMDA as other farmers seek resistant rams in the coming years. However, the past selection in the CAMDA flock for more resistant animals as breeding animals may be a source of bias in the study described here. The selection for (primarily) rams carrying the ARR allele and against rams carrying the VRQ allele would reduce the number of animals available to select from for economically important traits. It is general practice for rams with the top EBV's to be selected for breeding. However, it may be necessary to select rams with lower EBV's if there is not a sufficient pool of high EBV rams with the desired genotype, particularly in the early years of selection.

Hence, if rams were selected with slightly lower EBV's, due to having the desired genotype, it might lead to lower EBV's from some offspring carrying the resistant alleles.

There have been concerns about the National Scrapie Plan, and about related schemes in other countries that aim to change the frequency of resistant genotypes, since recent reports of atypical scrapie cases have emerged. It has been questioned whether there should be selection for only a small number of genotypes. The resistance and susceptibility conferred by certain alleles are well understood for the conventional scrapie strain. However, this is considered as a short-term solution to the current situation, and reducing the range of variability within the sheep population could be regarded as risky in the longterm if new scrapie strains were to affect the sheep population. It is believed that different scrapie strains already exist, and could partly explain why there are differences in allele frequencies between sheep breeds (Tranulis, 2002). It has been proposed that the persistence of several alleles, such as the VRQ allele that makes carriers susceptible to conventional scrapie, has been due to opposing selective regimes of scrapie strains that occurred in the past where different alleles conferred resistance to different strains (Moum *et al*, 2005). If this were the case, it would be important to preserve diversity of PrP polymorphisms in the sheep population. In Cyprus the first case of scrapie was reported in 1985 (Toumazos, 1988) and because the majority of sheep on the island had the ARQ allele that made them vulnerable to the particular scrapie strain, the disease went out of control (Baylis, 2006). In Cyprus 80 % of the sheep are at medium to high risk due to their genotype. In the UK, 20 % of sheep have medium to high risk genotypes and the incidence of scrapie is relatively low. If a new scrapie strain was to appear, and affect animals of the currently-selected genotype, then scrapie may move faster through the national flock than new resistant alleles could be bred back into it. Also, due to the long incubation period, a new scrapie strain could be present and have spread in the sheep population and yet be undetected for some years. Baylis and McIntyre (2004) suggested that the US approach to controlling scrapie (Detwiler and Baylis, 2003), where infected or source flocks are genotyped and susceptible animals are eliminated, could be more favourable in the longterm since diversity is still preserved at a national scale. The European

Food Safety Authority (EFSA) recommended that the NSP should continue and stated that it would not be necessary for the whole national flock to be bred for resistance to be successful, but suggested preserving semen and embryos from sheep with genotypes which are being outbred (Farmers Guardian, 2006). The Semen Archive was established in 2004 to collect semen from native British sheep breeds and other mainstream breeds, so that breeding populations could be re-established if potential repercussions, such as health and production traits being compromised, occur due to selecting in favour of the ARR allele.

CHAPTER 12

General Discussion

Preparation of the datasets used in this study was quite complex and time consuming. Data editing is a necessary process, as reliable results depend upon the quality of the data submitted. For genetic studies it is highly desirable to know the history and management of the animals that are included in datasets. Original data had to be checked for completeness and validity, and cleaning and recoding were both necessary. The analyses did not use all data that were in the original database, on the basis that inclusion of unusual observations or animals might bias the results or cause complication to analyses. This was thought to be acceptable as the main aim of the study was estimation of genetic parameters rather than breeding values of animals.

For both the Welsh Mountain and Beulah Speckled Face there were many flocks in the datasets, but some had very few animals. In the Beulah dataset flock size ranged from as little as 28 animals to 2957 animals. Small-sized flocks add very little information and can complicate the analyses, so for these they could be eliminated from the datasets. However, data from small-sized flocks can be informative when there are linkages between them and other flocks (i.e. when common sires are used) as is the case for the datasets used in this study. Appendix D shows the findings of a small study, using the Beulah Speckled Face dataset for illustration purposes. The removal of small flocks (i.e. those with fewer than 150 animals) had very little effect on estimates of variance components and heritabilities for weight and ultrasonically-scanned traits.

The general aim of this study was to obtain the best possible estimates of genetic parameters by means of appropriate model choice, and the importance of different fixed and random effects was investigated in all analyses. In Chapter 5 it was shown that model choice differed for eight-week weight, scan weight and the ultrasonically-scanned traits, and this demonstrated the importance of considering each trait individually. However, the findings in Chapters 6 and 7 showed that model choices for individual traits may vary depending on the dataset being analysed. In Chapter 5,

the models with maternal effects were not significantly better than models without these effects for muscle and fat depth, and only additive maternal genetic effect was significant for scan weight. In Chapters 6 and 7 the chosen model for estimating variance components and heritabilities for eight-week weight, scan weight, and ultrasonic muscle depth was one that contained direct additive effect, additive maternal genetic effect, maternal permanent environmental effect and maternal common environmental effect. The most appropriate model for ultrasonic fat depth varied with breed, but generally it omitted one maternal random effect. A reason for the different results described in Chapters 5 and 6, both using datasets for the Welsh Mountain breed, could be that the larger dataset used in Chapter 6 may have facilitated the disentangling of maternal effects.

Direct-maternal genetic covariance was not significant when included in models for either Welsh Mountain or Beulah Speckled Face breeds. Cytoplasmic effects, investigated in Chapter 10 for the Welsh Mountain breed, were also generally not significant and it is not necessary to include them in models for estimating genetic parameters.

It was found that testing for the significance of maternal effects was important, and when maternal effects were significant and not included direct heritability estimates were considerably inflated. Chapter 9 showed that estimates from bivariate analysis of genetic, environmental and phenotypic correlations also depend upon appropriate model choice in univariate analyses. For the estimation of accurate genetic covariances and correlations for the construction of a selection index, it is important that at least the maternal genetic effect is included in the univariate and bivariate models (if maternal effects are significant for the trait), because this allows the maternal component to be separated from the direct additive component. In the construction of indices, additive direct genetic covariances and correlations are important, whereas covariances and correlations of maternal components are not.

It appears that it is more important to include an effect than to exclude an effect. It could be argued that it would not matter if unnecessary non-significant random effects were included in a model, as they should not bias estimates or reduce the accuracy of estimates. For example, in Chapter 5 estimates of genetic parameters for scan weight

could be obtained from the same model used for eight-week weight (Model 5) including maternal environmental effects, rather than the model that was found to be appropriate with fewer effects (Model 2). Permanent environmental effect of the animal was significant for all litter traits in the Welsh Mountain but was not significant for litter size traits in the Beulah Speckled Face, although it improved the model slightly (Chapter 8). This could have been due to the smaller number of records of dams with more than one parity in the Beulah dataset. Again, it can be argued that if the model was improved by the addition of permanent environmental effect there would be no problem including the term even though it was not significant. Also bivariate analysis might be simpler if some traits had the same random effects included.

The same models were generally found to be appropriate for estimating genetic parameters for eight-week weight, scan weight, muscle depth and fat depth in both breeds. Compared to the Welsh Mountain results for weight and ultrasonically-scanned traits (Chapter 6) the estimates of direct heritability were lower for all traits of the Beulah breed (Chapter 7), particularly for eight-week weight. The additive maternal genetic effect was slightly higher in the Beulah Speckled Face than the Welsh Mountain, but was not significant for fat depth. Maternal permanent and temporary environmental effects tended to be higher in the Beulah Speckled Face than in the Welsh Mountain breed. Phenotypic variances were similar in both breeds, except for scan-weight the phenotypic variance was about 4 kg greater in the Beulah Speckled Face. Maternal environmental effects were consistently more important than additive maternal genetic effect in both breeds.

Maternal effects are certainly important for eight-week weight and continue to be present at the age of scanning (20/21 weeks). This finding should also be applicable to other sheep breeds, as in the majority of UK systems that produce lambs for meat production, the lamb is reared by the ewe until very close to marketing, so maternal effects are likely to be important in traits measured during this time.

Total maternal effect (sum of genetic and environmental maternal effects) for eight-week weight, scan weight, muscle depth and fat depth contributed 36 %, 26 %, 14 % and 0.20 % respectively to the total phenotypic variance in the Welsh Mountain, and

44 %, 32 %, 19 % and 23 % respectively in the Beulah Speckled Face. The greater contribution of total maternal effect in the Beulah Speckled Face could be because twins are more common than in the Welsh Mountain breed. In both breeds, maternal effect is greater for eight-week weight than for traits measured at scanning. This was expected, as the lamb becomes more dependent upon grass and less upon milk from the dam as it grows. Maternal effects were not significant for mature weight but contributed nearly 10 % of the phenotypic variance, suggesting that there are still carry-over effects at this age. As concluded in Chapter 5 it would be advisable to analyse data using models with maternal effects included; even if any of these effects are not significant the accuracy of the parameter estimates should not be affected.

12.1 Genetic Links Between The Flocks

The datasets of the two breeds examined comprised many flocks (Welsh Mountain = 40, Beulah Speckled Face = 28). In this thesis a comparison of breeding values of animals across flocks was not made. If this had been done it would then be appropriate to investigate the connectedness of the flocks, the importance of which has been discussed by Kuehn (2005). Connectedness described by Bourdon (1997) is the degree to which data can be compared from different contemporary groups within a population due to pedigree relationships between animals of different groups. Connectedness is established through the use of common sires in several flocks, providing a basis on which non-related animals can be compared. Reliable across-flock evaluation is only attained when a sufficient level of connectedness has been achieved (Lewis *et al*, 1999). Further work could look at the level of connectedness between flocks within the two datasets.

The genetic links between flocks were determined by examining the number of sires used across flocks. For the Welsh Mountain dataset (40 flocks) 452 sires were used, 7.2 % of them in two or more flocks and representing 23.9 % of lamb records. In addition to the sharing of sires within breeding groups there were some sires shared between the CAMDA, CAMP, and Llysfasi breeding groups. CAMDA had three common sires with both the other breeding groups, CAMP and Llysfasi. CAMP and Llysfasi shared eight common sires. Within the CAMP group there were 23 common sires, and clusters of flocks tended to share rams. Within the Llysfasi group there

were 17 common sires. In some cases the number of progeny of a common sire in a flock were low (as low as 1).

For the Beulah Speckled Face dataset (28 flocks) 226 sires were used, 9.7 % of them in two or more flocks and representing 35.0 % of lamb records. Four flocks only had one shared sire, but these flocks had only participated in the sire-referencing scheme for one year.

12.2 Development of a Selection Index

12.2.1 Application of genetic parameters

The aim of this study was to obtain genetic parameters for individual measured traits and to obtain genetic, environmental and phenotypic covariances and correlations between traits. Eight traits were investigated, namely eight-week weight, scan weight, ultrasonic muscle depth, ultrasonic fat depth, litter size born, litter size reared, total litter weight, and mature size. All these traits could be incorporated into a selection index.

The Welsh hill index derived from work by Roden (1999) is quite widely used (Table 12.1). It is designed for the improvement of maternal characteristics, growth traits and carcass traits. Conington *et al.* (2001) included additional goal and selection traits (Table 12.2).

Table 12.1 Selection goals and traits included in the indices derived by Roden (1999) for use in Welsh Mountain flocks.

Goal traits	Selection traits
Lean weight (LEAN)	Scan weight, Ultrasonic muscle depth,
Fat weight (FAT)	Ultrasonic fat depth
Maternal ability (MA)	Total lamb weight
Litter size (LS) †	Litter size

† Index 2 is similar to index 1 but with litter size included

Table 12.2 Selection goals and traits included in the index derived by Conington *et al.* (2001) for use in UK hill sheep production.

Goal traits	Selection traits
Mature size	Pre-mating live weights
Longevity (age at culling/death)	Age at culling / death
Lamb loss	Lamb loss from birth to weaning
No. of lambs reared	Litter size at weaning
Maternal weaning weight	Average weight of lambs weaned
Fleece weight	Fleece weight
Lamb weaning weight	Weaning weight
Carcass conformation	Ultrasonic muscle depth,
Carcass fat depth	Ultrasonic fat depth
Carcass weight	

12.2.2 Programs to construct a selection index

Some studies have already looked in detail at deriving economic values and constructing a selection index for hill sheep (Conington *et al*, 2004). Deriving economic values is complex, and they are just as important for selection indices as estimates of genetic parameters. Time constraints in this study precluded any work on deriving economic weights and evaluating selection indices in detail, but a small study was carried out using the program RESI.

There are various programs available for calculating selection index weights and genetic gains. INDEX, a macro written by Ap Dewi (1998) using the statistical software MINITAB, employs four matrices based upon the method of Schneeberger *et al.* (1992):

1. economic values for each trait in the objectives
2. genetic variances and covariances among the selection criteria
3. genetic covariances between the traits in the objective and the selection criteria
4. phenotypic variances and covariances between the selection criteria.

Tables for these matrices are shown in Appendix G. Not all genetic (co)variances could be obtained from the analyses done in this study, for example, some of those between objectives and selection criteria (e.g. genetic covariances between fat weight and ultrasonic fat depth, Tables G.1 and G.2). Estimates could have been obtained from other literature, but there is a problem in that measurements may not exactly have been made in the same way, or different models may have been used for data

analysis. For instance, Saatci (1998) reported results for carcass fat percentage and ultrasonic fat depth, but measurements were taken at a different time in the animals' lives than in this study. Roden (1999) gives estimates taken from literature, and phenotypic variances are similar to those reported in this study, so it might have been possible to take these values.

RESI (Restricted Selection Index) is a Fortran 77 program generally used in tree breeding to compute multi-trait selection indices (Cotterill and Dean, 1990). The user can input relative economic weights or desired gains, and a Kempthorne restriction can be applied to one or more traits to limit genetic gain in the traits to zero. Heritabilities, genetic correlations between traits, phenotypic variances and phenotypic correlations between traits are also required as inputs. This program is simpler to use than INDEX because it does not require genetic covariances between objective traits and selection criteria, but a limitation is that genetic gains are given for selection criteria, and not the goal traits of the breeding objective.

The eight traits studied in the Welsh Mountain, and the seven traits studied in the Beulah Speckled Face were all considered in separate analyses using RESI. Genetic and phenotypic correlations were not available for all pair-wise combinations of traits, and where they were not known they were set at zero. The genetic and phenotypic parameters estimated in Chapters 6, 7, 8 and 9 (presented in Tables 12.3, 12.4, 12.5 and 12.6) were used to build the matrices of phenotypic and additive genetic variances and covariances required by RESI.

Table 12.3 Direct heritabilities and phenotypic variances of selection criteria in the analysis of the Welsh Mountain breed.

	EWW	SW	MD	FD	MW	LSB	LSR	LW
σ^2_p	6.560	11.510	4.630	0.640	11.680	0.226	0.212	11.180
h^2	0.180	0.250	0.240	0.210	0.520	0.129	0.085	0.110

EWW eight-week weight; SW scan weight; MD muscle depth; FD fat depth; MW mature weight; LSB litter size born; LSR litter size reared; LW litter weight; σ^2_p phenotypic variance; h^2 direct heritability.

Table 12.4 Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between selection criteria in the Welsh Mountain breed

	EWW	SW	MD	FD	MW	LSB	LSR	LW
EWW	**1.000**	0.949	0.295	0.165	0.900	0.411	0.429	0.990
SW	0.769	**1.000**	0.370	0.189	0.000	0.459	0.467	0.995
MD	0.439	0.564	**1.000**	0.164	0.000	0.212	0.233	0.773
FD	0.337	0.466	0.361	**1.000**	0.000	0.125	0.203	0.860
MW	0.491	0.000	0.000	0.000	**1.000**	0.481	0.467	0.780
LSB	0.000	0.000	0.000	0.000	0.000	**1.000**	0.993	-0.100
LSR	0.000	0.000	0.000	0.000	0.000	0.846	**1.000**	-0.390
LW	0.000	0.000	0.000	0.000	0.000	-0.338	-0.299	**1.000**

Refer to Table 12.3 for trait abbreviations. Bold type – value for both genetic and phenotypic correlations.

Table 12.5 Direct heritabilities and phenotypic variances of selection criteria in the analysis of the Beulah Speckled Face.

	EWW	SW	MD	FD	LSB	LSR	LW
σ_p^2	6.67	15.41	4.83	0.60	0.282	0.250	13.870
h^2	0.09	0.18	0.19	0.20	0.13	0.09	0.11

σ_p^2 phenotypic variance; h^2 direct heritability. Refer to Table 12.3 for trait abbreviations.

Table 12.6 Genetic correlations (above diagonal) and phenotypic correlations (below diagonal) between selection criteria in the Beulah Speckled Face breed.

	EWW	SW	MD	FD	LSB	LSR	LW
EWW	**1.000**	0.564	0.150	0.223	0.417	0.451	0.976
SW	0.711	**1.000**	0.397	0.449	0.361	0.327	0.883
MD	0.453	0.610	**1.000**	0.200	0.110	0.171	0.793
FD	0.358	0.517	0.449	**1.000**	0.020	-0.010	0.742
LSB	0.000	0.000	0.000	0.000	**1.000**	0.937	-0.066
LSR	0.000	0.000	0.000	0.000	0.746	**1.000**	0.002
LW	0.000	0.000	0.000	0.000	-0.258	-0.208	**1.000**

Refer to Table 12.3 for trait abbreviations. Values in bold type are the same for both genetic and phenotypic correlations.

Some simple analyses were done for each breed. In the first analyses all traits were initially given a relative economic weighting of zero. Separately, the weighting of each trait was increased to +1, whilst the weighting for all other traits remained at zero. However, as fat is undesirable to the consumer the weighting for fat depth was decreased to –1. In other studies the economic weight for mature size has also been given a negative value, because smaller ewes cost less to maintain and are more profitable than larger ewes (Conington *et al*, 2004), so the weighting for mature size was also decreased to –1. Analyses were also done with increases in either fat depth or mature weight restricted to zero, while weightings on other traits were increased.

A second analysis was carried out using the weightings that have been used by the CAMDA Welsh Mountain flock: 0.01, 0.15, 0.24, and 0.60 for litter size, mature

weight, maternal ability and growth rate respectively. This index seems to contradict the index weightings of Conington *et al.* (2004) as there is a positive weighting to increase mature weight. This index was not investigated in the Beulah Speckled Face because there were no records for mature weight.

The third analysis used index weightings derived by Roden (1999) for two indices produced specifically for hill flocks. Index 1 had weightings of 0.49, -1.56, 1.11 and 0.83 for scan weight, ultrasonic fat depth, ultrasonic muscle depth and maternal ability. Index 2 had weightings of 0.49, -1.56, 1.12, 0.41 and 1.80 for scan weight, ultrasonic fat depth, ultrasonic muscle depth, maternal ability and litter size.

Results for the first analysis are shown in Tables G.7 to G.12, G.15 and G.16 in Appendix G. The majority of traits were positively genetically correlated so, as would be expected, when the weighting was increased on one trait there was genetic gain in all the other traits in the index. When the weighting on fat depth and mature weight was decreased to –1 the genetic gain was negative in all the other traits (Tables G7 and G15). Consumers demand less fat on their meat, and the indices examined show that positive genetic gains can be obtained in other traits when change in fat depth is restricted to zero in the index. When the change in fat depth and mature weight was restricted to zero and the weightings were increased on the other traits, the size of the genetic gain in the other traits was generally reduced, but they remained positive (Tables G8, G9, G11, G12 and G16). Predicted responses to selection from currently-used indices for the two breeds are shown in Tables 12.7, 12.8 and 12.9.

Table 12.7 Percentage gain in selection criteria using the index employed for CAMDA flock of the Welsh Mountain breed.

INDEX	EWW	SW	MD	FD	MW	LSB	LSR	LW
1	5.10	4.21	1.55	2.84	2.52	4.93	3.39	3.31
2	6.71	2.40	1.06	1.74	3.59	7.21	5.40	4.44

INDEX 1 – uses scan weight for growth rate weighting ; INDEX 2 – uses eight-week weight for growth rate weighting.

Table 12.8 Percentage gain in selection criteria using the two indexes derived by Roden (1999) for the Welsh Mountain breed.

INDEX	EWW	SW	MD	FD	MW	LSB	LSR	LW
1	5.41	3.23	2.39	1.88	2.64	5.57	3.96	3.94
2	5.15	3.37	2.46	1.23	2.47	5.61	3.99	3.55

Table 12.9 Percentage gain in selection criteria using the two indexes derived by Roden (1999) for the Beulah Speckled Face.

INDEX	EWW	SW	MD	FD	LSB	LSR	LW
1	1.51	2.62	2.24	3.29	1.82	1.74	2.31
2	1.49	2.63	2.22	2.44	2.39	2.19	2.09

The index that was used by CAMDA does not include weightings on ultrasonically-scanned traits. In both indexes derived by Roden (1999) these traits are weighted and included, and as a result there was a greater gain in ultrasonic muscle depth and reduced increase in fat depth, than in the index that was used by CAMDA. In Index 2 (Roden, 1999) there is a greater emphasis on increasing litter size resulting in slightly higher gains in scan weight and muscle depth and reduced gains in eight-week weight, fat depth and total litter weight, than for Index 1 (Table 12.8). The negative correlation between litter size and litter weight cause litter weight to be reduced, and eight-week weight is reduced because of its extremely high correlation with litter weight. In the Beulah Speckled Face there is a similar pattern (Table 12.9). Because of the extremely high genetic correlations between litter weight and eight-week weight, scan weight and ultrasonically-scanned traits (which are questionable because there were problems with convergence and some parameters were fixed at a boundary), analyses were carried out with these correlations set at zero for the Welsh Mountain breed, and the results are shown in Tables G10 to G14. For the indexes derived by Roden (1999), the percentage gain in selection criteria are lower for all traits except fat depth in the Beulah Speckled Face than in the Welsh Mountain.

To show the response from selection in the CAMDA flock that selects upon an index Figures 12.1 to 12.4 present average estimated breeding values by year of birth for the traits eight-week weight, scan weight, muscle depth and fat depth. Eight-week weight and scan weight show a yearly increase in EBVs. However, muscle depth and fat depth do not show any trend.

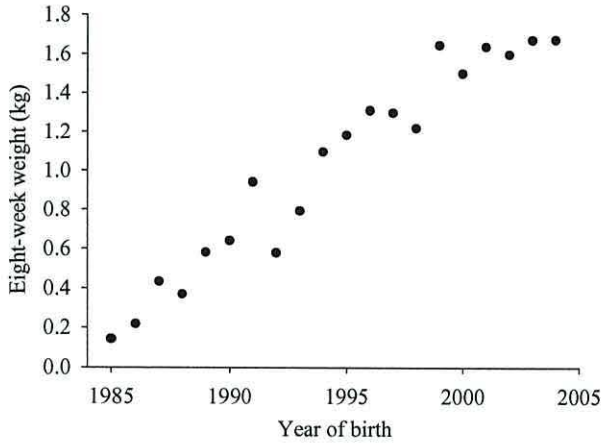


Figure 12.1 Estimated breeding values of eight-week weight (kg) according to year of birth.

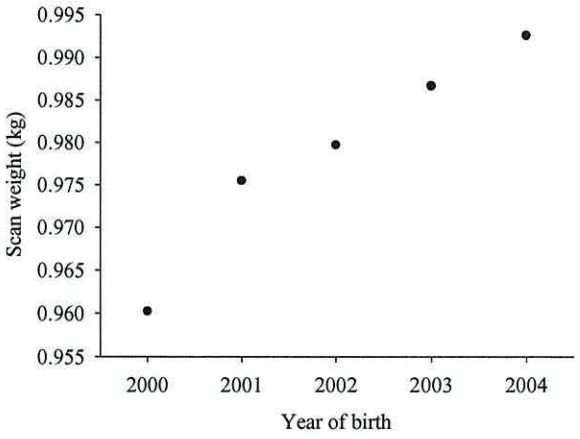
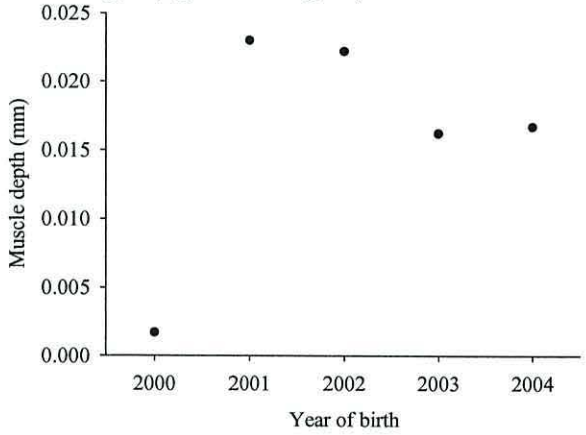
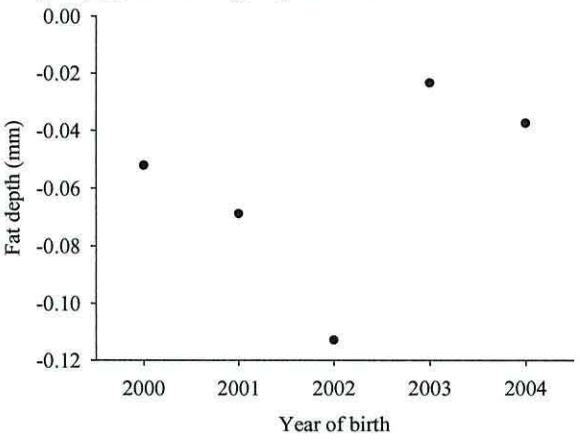


Figure 12.2 Estimated breeding values of scan weight (kg) according to year of birth.



12.3 Estimated breeding values of muscle depth (mm) according to year of birth.



12.4 Estimated breeding values of fat depth (mm) according to year of birth.

As a result of recent work investigating many disease resistance traits, selection indices incorporating these new disease traits are being established. They include measures such as fecal egg count as selection criteria because it is related to resistance to gastro-intestinal nematode infections. For these newly-incorporated traits, economic weightings need to be derived. Scrapie is a disease where PrP genotypes have been associated with resistance. However, incorporating scrapie resistance into a selection index may not be appropriate. The drive for selecting for scrapie resistance has only come about relatively recently through government involvement and the introduction of rules and schemes to eliminate 'susceptible' animals. Selection indices are constructed for the long term and selecting for scrapie resistance seems to be a short-term goal. Current rules mean that, sheep breeders taking part in schemes of the NSP have no choice but to get rid of their very susceptible animals, so there is no need to include resistance in an index. At present there is little evidence to

show any association between scrapie genotype and economically important traits, so scrapie genotype can be selected for independently. Even if scrapie resistance were included in an index, determining its economic weighting would not be easy. It would be difficult to determine, for example how much more a farmer would be willing to pay for a group 1 animal than a group 2 animal. This would depend on how abundant resistant animals are in the population. In a breed with a low number of resistant animals rams would be likely to fetch higher prices. Also, in the first few years sales of resistant animals may fetch high prices, but as the sheep population becomes more and more resistant, these animals would decline in worth over time.

Many studies investigating associations between scrapie genotype and economically important traits have used Bonferroni corrections in their analyses. This allows larger differences to be reported as not significant. The use of Bonferroni correction in some of these studies is questionable, but it produces results that are less likely to challenge the objectives of the National Scrapie Plan. Even if results from studies show that there is no association between scrapie genotype and traits of economic importance it might prove risky to reduce the range of variability within the sheep population in the long term as new scrapie strains may occur; these may have a different effect on PrP genotypes than the conventional strain, as recently observed with atypical scrapie. The finding of atypical scrapie means that the NSP is somewhat debatable and in years to come it will not be surprising if the current scheme is reversed.

12.3 FURTHER STUDY

- There was little evidence of cytoplasmic effects on weight and ultrasonically-scanned traits, but further studies could look at the cytoplasmic effects on litter traits of the Welsh Mountain. It may be better not to assign individuals to maternal lines, but to use methods based on DNA polymorphisms.

- Litter traits could be included in the further investigation of associations with scrapie genotype.

- An interesting investigation would be to look at the presence of fatty udder syndrome in sheep, a problem that has been suggested to mainly occur in cattle. Fatty udder syndrome occurs when excessive growth rates increase the fatty tissue in the udder during udder development and results in reduced lifetime milk production. This is more likely to be observed in lowland sheep with better nutrition than hill sheep. In these cases females could be genetically capable of supplying plenty of milk but do not because of over-nourishment when young.

- Other studies have included a higher number of goal traits; for example, Conington *et al.* (2004) also accounted for longevity, lamb survival, carcass conformation score and fat class, carcass weight, and fleece weight. The present study was not a comprehensive investigation of all traits, but a study of the range of traits that were available from MLC records. From the records available it would also have been possible to estimate parameters for lamb survival as a trait of the ewe. This would simply be number of lambs born (including lambs born dead, and lambs taken off the ewe) minus the number of lambs reared. Experimental flocks would have defined recording protocols for such traits, but because some of the data came from many unfamiliar, non-experimental flocks, it would have been necessary to make assumptions, which may not have reflected lamb survival in all flocks.

- Average daily weight gain is a measure of growth rate. This was calculated for animals in this study by dividing the weight traits (EWW and SW) by the age in days of the animal. This simple calculation does not take account of birth weight and therefore assumes that new-born lambs have a weight of 0 kg, but birth rearing type should account for the differences between singles and twins at birth. Heritability estimates for average daily weight gain up to eight weeks, and up to scanning age were very similar to the estimates for eight-week weight and scan weight. Eight-week weight and scan weight should be acceptable indirect measures of growth rate. However, further studies could examine the daily weight gain between eight weeks and scan age.

- This study used breeding groups that contained a number of flocks. Further work could look at the connectedness of flocks within breeding groups, as well as looking at genotype-environment interactions.

- A larger study could be carried out on the development of selection indices and their evaluation. A variety of indices could be evaluated based on alternative selection objectives, selection criteria and economic values.

- Determination of economic values for hill selection objectives under several scenarios, using a whole-farm economic model of a hill farm.

As illustrated in Figure 2.1 hill sheep are on the first stage of the stratified system. Selection decisions resulting in genetic gains in the hill sheep sector should gradually percolate down the other crossbreeding sectors. Overall, the main criteria which determine a farmer's income from sheep are (i) the number of lambs produced for slaughter, (ii) the size of the carcass and (iii) the conformation score and fat class and these are emphasised in selection indices. However, sectors differ in their selection objectives, and in the hill environment it is important to note the limits of the environment, and not to compromise animal welfare. In the hill sector ewe lambs or draft ewes are sold for cross breeding and maternal attributes are also important.

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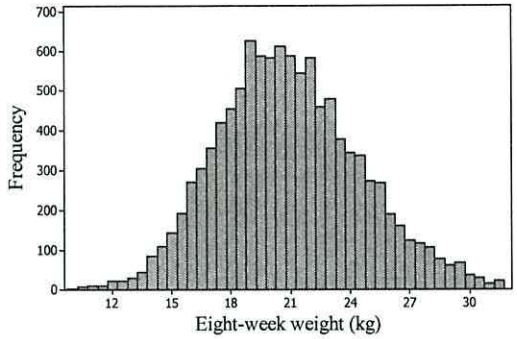
APPENDIX A

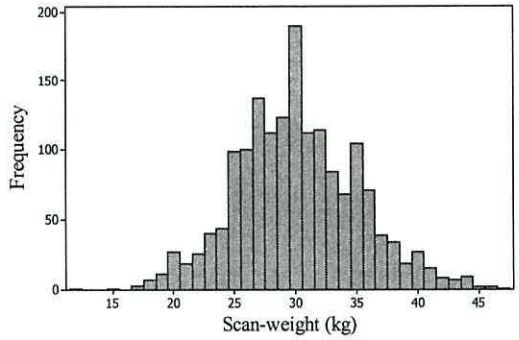
Table A.1 Reported estimates for weight and ultrasonically scanned measurements in different breeds of sheep.

Breed	Trait	h^2	m^2	Author
Beulah Speckled Face	Eight week weight Scan weight (151 days) Muscle depth Fat depth	0.17 0.16 0.18 0.17	0.05 0.17 0.07 0.18	(Hussain, *et al* 2006)
Bluefaced Leicester	Scan wt (147days) Fat depth Muscle depth	0.37 (0.05) 0.40 (0.05) 0.33 (0.05)		(van Heelsum, *et al* 1999)
Border Leicester	Live weight Fat depth Muscle depth	0.41 0.45 0.22		(Nsoso, *et al* 2004)
Coopworth	Live weight Fat depth Muscle depth	0.20 0.25 0.22		(Nsoso, *et al* 2004)
Corriedale	Live weight Fat depth Muscle depth	0.23 0.44 0.37		(Nsoso, *et al* 2004)
Corriedale	Birth weight Weaning weight 14 month weight	0.32 (0.07) 0.37 (0.10) 0.39 (0.09)	0.24 (0.06) 0.38 (0.08) 0.09 (0.03)	(Jara, *et al* 1998)
Dorset Down	Live weight Fat depth Muscle depth	0.42 0.31 0.31		(Nsoso, *et al* 2004)
Gotland breed	4 month weight	0.18	0.14	(Nasholm 2004)
Lleyn	Eight week weight	0.16		(Aslaminejad, *et al* 1998)
Rambouillet	Birth weight Weaning weight (120 d)	0.25-0.27 0.18	0.19-0.20 0.10	(Snowder, *et al* 2004)
Scottish Blackface	Birth wt Marking wt (~6 wks) Weaning wt (17 wks) Fat depth (17 wks) Muscle depth (17 wks)	0.07 (0.04) 0.02 (0.03) 0.14 (0.05) 0.27 (0.09) 0.16 (0.06)	0.06 0.16 0.09	(Conington, *et al* 1995)
Suffolk	8 week weight Scan weight (146 days) Muscle depth Fat depth	0.14 ± 0.009 0.20 ± 0.011 0.29 ± 0.010 0.27 ± 0.011	0.10 ± 0.007 0.07 ± 0.008 0.05 ± 0.009 0.07 ± 0.008	(Maniatis and Pollott 2002)
Swedish Finewool	Birth weight Weaning weight 120 day weight	0.07 0.12 0.16	0.30 0.13 0.11	(Nasholm and Danell 1996)
Welsh Mountain	Eighteen week weight Twelve week weight	0.09 0.21	 0.09	(Aslaminejad, *et al* 1999) (Saatci, *et al* 1999)

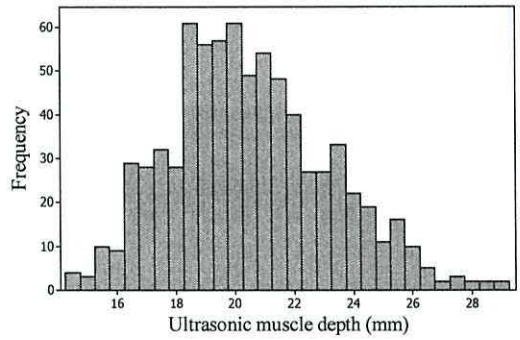
(a)



(b)



(c)



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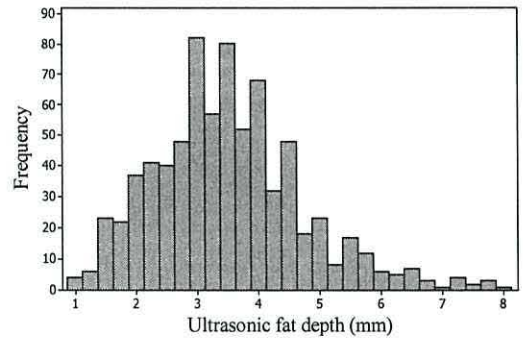
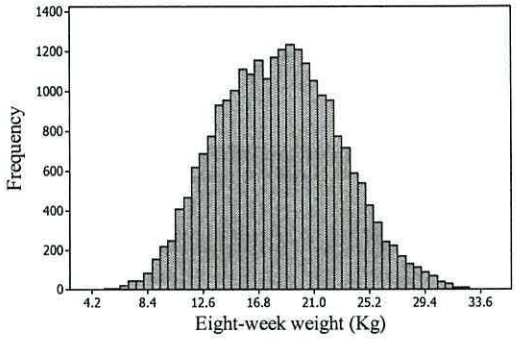
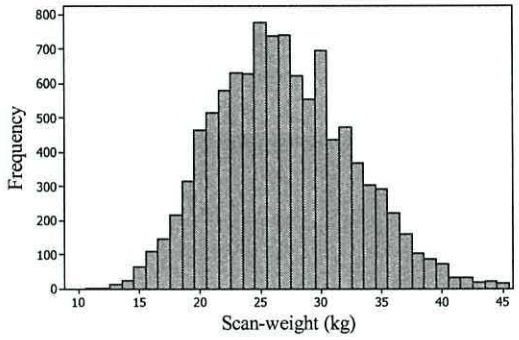


Figure A.1. Distributions of growth and ultrasonically scanned traits: eight-week weight (a), scan-weight (b), muscle depth (c) and fat depth (d).

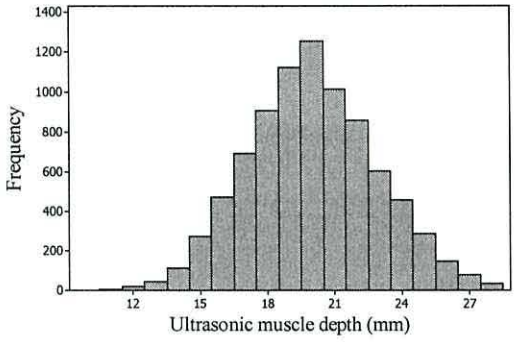
(a)



(b)



(c)



(d)

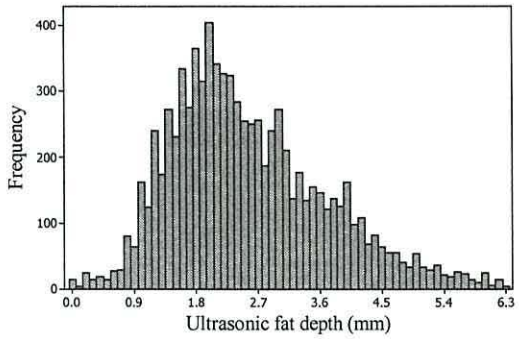


Figure B.1 Distributions of growth and ultrasonically scanned traits: eight-week weight (a), scan-weight (b), muscle depth (c) and fat depth (d).

Table B.1 Common sires used across flocks with the number of progeny in each flock of the Welsh Mountain dataset

Flock	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	All
Sire																																									
1	0	0	0	0	0	0	0	0	54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	81	0	0	0	0	0	0	0	0	0	0	0	0	135
2	0	0	0	0	0	0	0	8	31	16	0	32	0	0	22	89	0	0	0	0	0	0	0	0	0	0	0	0	0	32	0	0	0	0	0	3	15	0	0	0	248
3	0	0	0	18	0	44	0	0	0	0	0	0	0	0	0	0	27	11	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	0	0	6	0	0	132
4	0	0	0	0	0	9	0	0	0	0	0	0	0	0	0	0	8	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	26
5	0	179	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	182
6	0	118	0	0	0	0	2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	139
7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	20	0	0	0	0	0	0	0	0	0	0	0	0	0	39
8	0	0	0	0	0	0	99	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	104
9	0	0	0	0	0	66	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	68
10	0	0	0	0	0	170	0	0	0	0	0	0	0	0	0	0	0	0	22	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	192
11	0	0	0	15	0	0	5	0	12	19	0	17	14	0	0	0	0	5	14	0	0	0	0	0	0	25	0	25	0	0	0	0	0	0	0	0	26	8	10	0	195
12	0	0	0	0	0	0	0	0	31	0	0	15	59	0	0	0	0	18	11	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	12	0	7	6	6	0	172
13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17
14	0	177	14	0	0	0	0	24	0	25	19	21	16	24	25	23	0	0	0	0	0	0	0	0	0	0	23	21	17	26	25	21	27	0	0	0	0	0	22	0	550
15	0	26	52	0	0	0	263	70	31	45	49	21	52	34	54	51	18	0	0	0	0	0	0	0	0	0	43	24	25	25	67	27	24	0	0	6	12	0	0	70	0	1089
16	0	12	0	0	0	37	13	0	10	51	27	11	0	18	0	21	0	0	14	0	0	0	0	0	0	0	7	9	20	0	12	0	0	0	0	6	0	0	0	8	0	276
17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	30	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	44
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	2	0	0	0	0	0	0	0	0	0	0	0	0	18
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	17	14	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	42
20	11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	14	13	14	9	18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	79
21	24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	1	105	10	20	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	177
22	0	0	0	0	0	20	0	0	0	0	0	0	0	0	0	0	0	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	28
23	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	41	4	0	0	0	0	0	0	0	0	0	0	0	0	45
24	0	0	0	0	0	127	0	0	0	0	0	0	0	0	0	0	8	0	9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	144
25	0	0	0	0	0	214	0	0	0	0	0	0	0	0	0	0	21	0	23	6	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	7	287
26	0	0	0	0	0	37	0	0	0	0	0	0	0	0	0	0	18	0	13	5	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	0	0	0	4	86
27	0	0	0	0	0	0	211	27	16	48	28	10	24	36	28	75	0	0	0	0	0	0	0	0	0	102	73	25	0	0	0	0	0	16	0	0	18	0	34	0	771
28	0	0	0	0	12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	15	23	13	4	13	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	80
29	21	0	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	13	0	10	3	16	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	73
30	0	0	0	0	0	69	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	78
31	0	7	0	0	0	26	14	0	0	0	0	11	0	0	0	0	0	0	6	0	0	0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	0	1	0	69
32	0	0	14	0	0	0	169	0	11	11	0	18	0	0	0	0	0	0	0	0	0	0	0	0	0	9	34	0	0	0	0	0	0	0	0	4	0	0	8	0	278
33	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4	5	0	0	0	0	0	0	0	0	0	0	0	0	12
All	56	519	80	33	22	819	776	129	199	221	123	156	168	112	129	259	120	81	184	15	59	37	142	26	67	244	245	214	51	136	48	51	25	16	38	19	66	20	159	11	5875

Flocks: Plain coloured – CAMP, yellow – CAMDA, magenta – Llysfasi

Table B2. Counts, means, standard deviations for the fixed effect year of birth for traits eight-week weight, scan weight, muscle depth and fat depth

	Eight-week weight (kg)			Scan weight (kg)			Muscle depth (mm)			Fat depth (mm)		
	Count	**Mean**	**S.d**	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**
Year												
1985	580	20.39	3.92									
1986	614	19.43	3.33									
1987	645	20.24	3.35									
1988	665	19.06	3.33									
1989	530	20.54	3.49									
1990	608	20.97	3.19									
1991	546	21.42	3.49									
1992	567	18.94	2.90									
1993	522	21.94	3.32									
1994	854	19.93	3.70	49	35.38	2.95	49	22.55	1.80	49	3.95	1.07
1995	862	20.72	3.71	71	34.79	3.37	71	23.82	1.72	71	3.61	1.18
1996	951	21.10	3.98	118	31.16	3.47	118	20.98	1.88	118	2.85	0.89
1997	846	21.17	3.54									
1998	880	20.76	4.70									
1999	2105	17.05	4.23	1242	27.31	6.16	1242	20.04	2.88	1242	2.43	1.01
2000	3109	17.01	4.07	2194	27.76	5.76	2193	19.68	2.75	2192	2.94	1.07
2001	2421	17.07	4.07	1919	26.77	5.15	1072	18.42	2.42	1072	2.60	1.09
2002	2087	17.00	4.30	1621	26.67	5.18	1203	19.62	2.29	1203	3.13	1.08
2003	2714	16.61	4.71	1901	26.73	5.68	1371	20.85	2.95	1351	1.94	1.08
2004	2463	16.34	5.04	1394	23.90	5.24	1070	21.10	3.15	1071	1.87	0.70

Table B3. Counts, means, standard deviations for the fixed effects sex, dam age and birth rearing type for traits eight-week weight, scan weight, muscle depth and fat depth

	Eight-week weight (kg)			Scan weight (kg)			Muscle depth (mm)			Fat depth (mm)		
	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d
Sex												
Male	12037	19.17	4.83	4670	28.58	5.96	3418	20.09	2.95	3418	2.48	1.04
Female	12532	17.42	4.05	5839	25.34	5.03	4971	19.95	2.83	4951	2.61	1.19
Dam age												
2	5408	18.22	4.37	1795	25.00	5.59	1454	19.40	3.06	1453	2.36	1.08
3	6066	18.53	4.65	2420	26.14	5.48	2017	19.87	2.86	2003	2.45	1.10
4-6	12474	18.21	4.54	6036	27.62	5.63	4717	20.27	2.78	4714	2.67	1.14
7	621	17.67	4.43	258	25.53	5.98	201	19.67	3.12	199	2.42	1.21
BRT												
S:S	9985	19.35	4.80	4687	27.88	5.93	3667	20.55	2.85	3657	2.80	1.24
T:S	1327	17.74	4.55	513	26.69	5.69	451	20.05	2.81	451	2.44	1.04
T:T	13257	17.52	4.14	5309	25.82	5.30	4271	19.53	2.83	4261	2.36	0.99

S:S single born-single reared; T:S twin born-single reared; T:T twin born-twin reared.

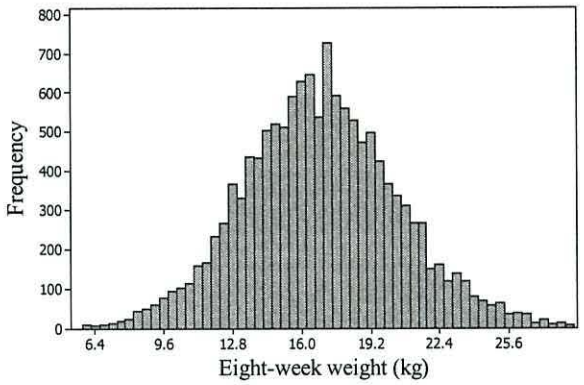
Table B4. Counts, means, standard deviations for the fixed effect flock for traits eight-week weight, scan weight, muscle depth and fat depth

	Eight-week weight (kg)			Scan weight (kg)			Muscle depth (mm)			Fat depth (mm)		
Flock	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**
1	77	19.90	2.92	60	37.29	4.67	60	23.18	2.36	60	2.45	0.84
2	11595	21.01	3.60	1617	29.42	4.72	835	21.18	3.11	836	3.00	1.03
3	114	17.44	4.18	93	28.50	4.94	93	20.57	2.23	93	3.07	1.11
4	33	14.50	3.12									
5	80	16.43	2.97	35	34.91	5.19	35	22.66	2.43	35	2.88	0.81
6	1489	18.01	4.08	1090	24.42	4.91	1081	19.05	2.76	1081	2.39	0.98
7	3425	16.91	3.85	2055	25.75	5.42	2052	19.55	2.82	2051	2.48	1.21
8	221	13.29	3.03	196	27.68	4.94	159	20.45	2.40	159	2.91	1.14
9	1547	12.13	2.32	1360	22.20	3.94	651	18.96	2.73	651	1.86	0.85
10	339	15.55	3.32	322	26.57	5.18	322	19.63	2.82	322	2.48	1.08
11	195	16.17	2.73	115	31.24	4.64	115	21.49	2.13	115	3.56	0.99
12	156	16.69	3.00	146	27.16	4.28	146	20.16	2.59	146	2.59	1.26
13	207	16.41	2.65	91	28.86	4.51	55	21.49	2.09	55	4.05	0.96

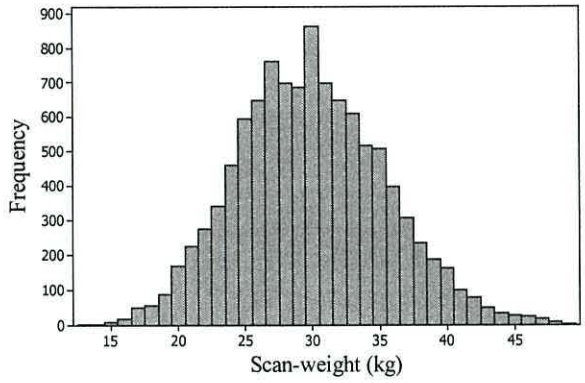
Table B.4 continued

	Eight-week weight (kg)			Scan weight (kg)			Muscle depth (mm)			Fat depth (mm)		
Flock	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**	**Count**	**Mean**	**S.d**
14	237	14.42	2.50	227	27.72	5.44	139	20.12	2.42	139	3.10	1.19
15	228	17.57	3.71	180	29.97	4.17	138	20.28	2.03	138	3.21	1.11
16	377	16.41	3.40	308	30.89	4.75	211	20.90	2.41	211	3.30	0.99
17	1220	14.12	2.99	443	23.12	4.52	440	19.15	2.70	421	1.63	0.77
18	99	15.58	2.32	15	26.93	2.63	15	19.47	1.36	15	2.55	0.80
19	313	16.77	3.24	242	26.49	4.38	237	19.35	2.23	237	2.28	0.82
20	15	17.76	3.65	10	24.20	3.65	10	19.20	2.35	10	3.03	0.75
21	91	17.90	3.71	50	33.14	4.71	50	21.02	2.71	50	2.14	0.43
22	88	19.42	2.76	80	36.78	4.66	80	22.15	2.23	80	2.10	0.62
23	142	16.24	3.44	84	29.31	5.91	84	20.41	3.52	84	1.71	0.62
24	66	17.33	3.04	44	34.81	5.86	44	20.80	2.32	44	2.35	0.70
25	96	16.02	2.58	69	34.97	5.08	69	23.30	2.42	69	2.47	0.68
26	326	15.43	2.84	269	27.98	5.47	213	20.21	2.57	213	2.79	1.07
27	245	16.03	3.66	199	27.88	5.31	134	20.41	2.81	134	2.77	0.98
28	286	13.35	2.92	234	25.95	4.69	234	19.56	2.27	234	2.75	0.93
29	84	15.23	2.09	77	29.17	3.96	77	20.25	1.98	76	3.18	1.14
30	300	15.12	2.53	278	29.17	4.53	194	23.34	2.00	194	2.93	0.97
31	76	17.37	3.18	63	30.51	4.44	63	20.03	2.34	63	3.46	1.03
32	83	15.59	1.88	79	27.49	3.48	79	19.35	2.53	79	3.29	0.93
33	25	16.47	2.28	13	31.19	3.28	13	23.46	1.66	13	3.40	0.59
34	16	15.68	1.17									
35	58	12.91	2.22	21	25.86	3.65	21	21.67	2.69	21	1.80	0.53
36	147	15.45	2.86	86	26.73	4.19	86	21.47	2.76	86	3.39	1.01
37	122	16.16	3.54	101	27.28	5.45	100	21.08	2.51	100	1.89	0.95
38	84	19.04	3.73									
39	256	17.30	2.87	152	30.02	4.19	49	19.53	2.19	49	3.51	1.11
40	11	17.63	2.69	5	37.00	3.26	5	21.40	1.34	5	3.80	0.89

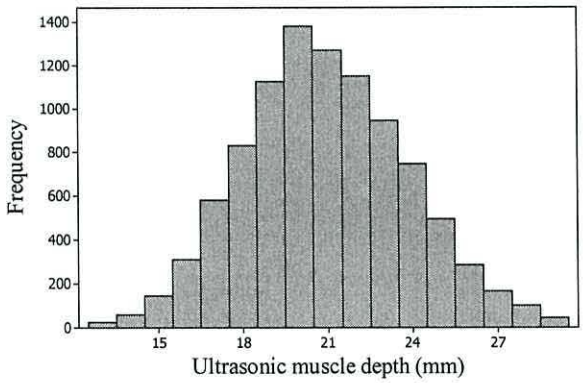
(a)



(b)



(c)



(d)

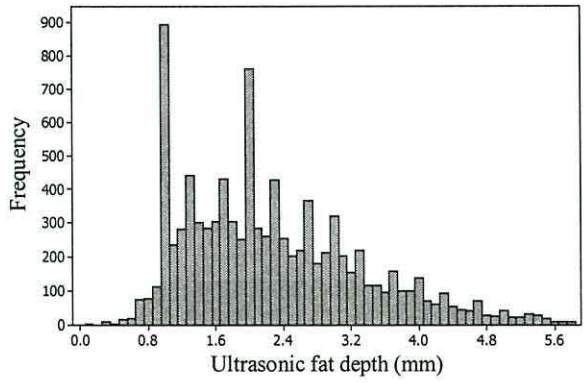


Figure C.1 Distributions of weight and ultrasonically scanned traits: eight-week weight (a), scan-weight (b), muscle depth (c) and fat depth (d).

Table C.1. Flocks in the Beulah Sire Referencing Scheme with shaded blocks representing years from 1985 to 2004 where records are available.

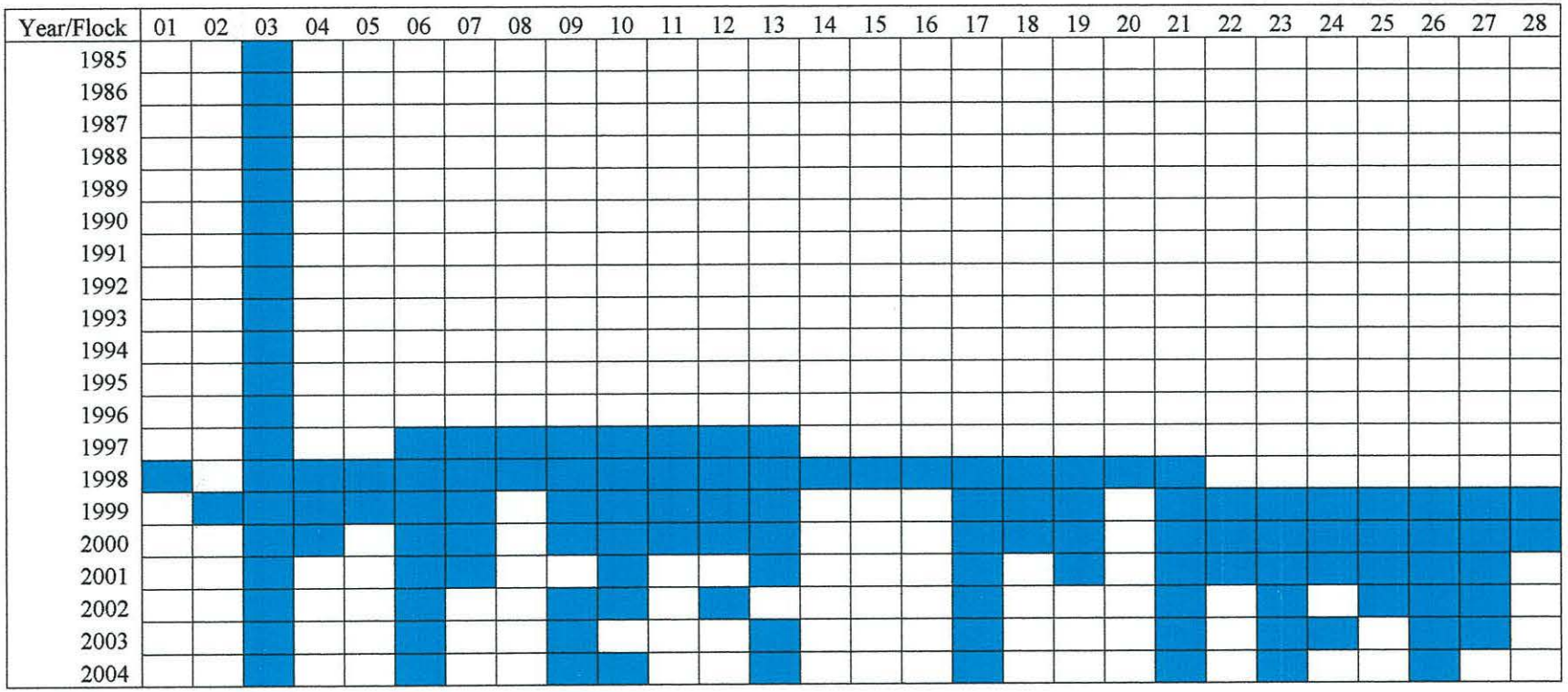


Table C.2. Counts, means and standard deviations for the fixed effect year of birth for the traits eight-week weight, scan weight, muscle depth and fat depth.

	Eight-week weight (kg)			Scan weight (kg)			Muscle depth (mm)			Fat depth (mm)		
	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d
Year												
1985	174	14.854	3.181									
1986	229	16.885	2.948									
1987	202	17.293	2.553									
1988	227	17.129	2.971									
1989	117	16.126	2.808									
1990	175	13.804	2.29									
1991	177	13.87	3.083									
1992	120	20.488	3.451				19	20.421	2.61	19	3.018	1.601
1993	139	12.219	3.244									
1994	113	16.147	3.722				15	19.533	2.232	15	1.844	0.653
1995	138	13.451	2.622	107	25.888	3.707	107	17.467	1.798	107	1.3864	0.5023
1996	132	14.205	3.262	96	28.26	4.682	96	20.208	2.147	96	2.1668	0.8718
1997	1245	17.214	3.653	1000	29.772	5.088	1000	20.81	2.454	1000	1.9957	0.9208
1998	1251	16.858	3.272	1069	29.317	5.944	1069	21.914	2.993	1069	1.9009	0.9999
1999	1674	16.077	3.381	1562	28.55	5.733	1562	20.091	2.611	1562	1.9347	0.9662
2000	1863	16.658	3.417	1701	28.957	5.45	1701	20.382	2.806	1701	2.0927	0.867
2001	1588	16.746	3.537	1405	30.498	5.314	1158	20.916	2.963	1158	2.7154	1.0928
2002	1424	17.753	3.362	1303	31.108	5.048	1069	20.992	2.981	1070	2.8725	1.1104
2003	1260	18.51	3.563	1184	30.459	5.504	878	20.773	2.684	878	2.5964	1.0652
2004	1250	17.052	3.677	1108	31.511	5.352	977	22.732	2.625	977	2.5404	1.0371

Table C.3. Counts, means and standard deviations for the fixed effects sex, dam age and birth rearing type (BRT) for the traits eight-week weight, scan weight, muscle depth and fat depth.

	Eight-week weight (kg)			Scan weight (kg)			Muscle depth (mm)			Fat depth (mm)		
	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d
Sex												
Male	6596	17.521	3.72	5045	31.532	5.72	4556	21.059	2.939	4556	2.1419	0.9973
Female	6902	16.185	3.335	5524	28.4	4.887	5095	20.794	2.836	5096	2.4081	1.1008
Dam age												
1	158	19.595	2.581	179	25.112	4.654	158	19.595	2.581	158	1.7554	0.791
2	2194	20.65	2.834	2421	29.1	5.457	2194	20.65	2.834	2194	2.2763	1.0696
3	2437	21.188	2.938	2672	30.371	5.581	2437	21.188	2.938	2437	2.3518	1.0836
4 - 6	4529	20.95	2.88	4946	30.227	5.455	4529	20.95	2.88	4530	2.2768	1.0501
7	519	16.588	3.522	351	29.507	5.251	333	20.931	2.819	333	2.1428	1.0282
BRT												
S:S	3201	18.76	3.679	2476	32.532	5.689	2266	21.822	2.904	2266	2.6816	1.1607
S:T	39	17.362	3.18	32	29.25	5.316	32	20.125	3.003	32	2.007	1.147
T:S	831	16.936	3.853	627	30.458	5.972	579	20.779	3.05	579	2.3645	1.0922
T:T	8556	16.247	3.277	6737	29.02	5.105	6101	20.641	2.792	6101	2.1556	0.9857
Tr:S	75	16.857	3.186	65	30.969	5.593	62	21.226	2.731	62	2.444	1.154
Tr:T	483	15.886	3.342	387	29.054	5.382	375	20.704	2.92	375	2.0893	0.9682
Tr:Tr	313	14.464	3.107	245	26.984	4.844	236	20.14	2.931	237	1.8318	0.9313

S:S single born-single reared; S:T single born-twin reared; T:S twin born-single reared; T:T twin born-twin reared; Tr:S triplet born-single reared; Tr:T triplet born-twin reared; Tr:Tr triplet born-triplet reared.

Table C.4. Counts, means and standard deviations for the fixed effect of flock for the traits eight-week weight, scan weight, muscle depth and fat depth.

	Eight-week weight (kg)			Scan weight (kg)			Muscle depth (mm)			Fat depth (mm)		
Flock	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d	Count	Mean	S.d
1	56	17.27	3.30	45	34.96	4.60	45	22.11	2.05	45	3.44	1.08
2	28	15.37	2.64	25	33.74	3.58	25	20.72	1.54	25	2.83	0.87
3	2957	15.71	3.53	1202	28.36	5.33	1200	19.53	2.63	1200	1.98	0.97
4	176	17.85	2.83	175	34.87	5.61	175	21.51	2.49	175	2.64	1.20
5	69	17.30	3.20	29	31.50	5.14	29	22.14	2.49	29	2.18	0.75
6	1058	18.13	3.54	988	31.47	5.81	988	23.59	2.74	988	2.92	0.88
7	312	15.29	3.32	287	30.40	4.89	287	20.58	2.40	287	1.83	0.80
8	29	16.32	2.93	27	30.09	4.11	27	20.52	2.78	27	1.47	0.59
9	439	16.03	3.07	389	31.01	5.33	389	21.89	2.87	389	1.95	0.93
10	507	18.86	3.79	311	34.96	4.66	311	23.17	2.60	311	2.56	1.11
11	109	15.97	3.67	88	26.71	4.64	88	19.40	2.70	88	1.44	0.64
12	138	17.20	3.76	128	29.70	5.47	128	21.23	2.48	128	1.70	0.81
13	2893	17.15	3.28	2663	29.14	5.21	2246	20.68	2.62	2247	2.28	1.07
14	199	18.42	3.14	159	28.92	4.18	159	19.94	2.25	159	2.25	1.00
15	50	17.24	2.45	49	31.35	5.76	49	21.47	2.61	49	2.29	0.89
16	120	18.02	2.91	77	34.04	4.07	77	20.47	2.18	77	2.87	0.96
17	202	14.32	3.81	159	24.54	5.45	132	19.74	3.02	132	1.45	0.54
18	96	15.34	3.50	73	27.42	5.33	73	19.82	3.21	73	1.48	0.44
19	169	16.55	3.92	159	29.53	5.54	159	21.08	3.03	159	2.16	1.10
20	41	17.10	3.21	38	30.82	6.52	38	22.11	2.52	38	1.58	0.84
21	955	18.43	3.50	822	29.85	5.15	658	20.65	2.75	658	1.64	0.75
22	320	14.92	3.54	270	27.86	4.83	216	19.50	2.36	216	2.29	0.89
23	632	16.03	3.38	587	28.68	5.31	586	21.17	2.59	586	1.72	0.82
24	332	18.28	3.33	303	31.40	5.05	242	20.26	2.32	242	2.82	1.00
25	456	16.58	3.61	414	30.66	5.27	414	19.91	2.43	414	2.72	0.99
26	791	16.42	3.26	748	31.12	5.09	616	20.73	2.85	616	2.91	1.06
27	309	18.52	2.89	299	31.48	5.36	239	20.02	2.38	239	2.78	0.94
28	55	17.64	3.18	55	33.22	4.53	55	22.13	2.44	55	3.37	0.89

Table C.5. Common sires used across flocks with the number of progeny in each flock (shown highlighted) of the Beulah Sire Referencing scheme.

Flock Sire	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	0	0	24	0	0	0	0	0	16	0	0	0	0	0	0	0	10	0	0	0	131	0	14	0	0	0	0	0
2	0	0	24	0	0	0	0	0	0	0	0	0	0	0	0	0	12	0	0	0	16	0	27	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	34	0	47	0
4	0	0	0	0	0	1	0	0	0	0	0	0	173	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	49	0	0	0	0	0	13	8	0	0	0	0	0	0	10	0	0	0	0	0	16	40	0	20	31	0
6	0	0	42	0	0	0	0	0	17	0	0	0	91	0	0	0	0	0	0	0	0	0	13	0	0	26	0	0
7	0	0	22	0	0	0	0	0	18	0	0	0	0	0	0	0	22	0	0	0	0	0	12	0	0	0	0	0
8	0	0	95	0	0	24	23	21	17	38	19	17	25	15	15	50	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	15	0	5	0	0	0	0	0	0	147	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	34	0	0	0	22	0	16	0	0	2	0	4	0	0	0	0	0	41	0	0	0	0	0	0	0	0
11	15	0	43	0	5	38	25	0	15	19	18	0	57	33	0	0	35	0	0	0	13	19	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0	0	0	0	0	254	0	0	0	0	0	0	0	0	0	15	0	0	0	0	0
13	0	0	0	0	0	0	0	0	0	0	0	0	177	0	0	0	0	0	0	0	0	0	54	0	0	0	0	0
14	18	17	52	37	36	13	13	4	30	25	28	12	15	7	0	0	26	19	5	0	31	20	24	25	13	0	19	29
15	0	0	21	0	11	21	0	0	0	9	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0	0
16	0	0	52	0	0	0	37	0	13	0	13	30	0	0	0	0	0	11	31	0	0	0	0	1	0	34	39	0
17	0	0	56	43	0	37	3	0	17	0	0	0	55	0	0	0	7	0	3	0	8	18	17	41	26	61	76	26
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	7	21	19	0
19	0	0	0	0	0	0	0	0	0	7	0	0	117	0	0	0	0	0	14	0	0	15	57	0	0	0	0	0
20	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0
21	0	0	15	0	0	0	28	0	0	53	0	0	23	0	0	0	20	0	15	0	8	11	0	6	139	16	37	0
22	0	0	26	0	0	35	21	0	11	43	14	12	21	0	0	0	11	24	0	0	20	19	18	0	0	0	0	0

APPENDIX D

Examining the effect of flock size and the number of animals in the dataset in the Beulah Speckled Face breed

The number of records obtained from different flocks ranged greatly, from as little as 28 animals to 2957 animals. It was thought that including flocks with few animals might complicate the analysis. Therefore, it was decided to examine whether applying a minimum threshold to the number of animals per flock affected the estimates of genetic parameters. Analysis involved data from all flocks, and the minimum thresholds shown in Table D.1. The interval between thresholds was 50 up to a threshold of 250, and then increased to 250. The number of flocks and the number of animals in each analysis are also shown are shown in Table D.1.

Table D.1 Number of flocks and animals used to estimate genetic parameters for eight-week weight (EWW), scan weight (SW), muscle depth (MD) and fat depth (FD) for the whole dataset and different subsets.

Minimum threshold	Number of flocks	Number of Animals			
		EWW	SW	MD	FD
All flocks	28	13527	10569	9651	9652
>50 animals	25	13429	10479	9561	9562
>100 animals	20	13074	10228	9310	9311
>150 animals	17	12707	9935	9017	9018
>200 animals	14	12163	9442	8524	8525
>250 animals	13	11961	9283	8392	8393
>500 animals	7	9793	7321	6605	6606
>750 animals	5	8654	6423	5708	5709
>1000 animals	3	6908	4853	4434	4435

There were some differences in variance component estimates and heritabilities among the different flock size thresholds used. It is noteworthy that the different analyses mostly contain the same populations (i.e. animals in the analysis of >1000 are also in analysis of all flocks), so estimates would be expected to be similar. As more flocks are eliminated, standard errors tend to increase. Because very small flocks might complicate procedures and add little information to the overall analysis, it may be sensible for them to be removed from a dataset. In the case of eight-week weight, scan weight, ultrasonic muscle and fat depth, the removal of flocks with fewer than 150 animals would make little difference to the overall results.

Table D.2 The estimation of variance components and genetic parameters for eight-week weight of Beulah Speckleface lambs.

Flock size					
	>0	>50	>100	>150	>200
σ^2_A	0.57	0.57	0.56	0.54	0.39
σ^2_M	0.46	0.46	0.47	0.48	0.51
σ^2_{PE}	0.76	0.76	0.76	0.76	0.80
σ^2_{CE}	1.75	1.75	1.75	1.73	1.71
σ^2_E	3.13	3.13	3.14	3.19	3.27
σ^2_P	6.669 ± 0.100	6.678 ± 0.101	6.679 ± 0.102	6.701 ± 0.103	6.682 ± 0.104
h^2	0.086 ± 0.02	0.085 ± 0.02	0.084 ± 0.02	0.080 ± 0.02	0.059 ± 0.02
m^2	0.069 ± 0.02	0.070 ± 0.02	0.071 ± 0.02	0.072 ± 0.02	0.076 ± 0.02
pe^2	0.114 ± 0.02	0.114 ± 0.02	0.114 ± 0.02	0.114 ± 0.02	0.120 ± 0.02
ce^2	0.263 ± 0.02	0.263 ± 0.02	0.261 ± 0.02	0.258 ± 0.02	0.256 ± 0.02
h^2_T	0.120	0.121	0.119	0.116	0.098

Flock size				
	>250	>500	>750	>1000
σ^2_A	0.40	0.36	0.41	0.35
σ^2_M	0.52	0.58	0.62	0.51
σ^2_{PE}	0.80	0.82	0.82	0.94
σ^2_{CE}	1.70	1.58	1.54	1.43
σ^2_E	3.28	3.33	3.38	3.52
σ^2_P	6.697 ± 0.106	6.661 ± 0.116	6.769 ± 0.126	6.755 ± 0.140
h^2	0.059 ± 0.02	0.054 ± 0.02	0.060 ± 0.02	0.052 ± 0.02
m^2	0.078 ± 0.02	0.087 ± 0.02	0.091 ± 0.02	0.075 ± 0.03
pe^2	0.120 ± 0.02	0.123 ± 0.02	0.122 ± 0.02	0.140 ± 0.03
ce^2	0.254 ± 0.02	0.237 ± 0.02	0.227 ± 0.02	0.212 ± 0.02
h^2_T	0.097	0.097	0.106	0.090

σ^2_A direct additive effect; σ^2_M maternal additive genetic variance; σ^2_{PE} maternal permanent environmental variance; σ^2_{CE} maternal temporary environmental variance; σ^2_E error variance; σ^2_P phenotypic variance, h^2 direct heritability, m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance; h^2_T total heritability.

Table D.3 The estimation of (co)variance components and genetic parameters for scan weight of Beulah Speckleface lambs.

Flock size	>0	>50	>100	>150	>200
σ^2_A	2.73	2.74	2.38	2.73	2.72
σ^2_M	1.25	1.25	1.24	1.26	1.37
σ^2_{PE}	1.15	1.15	1.15	1.16	1.12
σ^2_{CE}	2.44	2.43	2.38	2.39	2.44
σ^2_E	7.83	7.83	7.90	7.90	7.85
σ^2_P	15.41 ± 0.269	15.39 ± 0.269	15.39 ± 0.272	15.44 ± 0.276	15.49 ± 0.284
h^2	0.177 ± 0.030	0.178 ± 0.031	0.178 ± 0.031	0.178 ± 0.031	0.175 ± 0.031
m^2	0.081 ± 0.023	0.081 ± 0.025	0.081 ± 0.025	0.082 ± 0.025	0.088 ± 0.025
pe^2	0.075 ± 0.023	0.074 ± 0.023	0.075 ± 0.023	0.075 ± 0.023	0.072 ± 0.024
ce^2	0.159 ± 0.018	0.158 ± 0.018	0.154 ± 0.018	0.160 ± 0.019	0.157 ± 0.019
h^2_T	0.218	0.218	0.195	0.218	0.219

Flock size	>250	>500	>750	>1000
σ^2_A	2.73	2.85	2.68	2.58
σ^2_M	1.39	1.35	1.48	1.49
σ^2_{PE}	1.13	1.23	1.03	1.28
σ^2_{CE}	2.43	2.21	1.99	2.26
σ^2_E	7.89	7.501	7.70	7.32
σ^2_P	15.57 ± 0.288	15.13 ± 0.318	14.89 ± 0.331	14.93 ± 0.385
h^2	0.176 ± 0.031	0.188 ± 0.034	0.180 ± 0.036	0.173 ± 0.038
m^2	0.089 ± 0.026	0.089 ± 0.027	0.100 ± 0.029	0.100 ± 0.033
pe^2	0.073 ± 0.024	0.081 ± 0.025	0.069 ± 0.026	0.085 ± 0.030
ce^2	0.156 ± 0.019	0.146 ± 0.020	0.134 ± 0.021	0.152 ± 0.024
h^2_T	0.220	0.233	0.230	0.223

σ^2_A direct additive effect; σ^2_M maternal additive genetic variance; σ^2_{PE} maternal permanent environmental variance; σ^2_{CE} maternal temporary environmental variance; σ^2_E error variance; σ^2_P phenotypic variance, h^2 direct heritability, m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance; h^2_T total heritability.

Table D.4 The estimation of (co)variance components and genetic parameters for muscle depth of Beulah Speckleface lambs.

Flock size					
	>0	>50	>100	>150	>200
σ^2_A	0.90	0.90	0.88	0.87	0.86
σ^2_M	0.14	0.14	0.14	0.15	0.18
σ^2_{PE}	0.19	0.18	0.18	0.18	0.16
σ^2_{CE}	0.59	0.59	0.58	0.56	0.55
σ^2_E	3.01	3.02	3.04	3.07	3.11
σ^2_P	4.826 ± 0.084	4.831 ± 0.085	4.824 ± 0.085	4.835 ± 0.087	4.862 ± 0.089
h^2	0.186 ± 0.032	0.186 ± 0.032	0.183 ± 0.032	0.181 ± 0.032	0.177 ± 0.032
m^2	0.029 ± 0.020	0.030 ± 0.020	0.029 ± 0.020	0.030 ± 0.020	0.036 ± 0.021
pe^2	0.039 ± 0.021	0.038 ± 0.021	0.038 ± 0.021	0.038 ± 0.021	0.034 ± 0.021
ce^2	0.123 ± 0.028	0.122 ± 0.021	0.119 ± 0.021	0.117 ± 0.021	0.114 ± 0.022
h^2_T	0.201	0.200	0.198	0.196	0.196

Flock size				
	>250	>500	>750	>1000
σ^2_A	0.85	0.88	0.84	0.74
σ^2_M	0.18	0.16	0.18	0.19
σ^2_{PE}	0.17	0.18	0.15	0.15
σ^2_{CE}	0.55	0.53	0.54	0.62
σ^2_E	3.12	3.02	3.10	3.04
σ^2_P	4.856 ± 0.089	4.771 ± 0.099	4.803 ± 0.105	4.738 ± 0.117
h^2	0.175 ± 0.032	0.185 ± 0.034	0.175 ± 0.035	0.155 ± 0.038
m^2	0.036 ± 0.021	0.034 ± 0.021	0.037 ± 0.023	0.041 ± 0.026
pe^2	0.034 ± 0.022	0.038 ± 0.022	0.030 ± 0.024	0.032 ± 0.026
ce^2	0.112 ± 0.022	0.110 ± 0.024	0.112 ± 0.025	0.131 ± 0.028
h^2_T	0.193	0.202	0.193	0.176

σ^2_A direct additive effect; σ^2_M maternal additive genetic variance; σ^2_{PE} maternal permanent environmental variance; σ^2_{CE} maternal temporary environmental variance; σ^2_E error variance; σ^2_P phenotypic variance, h^2 direct heritability, m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance; h^2_T total heritability.

Table D.5 The estimation of variance components and genetic parameters for fat depth of Beulah Speckleface lambs.

Flock size					
	>0	>50	>100	>150	>200
σ^2_A	0.12	0.12	0.12	0.12	0.13
σ^2_M	0.00	0.00	0.00	0.00	0.00
σ^2_{PE}	0.06	0.06	0.06	0.06	0.06
σ^2_{CE}	0.07	0.07	0.07	0.07	0.07
σ^2_E	0.34	0.34	0.34	0.34	0.33
σ^2_P	0.597 ± 0.012	0.597 ± 0.012	0.596 ± 0.011	0.601 ± 0.011	0.592 ± 0.011
h^2	0.204 ± 0.032	0.204 ± 0.032	0.206 ± 0.032	0.207 ± 0.032	0.211 ± 0.032
m^2	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000	0.000 ± 0.000
pe^2	0.108 ± 0.017	0.108 ± 0.017	0.106 ± 0.017	0.108 ± 0.017	0.108 ± 0.017
ce^2	0.119 ± 0.021	0.120 ± 0.021	0.122 ± 0.021	0.123 ± 0.021	0.126 ± 0.022
h^2_T	0.122	0.122	0.123	0.125	0.125

Flock size				
	>250	>500	>750	>1000
σ^2_A	0.13	0.13	0.14	0.13
σ^2_M	0.00	0.00	0.00	0.00
σ^2_{PE}	0.65	0.65	0.07	0.07
σ^2_{CE}	0.75	0.76	0.07	0.08
σ^2_E	0.33	0.30	0.30	0.28
σ^2_P	0.598 ± 0.011	0.571 ± 0.012	0.571 ± 0.013	0.557 ± 0.015
h^2	0.212 ± 0.032	0.226 ± 0.035	0.244 ± 0.040	0.239 ± 0.044
m^2	0.000 ± 0.000	0.000 ± 0.000	0.001 ± 0.017	0.002 ± 0.018
pe^2	0.110 ± 0.017	0.114 ± 0.019	0.116 ± 0.023	0.119 ± 0.025
ce^2	0.125 ± 0.022	0.132 ± 0.023	0.116 ± 0.024	0.136 ± 0.027
h^2_T	0.126	0.129	0.140	0.134

σ^2_A direct additive effect; σ^2_M maternal additive genetic variance; σ^2_{PE} maternal permanent environmental variance; σ^2_{CE} maternal temporary environmental variance; σ^2_E error variance; σ^2_P phenotypic variance, h^2 direct heritability, m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance; h^2_T total heritability.

APPENDIX E

Table E.1 Variance components obtained from univariate analysis used in bivariate analysis of Welsh Mountain.

	σ^2_a	σ^2_m	σ^2_{pe}	σ^2_{ce}	σ^2_{pea}	σ^2_e	σ^2_p
EWW	1.208	0.360	0.414	1.568		3.006	6.56
SW	2.874	0.553	0.844	1.577		5.690	11.51
MD	1.125	0.101	0.394	0.156		2.845	4.63
FD	0.137	0.029		0.101		0.374	0.64
MW	6.130					5.553	11.68
LSB	0.029				0.018	0.178	0.226
LSR	0.018				0.015	0.178	0.212
LW	1.230				0.846	9.100	11.18

EWW eight week weight; SW scan weight; MD muscle depth; FD fat depth; MW mature weight; LSB litter size born; LSR litter size reared; LW litter weight; σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal temporary environmental variance; σ^2_{pea} permanent environmental variance of the animal; σ^2_e error variance; σ^2_p phenotypic variance.

Table E.2. Variance components obtained from univariate analysis used in bivariate analysis of Beulah Speckled face.

	σ^2_a	σ^2_m	σ^2_{pe}	σ^2_{ce}	σ^2_{pea}	σ^2_e	σ^2_p
EWW	0.572	0.461	0.758	1.753		3.125	6.67
SW	2.732	1.253	1.148	2.443		7.830	15.41
MD	0.897	0.142	0.186	0.593		3.008	4.83
FD	0.122		0.064	0.071		0.340	0.60
LSB	0.036					0.245	0.282
LSR	0.019					0.231	0.250
LW	1.372				1.39	11.107	11.11

See Table E.1 for definition of abbreviations.

Table E.3. (Co)variance components for bivariate analysis of growth and ultrasonically scanned traits of the Welsh Mountain.

TRAIT 1 TRAIT 2	EWW SW	EWW MD	EWW FD	SW MD	SW FD	MD FD	EWW MW
σ^2_p T1	6.551	6.548	6.551	11.500	11.460	4.656	6.540
σ^2_p T2	13.270	4.912	0.667	4.729	0.647	0.642	12.42
σ^2_p T1/T2	7.172	2.491	0.788	4.155	1.269	0.625	4.427
σ^2_e T1	3.045	3.034	3.041	5.705	5.666	2.712	3.039
σ^2_e T1/T2	2.870	1.096	0.271	2.180	0.711	0.336	1.807
σ^2_e T2	6.668	2.829	0.387	2.766	0.385	0.372	5.923
σ^2_a T1	1.132	1.152	1.136	2.787	2.859	1.359	1.305
σ^2_a T1/T2	1.745	0.372	0.067	0.719	0.118	0.073	2.620
σ^2_a T2	2.985	1.384	0.142	1.354	0.136	0.146	6.502
σ^2_{am} T1	0.065	0.056	0.065	0.083	0.010	-0.258	
σ^2_m T1 σ^2_a T2	0.097	0.098	0.004	0.140	-0.004	0.005	

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TRAIT 1 TRAIT 2	EWW SW	EWW MD	EWW FD	SW MD	SW FD	MD FD	EWW MW
σ^2_m T1	0.340	0.334	0.370	0.537	0.633	0.283	0.299
σ^2_m T2 σ^2_a T1	-0.057	-0.060	0.025	0.066	0.031	0.045	
σ^2_{am} T2	-0.074	-0.294	-0.006	-0.233	0.000	-0.009	
σ^2_m T1/T2	0.544	0.065	0.103	0.040	0.131	0.035	
σ^2_m T2	1.026	0.264	0.037	0.200	0.028	0.035	
σ^2_{pe} T1	0.402	0.404	0.345	0.807	0.446	0.112	0.410
σ^2_{pe} T1/T2	0.486	0.275		0.427			
σ^2_{pe} T2	0.598	0.191		0.231			
σ^2_{ce} T1	1.566	1.568	1.594	1.579	1.847	0.447	1.489
σ^2_{ce} T1/T2	1.487	0.645	0.318	0.584	0.282	0.131	
σ^2_{ce} T2	2.064	0.537	0.106	0.412	0.098	0.098	

See Table E.1 for definition of abbreviations. T1 trait 1; T2 trait 2.

Table E.4. (Co)variance components for bivariate analysis of litter traits of the Welsh Mountain.

TRAIT 1 TRAIT 2	LSB LSR	LSB LW	LSR LW
σ^2_p T1	0.224	0.223	0.210
σ^2_p T2	0.211	11.78	11.61
σ^2_p T1/T2	0.184	-0.485	-0.207
σ^2_e T1	0.176	0.176	0.177
σ^2_e T1/T2	0.144	-0.444	-0.216
σ^2_e T2	0.177	9.789	9.636
σ^2_a T1	0.028	0.028	0.017
σ^2_a T1/T2	0.022	-0.018	-0.006
σ^2_a T2	0.018	1.186	1.200
σ^2_{pea} T1	0.019	0.019	0.016
σ^2_{pea} T1/T2	0.017	-0.023	0.015
σ^2_{pea} T2	0.016	0.810	0.769

See Table E.1 for definition of abbreviations. T1 trait 1; T2 trait 2.

Table E.5. (Co)variance components for bivariate analysis of growth, ultrasonically scanned traits and litter traits of the Welsh Mountain.

TRAIT 1 TRAIT 2	LSB MW	LSB EWW	LSB SW	LSB MD	LSB FD	LSR MW	LSR EWW
σ^2_p T1	0.224	0.224	0.224	0.224	0.223	0.211	0.211
σ^2_p T2	11.87	6.605	11.58	4.419	0.641	11.82	6.606
σ^2_p T1/T2	0.211	0.077	0.130	0.037	0.008	0.158	0.063
σ^2_e T1	0.176	0.176	0.176	0.176	0.176	0.178	0.178
σ^2_e T1/T2	0.00	0.00	0.00	0.00	0.00	0.00	0.00
σ^2_e T2	5.237	3.006	5.690	2.845	0.375	5.303	3.006
σ^2_a T1	0.029	0.028	0.029	0.028	0.028	0.018	0.017
σ^2_a T1/T2	0.211	0.076	0.132	0.037	0.008	0.158	0.063
σ^2_a T2	6.630	1.232	2.874	1.107	0.136	6.517	1.239
σ^2_{pea} T1	0.018	0.019	0.019	0.019	0.019	0.015	0.015
σ^2_m T2		0.662	1.244	0.181	0.029		0.660
σ^2_{pe} T2		<0.00	<0.00	0.014			<0.00B
σ^2_{ce} T2		1.704	1.778	0.472	0.101		1.701

TRAIT 1 TRAIT 2	LSR SW	LSR MD	LSR FD	LW MW	LW EWW	LW SW	LW MD	LW FD
σ^2_p T1	0.211	0.210	0.210	11.44	11.68	11.06	11.40	11.41
σ^2_p T2	11.57	4.621	0.641	11.28	6.760	10.79	4.627	0.647
σ^2_p T1/T2	0.104	0.032	0.010	1.992	3.481	1.768	1.079	0.371
σ^2_e T1	0.177	0.178	0.178	9.424	8.017	9.347	9.387	9.396
σ^2_e T1/T2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
σ^2_e T2	5.690	2.845	0.375	5.874	2.236	5.744	2.707	0.353
σ^2_a T1	0.017	0.017	0.017	1.206	3.664B	1.108	1.371	1.324
σ^2_a T1/T2	0.010	0.032	0.010	1.992	3.481B	1.768	1.079	0.371
σ^2_a T2	2.863	1.115	0.136	5.405	3.374B	2.849	1.422	0.194
σ^2_{pea} T1	0.015	0.016	0.016	0.811	0.00B	0.600	0.641	0.689
σ^2_m T2	1.241	0.181	0.030		0.00B	0.085	0.086	0.014
σ^2_{pe} T2	0.00	0.011			0.00B	0.543	0.044	
σ^2_{ce} T2	1.780	0.469	0.100		1.150	1.566	0.369	0.086

See Table E.1 for definition of abbreviations. T1 trait 1; T2 trait 2.

Table E.6. (Co)variance components for bivariate analysis of litter traits of the Beulah Speckled Face

TRAIT 1 TRAIT 2	LSB LSR	LSB LW	LSR LW
σ^2_p T1	0.285	0.285	0.250
σ^2_p T2	0.252	13.40	14.57
σ^2_p T1/T2	0.200	-0.514	-0.397
σ^2_e T1	0.247	0.247	0.231
σ^2_e T1/T2	0.175	-0.498	-0.397
σ^2_e T2	0.233	12.067	13.199
σ^2_a T1	0.037	0.037	0.019
σ^2_a T1/T2	0.025	-0.016	<0.00
σ^2_a T2	0.019	1.333	1.375
σ^2_{pea} T2		1.456	1.490

Table E.7. (Co)variance components for bivariate analysis of growth and ultrasonically scanned traits of the Beulah Speckled Face.

TRAIT 1 TRAIT 2	EWW SW	EWW MD	EWW FD	SW MD	SW FD	MD FD
σ^2_p T1	6.704	6.679	6.672	15.41	15.41	4.841
σ^2_p T2	15.86	4.925	0.604	4.893	0.601	0.595
σ^2_p T1/T2	7.328	2.597	0.719	5.296	1.574	0.763
σ^2_e T1	3.034	3.062	3.060	7.708	7.658	2.947
σ^2_e T1/T2	3.320	1.306	0.287	2.871	0.748	0.400
σ^2_e T2	8.155	3.040	0.345	2.985	0.345	0.344
σ^2_a T1	0.754	0.701	0.699	2.986	3.055	0.982
σ^2_a T1/T2	0.794	0.117	0.064	0.672	0.275	0.068
σ^2_a T2	2.627	0.881	0.119	0.959	0.123	0.116
σ^2_{am} T1	-0.312	-0.259	-0.167	-0.627	-0.271	-0.122
σ^2_m T1 σ^2_a T2	0.035	-0.057	-0.008	-0.084	-0.026	0.019
σ^2_m T1	0.781	0.659	0.467	1.737	1.083	0.193
σ^2_m T2 σ^2_a T1	-0.182	-0.080		-0.276		
σ^2_{am} T2	-0.299	-0.074		-0.111		
σ^2_m T1/T2	0.943	0.274		0.512		
σ^2_m T2	1.543	0.218		0.233		
σ^2_{pe} T1	0.725	0.779	0.868	1.191	1.435	0.238
σ^2_{pe} T1/T2	0.980	0.365	0.187	0.474	0.277	0.103
σ^2_{pe} T2	1.352	0.175	0.069	0.192	0.064	0.065
σ^2_{ce} T1	1.722	1.738	1.744	2.419	2.452	0.604
σ^2_{ce} T1/T2	1.437	0.671	0.189	1.127	0.299	0.172
σ^2_{ce} T2	2.486	0.685	0.072	0.635	0.070	0.070

Table E.8. (Co)variance components for bivariate analysis of growth, ultrasonically scanned traits and litter traits of the Beulah Speckled Face.

TRAIT 1 TRAIT 2	LSB EWW	LSB SW	LSB MD	LSB FD	LSR EWW	LSR SW
σ^2_p T1	0.282	0.282	0.281	0.282	0.251	0.250
σ^2_p T2	6.690	15.44	4.825	0.597	6.695	15.43
σ^2_p T1/T2	0.067	0.118	0.020	0.001	0.053	0.077
σ^2_e T1	0.244	0.245	0.245	0.245	2.30	0.231
σ^2_e T1/T2	0.00	0.00	0.00	0.00	0.00	0.00
σ^2_e T2	3.077	7.753	3.010	0.339	3.066	7.765
σ^2_a T1	0.038	0.037	0.036	0.037	0.020	0.019
σ^2_a T1/T2	0.067	0.118	0.020	0.001	0.053	0.077
σ^2_a T2	0.674	2.899	0.894	0.123	0.694	2.869
σ^2_{pea} T1						
σ^2_m T2	0.438	1.178	0.145		0.430	1.187
σ^2_{pe} T2	0.760	1.178	0.183	0.064	0.763	1.172
σ^2_{ce} T2	1.741	2.433	0.593	0.071	1.742	2.440

TRAIT 1 TRAIT 2	LSR MD	LSR FD	LW EWW	LW SW	LW MD	LW FD
σ^2_p T1	0.250	0.250	15.58	16.57	14.82	15.39
σ^2_p T2	4.825	0.597	5.210	12.84	5.194	0.596
σ^2_p T1/T2	0.022	<0.00	0.877	1.916	1.098	0.379
σ^2_e T1	0.232	0.232	12.583	12.553	12.559	12.446
σ^2_e T1/T2	0.00	0.00	0.00[F]	0.00[F]	0.00[F]	0.00[F]
σ^2_e T2	3.009	0.340	3.107	7.719	2.906	0.308
σ^2_a T1	0.019	0.019	1.214	1.508	1.665	2.562
σ^2_a T1/T2	0.022	<0.00	0.877[F]	1.916[F]	1.098[F]	0.623
σ^2_a T2	0.894	0.122	0.664	3.124	1.153	0.199
σ^2_{pea} T1			0.649	0.741	1.008	0.670
σ^2_m T2	0.144		0.046	0.281	0.022	0.042
σ^2_{pe} T2	0.184	0.064	0.649	0.973	0.106	
σ^2_{ce} T2	0.594	0.071	1.783	2.510	0.593	0.067

[F] Parameter fixed

Table E.9 Bivariate analysis between eight-week weigh (EWW) and scan weight (SW) of Beulah Speckled Face.

	Model 1	Model 2	Model 3	Model 4	Model 5
$\sigma^2_p EWW$	7.18 (0.12)	6.91 (0.11)	6.74 (0.11)	6.77 (0.10)	6.70 (0.10)
$\sigma^2_p SW$	5.07 (0.09)	16.27 (0.28)	15.94 (0.27)	16.02 (0.27)	15.86 (0.27)
COV_P	2.89 (0.08)	7.18 (0.28)	7.20 (0.25)	7.32 (0.26)	7.33 (0.24)
$h^2 EWW$	0.48 (0.02)	0.14 (0.03)	0.16 (0.03)	0.10 (0.03)	0.11 (0.03)
$h^2 SW$	0.33 (0.03)	0.17 (0.03)	0.19 (0.03)	0.16 (0.03)	0.17 (0.03)
r_G	0.57 (0.04)	0.58 (0.10)	0.59 (0.09)	0.54 (0.12)	0.56 (0.11)
r_E	0.43 (0.02)	0.66 (0.01)	0.66 (0.01)	0.67 (0.02)	0.67 (0.02)
r_P	0.48 (0.01)	0.68 (0.02)	0.70 (0.02)	0.70 (0.02)	0.71 (0.02)

σ^2_P phenotypic variance; h^2 direct heritability; COV_P phenotypic covariance; r_G genetic correlation; r_E residual correlation; r_P phenotypic correlation.

Table E.10. Bivariate analysis between eight-week weight (EWW) and muscle depth (MD) of the Beulah Speckled Face breed.

	Model 1	Model 2	Model 3	Model 4	Model 5
$\sigma^2_p EWW$	7.18 (0.12)	6.90 (0.11)	6.72 (0.11)	6.75 (0.10)	6.68 (0.10)
$\sigma^2_p MD$	5.07 (0.09)	4.98 (0.09)	4.93 (0.09)	4.94 (0.09)	4.93 (0.09)
COV_P	2.89 (0.08)	2.47 (0.14)	2.54 (0.12)	2.56 (0.13)	2.60 (0.12)
$h^2 EWW$	0.48 (0.02)	0.13 (0.03)	0.15 (0.03)	0.09 (0.03)	0.10 (0.03)
$h^2 MD$	0.33 (0.03)	0.19 (0.04)	0.20 (0.04)	0.18 (0.04)	0.18 (0.04)
r_G	0.57 (0.04)	0.22 (0.14)	0.24 (0.14)	0.12 (0.17)	0.15 (0.16)
r_E	0.43 (0.02)	0.45 (0.02)	0.44 (0.02)	0.43 (0.02)	0.43 (0.03)
r_P	0.48 (0.01)	0.42 (0.02)	0.44 (0.02)	0.44 (0.02)	0.45 (0.02)

See Table E.9 for definition of abbreviations

Table E.11. Bivariate analysis between eight-week weight (EWW) and fat depth (FD) of the Beulah Speckled Face breed.

	Model 1	Model 2	Model 3	Model 4	Model 5
$\sigma^2_p EWW$	7.18 (0.12)	6.91 (0.11)	6.71 (0.10)	6.74 (0.08)	6.67 (0.10)
$\sigma^2_p FD$	0.62 (0.01)	0.61 (0.01)	0.60 (0.01)	0.61 (0.01)	0.60 (0.01)
COV_P	0.79 (0.03)		0.72 (0.03)	0.69 (0.02)	0.72 (0.03)
$h^2 EWW$	0.48 (0.02)	0.13 (0.03)	0.15 (0.03)	0.07 (0.00)	0.10 (0.03)
$h^2 FD$	0.37 (0.03)	0.18 (0.03)	0.21 (0.03)	0.19 (0.00)	0.20 (0.03)
r_G	0.47 (0.04)	0.31 (0.13)	0.26 (0.13)	0.26 (0.00)	0.22 (0.15)
r_E	0.30 (0.02)	0.30 (0.02)	0.31 (0.02)	0.27 (0.02)	0.28 (0.03)
r_P	0.37 (0.01)	0.31 (0.02)	0.36 (0.01)	0.34 (0.01)	0.36 (0.01)

See Table E.9 for definition of abbreviations

Table E.12. Bivariate analysis between scan weight (SW) and muscle depth (MD) of the Beulah Speckled Face breed.

	Model 1	Model 2	Model 3	Model 4	Model 5
$\sigma^2_p SW$	16.29 (0.30)	15.68 (0.28)	15.45 (0.28)	15.51 (0.28)	15.41(0.27)
$\sigma^2_p MD$	5.03 (0.09)	4.94 (0.09)	4.90 (0.09)	4.91 (0.09)	4.89 (0.09)
COV_P	5.80 (0.14)	5.09 (0.24)	5.24 (0.21)	5.24 (0.22)	5.30 (0.21)
$h^2 SW$	0.47 (0.03)	0.20 (0.04)	0.21 (0.04)	0.19 (0.04)	0.19 (0.04)
$h^2 MD$	0.34 (0.03)	0.21 (0.04)	0.21 (0.04)	0.19 (0.04)	0.20 (0.04)
r_G	0.68 (0.03)	0.44 (0.11)	0.44 (0.10)	0.38 (0.12)	0.40 (0.12)
r_E	0.63 (0.02)	0.64 (0.02)	0.64 (0.02)	0.60 (0.02)	0.60 (0.02)
r_P	0.64 (0.01)	0.58 (0.03)	0.60 (0.02)	0.60 (0.02)	0.61 (0.02)

See Table E.9 for definition of abbreviations

Table E.13. Bivariate analysis between scan weight (SW) and fat depth (FD) of the Beulah Speckled Face breed.

	Model 1	Model 2	Model 3	Model 4	Model 5
$\sigma^2_p SW$	16.30 (0.30)	15.71 (0.29)	15.44 (0.28)	15.53 (0.20)	15.41 (0.27)
$\sigma^2_p FD$	0.62 (0.01)	0.60 (0.01)	0.60 (0.01)	0.60 (0.01)	0.60 (0.01)
COV_P	1.68 (0.05)	1.45 (0.08)	1.57 (0.05)	1.50 (0.03)	1.57 (0.05)
$h^2 SW$	0.47 (0.03)	0.21 (0.04)	0.22 (0.04)	0.19 (0.00)	0.20 (0.04)
$h^2 FD$	0.37 (0.03)	0.20 (0.03)	0.21 (0.03)	0.20 (0.00)	0.20 (0.03)
r_G	0.57 (0.04)	0.46 (0.10)	0.47 (0.10)	0.44 (0.00)	0.45 (0.10)
r_E	0.51 (0.02)	0.50 (0.02)	0.49 (0.02)	0.46 (0.02)	0.46 (0.03)
r_P	0.53 (0.01)	0.47 (0.02)	0.52 (0.01)	0.49 (0.01)	0.52 (0.01)

See Table E.9 for definition of abbreviations

Table E.14. Bivariate analysis between muscle depth (MD) and fat depth (FD) of the Beulah Speckled Face breed.

	Model 1	Model 2	Model 3	Model 4	Model 5
$\sigma^2_p MD$	4.97 (0.09)	4.86 (0.09)	4.84 (0.09)	4.84 (0.09)	4.84 (0.09)
$\sigma^2_p FD$	0.61 (0.01)	0.60 (0.01)	0.59 (0.01)	0.60 (0.01)	0.60 (0.01)
COV_P	0.80 (0.03)	0.78 (0.04)	0.76 (0.03)	0.80 (0.04)	0.76 (0.03)
$h^2 MD$	0.34 (0.03)	0.19 (0.04)	0.22 (0.04)	0.18 (0.04)	0.20 (0.04)
$h^2 FD$	0.37 (0.03)	0.17 (0.03)	0.20 (0.03)	0.17 (0.03)	0.20 (0.03)
r_G	0.52 (0.05)	0.10 (0.14)	0.23 (0.12)	0.08 (0.15)	0.20 (0.13)
r_E	0.42 (0.02)	0.46 (0.02)	0.45 (0.02)	0.41 (0.03)	0.40 (0.03)
r_P	0.46 (0.01)	0.46 (0.02)	0.45 (0.01)	0.47 (0.02)	0.45 (0.01)

See Table E.9 for definition of abbreviations

Table F.1 Estimates of variance components and genetic parameters for Welsh Mountain lambs

	EWW	SW	MD	FD
σ^2_a	1.49	3.39	0.46	0.11
σ^2_m	0.63	0.21		
σ^2_{pe}	0.32	1.65		
σ^2_{ce}	1.76			
σ^2_e	3.36	6.90	3.63	0.54
σ^2_p	7.50 ± 0.128	12.15 ± 0.53	4.10 ± 0.212	0.65 ± 0.034
h^2	0.20 ± 0.015	0.28 ± 0.088	0.11 ± 0.071	0.16 ± 0.075
m^2	0.08 ± 0.017	0.02 ± 0.040		
pe^2	0.04 ± 0.014	0.14 ± 0.041		
ce^2	0.23 ± 0.015			

σ^2_a direct additive effect; σ^2_m maternal additive genetic variance; σ^2_{pe} maternal permanent environmental variance; σ^2_{ce} maternal temporary environmental variance; σ^2_e error variance; σ^2_p phenotypic variance; h^2 direct heritability; m^2 maternal heritability; pe^2 maternal permanent environmental variance expressed as a proportion of phenotypic variance; ce^2 maternal temporary environmental variance expressed as a proportion of the phenotypic variance.

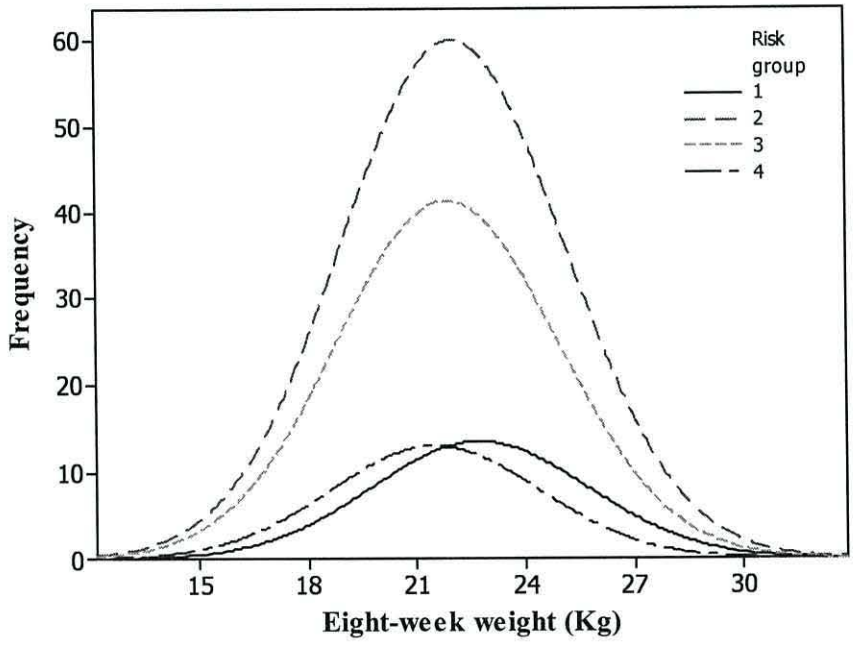

Figure F. 1 Distribution of risk groups for eight-week weight

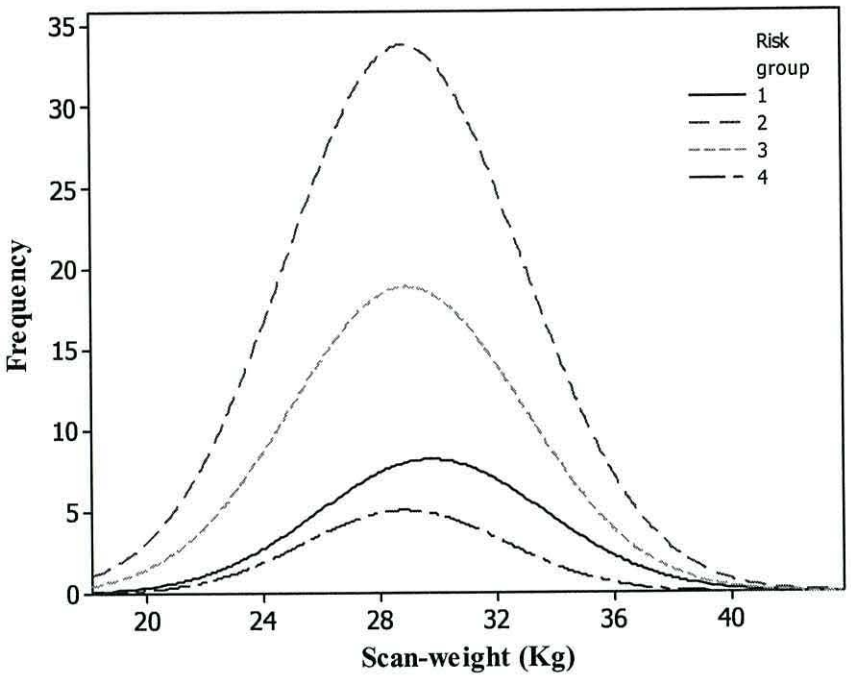

Figure F. 2 Distribution of risk groups for scan weight

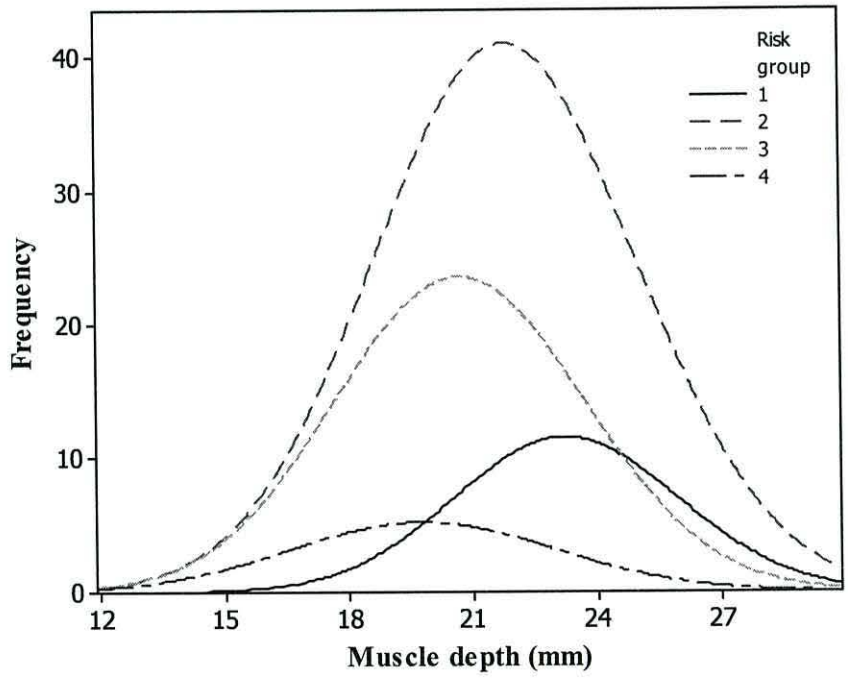

Figure F. 3 Distribution of risk groups for muscle depth

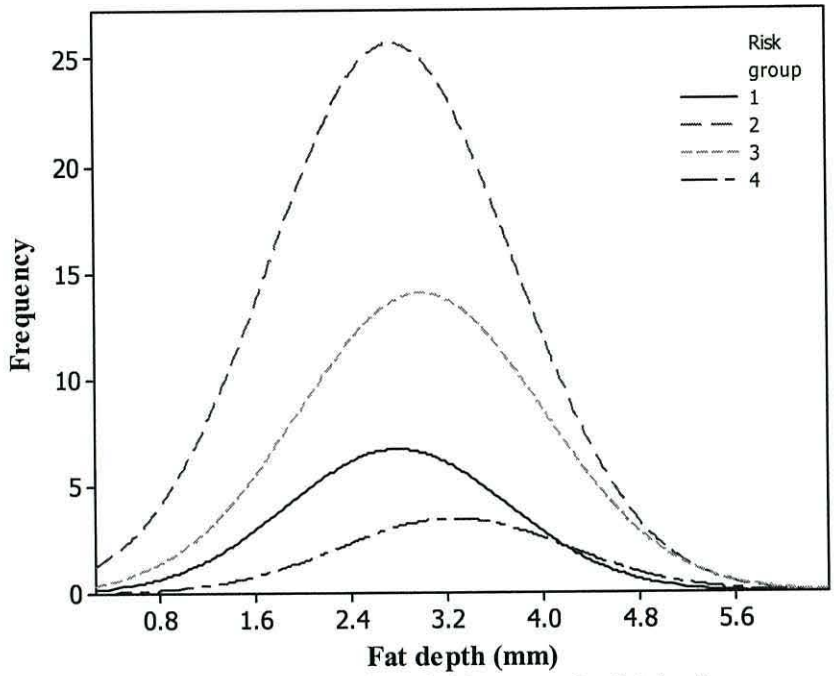

Figure F. 4 Distribution of risk groups for fat depth

Table F.2 Analysis 1: Counts, estimated means (and standard error) of analysed traits by genotype

Genotype	EWW (kg)		SW (kg)		MD (mm)		FD (mm)	
	Mean (se)	Count	Mean (se)	Count	Mean (se)	Count	Mean (se)	Count
ARR/ARR	21.14 (0.31)	101	30.17 (0.61)	80	22.45 (0.35)	78	3.18 (0.14)	78
ARR/AHQ	21.36 (0.25)	227	30.27 (0.53)	169	21.74 (0.28)	160	3.04 (0.12)	160
ARR/ARQ	21.13 (0.24)	235	30.31 (0.53)	175	21.87 (0.28)	167	3.07 (0.12)	167
AHQ/AHQ	21.60 (0.37)	61	31.80 (0.72)	35	22.63 (0.44)	31	3.15 (0.18)	31
AHQ/ARQ	21.32 (0.26)	166	30.68 (0.57)	109	21.87 (0.32)	104	3.04 (0.13)	105
ARQ/ARQ	21.19 (0.32)	87	30.63 (0.69)	44	21.92 (0.40)	43	3.11 (0.16)	43
ARR/VRQ	20.67 (0.47)	32	29.77 (0.90)	18	21.34 (0.54)	17	3.14 (0.22)	17
AHQ/VRQ	20.78 (0.52)	24	30.69 (1.13)	10	21.88 (0.69)	10	3.48 (0.27)	10
ARQ/VRQ	21.67 (0.46)	35	33.11 (1.05)	13	23.84 (0.65)	12	3.26 (0.26)	12

Table F.3 Analysis 1: t-values from comparisons between genotype risk groups for eight-week weight (below the diagonal) and scan weight (above the diagonal).

Genotype	ARR/ ARR	ARR/ AHQ	ARR/ ARQ	AHQ/ AHQ	AHQ/ ARQ	ARQ/ ARQ	ARR/ VRQ	AHQ/ VRQ	ARQ/ VRQ
ARR/ARR		0.05	0.30	**2.33**	0.99	0.71	0.46	0.47	**2.84**
ARR/AHQ	0.71		0.10	**2.48**	1.00	0.62	0.61	0.39	**2.86**
ARR/ARQ	0.06	0.97		**2.36**	0.92	0.58	0.66	0.36	**2.86**
AHQ/AHQ	1.09	0.68	1.29		1.73	1.50	**2.09**	0.93	1.18
AHQ/ARQ	0.53	0.15	0.75	0.76		0.09	1.08	0.01	**2.44**
ARQ/ARQ	0.12	0.52	0.20	0.97	0.39		0.92	0.05	**2.34**
ARR/VRQ	0.93	1.46	0.97	1.70	1.35	1.01		0.71	**2.71**
AHQ/VRQ	0.66	1.11	0.67	1.40	1.02	0.73	0.16		1.73
ARQ/VRQ	1.05	0.68	1.19	0.13	0.76	0.96	1.64	1.38	

Table F.4 Analysis 1: t-values from comparisons between genotype risk groups for muscle depth (below the diagonal) and fat depth (above the diagonal).

Genotype	ARR/ ARR	ARR/ AHQ	ARR/ ARQ	AHQ/ AHQ	AHQ/ ARQ	ARQ/ ARQ	ARR/ VRQ	AHQ/ VRQ	ARQ/ VRQ
ARR/ARR		1.19	0.91	0.17	1.02	0.42	0.19	-1.07	-0.33
ARR/AHQ	0.59		-0.37	-0.66	-0.04	-0.46	-0.47	-1.64	-0.89
ARR/ARQ	**2.05**	-0.55		-0.44	0.29	-0.24	-0.30	-1.51	-0.76
AHQ/AHQ	-0.38	**-2.20**	-1.85		0.62	0.19	0.04	-1.13	-0.42
AHQ/ARQ	1.76	-0.51	-0.03	1.82		-0.43	-0.44	-1.62	-0.88
ARQ/ARQ	1.74	-0.35	**-2.14**	1.52	-0.12		-0.12	-1.28	-0.59
ARR/VRQ	**2.01**	0.76	1.01	**2.07**	0.99	0.97		-1.06	-0.41
AHQ/VRQ	0.82	-0.21	-0.02	1.01	-0.01	0.05	-0.66		0.61
ARQ/VRQ	**-2.09**	**-3.32**	**-3.15**	-1.71	**-3.12**	**-2.86**	**-3.21**	**-2.26**	

Table F.5 Analysis 2: Counts and estimated means (and standard error) of analysed traits by risk group.

	EWW (kg)		SW (kg)		MD (mm)		FD (mm)	
Risk Group	Mean (se)	Count	Mean (se)	Count	Mean (se)	Count	Mean (se)	Count
1	21.15 (0.314)	101	30.22 (0.614)	80	22.47 (0.345)	78	3.18 (0.144)	78
2	21.24 (0.214)	462	30.31 (0.498)	344	21.80 (0.255)	327	3.08 (0.110)	327
3	21.33 (0.229)	314	30.88 (0.526)	188	21.98 (0.285)	178	3.07 (0.121)	179
4	21.10 (0.315)	94	31.14 (0.675)	44	22.14 (0.396)	42	3.21 (0.162)	42

Table F.6 Analysis 3: Counts and estimated means (and standard error) of analysed traits by allele number.

		EWW (kg)		SW (kg)		MD (mm)		FD	
Allele	No.	Mean (se)	Count	Mean (se)	Count	Mean (se)	Count	Mean (se)	Count
ARR	2	21.14 (0.314)	101	30.21 (0.614)	80	22.47 (0.343)	78	3.19 (0.144)	78
	1	21.20 (0.211)	494	30.30 (0.491)	362	21.79 (0.251)	344	3.08 (0.110)	344
	0	21.33 (0.222)	376	31.05 (0.518)	214	22.09 (0.280)	203	3.10 (0.120)	204
AHQ	2	21.59 (0.370)	61	31.81 (0.724)	35	22.57 (0.438)	31	3.15 (0.177)	31
	1	21.30 (0.217)	417	30.45 (0.510)	288	21.74 (0.266)	274	3.06 (0.114)	275
	0	21.15 (0.213)	493	30.41 (0.507)	333	22.00 (0.261)	320	3.12 (0.112)	320
ARQ	2	21.19 (0.322)	87	30.62 (0.696)	44	21.83 (0.398)	43	3.10 (0.164)	43
	1	21.24 (0.216)	436	30.61 (0.502)	297	21.90 (0.261)	283	3.07 (0.113)	284
	0	21.26 (0.216)	448	30.50 (0.501)	315	21.96 (0.261)	299	3.12 (0.113)	299
VRQ	1	21.10 (0.315)	94	31.12 (0.674)	44	22.12 (0.396)	42	3.21 (0.162)	42
	0	21.26 (0.198)	877	30.50 (0.483)	612	21.90 (0.248)	583	3.08 (0.107)	584

Genetic Resistance to Scrapie in a flock of Welsh Mountain Sheep.

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Introduction There is considerable interest in the eradication of all transmissible spongiform encephalopathies (TSE's) in food producing animals, to minimise any possible risk to human health. Scrapie, a TSE and a notifiable disease, is a fatal neuro-degenerative disease of sheep and goats. Susceptibility is strongly linked to the prion protein (PrP) genotype on three codons 136, 154 and 171. The ARR alleles confer the greatest resistance to disease; ARQ and ARH are intermediates, whereas VRQ confers greatest susceptibility. UK and EU eradication policies are presently selecting for resistance to scrapie and farmers are taking advantage of genotyping schemes to position themselves better in the market place should scrapie resistance become a major market requirement. The objectives of the study were to find out PrP genotypic frequencies and thus PrP gene-associated susceptibility to scrapie in a flock of Welsh mountain sheep and to predict changes in scrapie genotypes as a result to selection.

Materials and Methods Blood samples were collected by animal health officers from 449 Welsh Mountain Sheep (268 breeding ewes and 181 lambs born in 2001 and 2002) from the CAMDA nucleus flock, genotyped through the National Scrapie Plan Scheme (NSP). The animals genotyped were potential replacement animals rather than animals of the whole flock. Each animal had a bolus inserted to provide a NSP electronic identification number. Other information that was recorded included identification provided by the owner, sex, and age group at time of test. Distributions of the genotypes and gene frequencies were calculated for the different sub-groups (grouping based on sex, age group and year of birth) and allocated into risk groups designated by the NSP (DEFRA, 2003). Emphasis placed when selecting rams in the autumn of 2001 was on choosing rams from resistant genotype groups. Of the 8 rams used 6 were in group 1 or 2.

Results A total of 10 genotypes out of 15, falling into all five groups designated by the National Scrapie Plan, were found. Overall the most common genotype was AHQ/ARQ (24.5%) and the least common was VRQ/VRQ (0.7%). Four allelic variants occurred in the CAMDA flock, these were ARQ (34.7%), AHQ (31.9%), ARR (20.7%) and VRQ (12.7%). The ARR allele occurred in about 35.3 % of animals. The genotype associated with full resistance, ARR homozygous, was found in 5.3% of total sheep examined and therefore at low risk to scrapie, 22.9% were AHQ/ARR and ARQ/ARR heterozygotes, also with some resistance in individual sheep. However, 7.1% of the ARR heterozygotes were ARR/VRQ, which are in the low resistant group. There was an increase in the number of animals in the more resistant genotypes in the lambs born in 2002 compared with lambs born the previous year. Proportions of scrapie susceptible genotypes (Groups 4 & 5) were present in 25.2% and 2.6% of the lambs born in 2001 and 2002 respectively and are shown in Table 1. The genotype associated to highest susceptibility (VRQ/VRQ) was only found in 2001 lambs.

Table 1. Frequency distribution of sheep into scrapie risk categories

Risk Type (NSP)	Overall data %	Adult Females %	2001 lambs %	2002 lambs %
1	5.3	5.2	2.8	15.8
2	22.9	22.0	14.7	60.5
3	47.0	45.1	57.3	21.1
4	7.1	8.2	6.3	2.6
5	17.5	19.4	18.9	0.0

Conclusions The results show a response to selection by an increase in the proportion of animals with genotypes higher in resistance to scrapie in lambs born in 2002 compared with 2001 due to the use of more resistant rams on ewes in the Autumn of 2001. By using a ram with an ARR/ARR genotype on ewes that may be of a more susceptible genotype, any offspring produced would be at least in group 2 with 1 ARR allele. The results demonstrate that the proportion of a flock resistant to scrapie can be increased rapidly as a response to the use of scrapie resistant rams.

References

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Table G.1. Genetic (co)variances between the selection criteria and objectives that are available from this study or required for the Welsh Mountain.

	EWW	SW	MD	FD	MW	LS	LW
GR (EWW)	✓	✓	✓	✓	✓	✓	✓
LEAN	*required*	*required*	*required*	*required*	*required*	*required*	*required*
FAT	*required*	*required*	*required*	*required*	*required*	*required*	*required*
MS (MW)	✓	*required*	*required*	*required*	✓	✓	✓
MA (LW)	✓	✓	✓	✓	✓	✓	✓
LS	✓	✓	✓	✓	✓	✓	✓

✓ genetic (co)variances available from this study
required – records not available from this study i.e. obtain estimates from other studies

Table G.2 Genetic (co)variances between the selection criteria and objectives for the Welsh Mountain

	EWW	SW	MD	FD	MW	LSB	LW
GR (EWW)	1.208	1.745	0.372	0.067	2.62	0.076	3.481
LEAN	*required*	*required*	*required*	*required*	*required*	*required*	*required*
FAT	*required*	*required*	*required*	*required*	*required*	*required*	*required*
MS (MW)	2.62	*required*	*required*	*required*	6.13	0.211	1.992
MA (LW)	3.481	1.768	1.079	0.371	1.992	0	1.23
LS	0.076	0.132	0.037	0.008	0.211	0.03	0

	EWW	SW	MD	FD	MW	LSB	LW
GR (EWW)	1.208	**1.745**	**0.372**	**0.067**	2.62	0.076	3.481
LEAN	*0.0*	**1.31**	**0.625**	**0.153**	*0.0*	*0.0*	*0.0*
FAT	*0.0*	**1.66**	**0.276**	**0.337**	*0.0*	*0.0*	*0.0*
MS (MW)	2.62	**3.034**	**0.851**	**0.027**	6.13	0.211	1.992
MA (LW)	3.481	1.768	1.079	0.371	1.992	0.0	1.23
LS	0.076	0.132	0.037	0.008	0.211	0.03	0.0

Genetic variances of lean weight and fat weight were taken from Roden 1999 and were used to calculate genetic covariances with scan weight, muscle depth and fat depth (in blue print). Values for correlations between mature weight and scan weight, muscle depth and fat depth from Conington *et al.* (2001) were used to calculate genetic covariances (in red print).

Table G.3 Matrix of genetic variances (in bold) of the selection criteria and covariances between selection criteria for the Welsh Mountain.

	EWW	SW	MD	FD	MW	LSB	LW
EWW	**1.208**	1.745	0.372	0.067	2.6502	0.076	3.481
SW	1.745	**2.874**	0.719	0.118	0	0.132	1.768
MD	0.372	0.719	**1.125**	0.073	0	0.037	1.079
FD	0.067	0.118	0.073	**0.137**	0	0.008	0.371
MW	2.650	0	0	0	**6.130**	0.211	1.992
LSB	0.076	0.132	0.037	0.008	0.211	**0.029**	0
LW	3.481	1.768	1.079	0.371	1.992	0	**1.230**

Table G.4 Matrix of phenotypic variances for each of the selection criteria and phenotypic covariances between the selection criteria for the Welsh Mountain.

	EWW	SW	MD	FD	MW	LSB	LW
EWW	**6.56**	7.172	2.491	0.788	4.427	0.077	3.481
SW	7.172	**11.51**	4.155	1.269	0.00	0.130	1.768
MD	2.491	4.155	**4.63**	0.625	0.00	0.037	1.079
FD	0.788	1.269	0.625	**0.64**	0.00	0.008	0.371
MW	4.427	0.00	0.00	0.00	**0.226**	0.211	1.992
LSB	0.077	0.130	0.037	0.008	0.211	**0.212**	-0.485
LW	3.481	1.768	1.079	0.371	1.992	-0.485	**11.68**

Table G.5 Matrix of genetic variances (in bold) of the selection criteria and covariances between selection criteria for the Beulah Speckled Face.

	EWW	SW	MD	FD	LSB	LSR	LW
EWW	**0.572**	0.794	0.117	0.064	0.067	0.053	0.877
SW	0.794	**2.732**	0.672	0.275	0.118	0.077	1.916
MD	0.117	0.672	**0.897**	0.068	0.020	0.022	1.098
FD	0.064	0.275	0.068	**0.122**	0.001	0.00	0.623
LSB	0.067	0.118	0.020	0.001	**0.036**	0.025	-0.016
LSR	0.053	0.077	0.022	0.00	0.025	**0.019**	0.00
LW	0.877	1.916	1.098	0.623	-0.016	0.00	**1.372**

Table G.6 Matrix of phenotypic variances for each of the selection criteria and phenotypic covariances between the selection criteria for the Beulah Speckled Face.

	EWW	SW	MD	FD	LSB	LSR	LW
EWW	**6.67**	7.328	2.597	0.719	0.067	0.053	0.877
SW	7.328	**15.41**	5.296	1.574	0.118	0.077	1.916
MD	2.597	5.296	**4.83**	0.763	0.020	0.022	1.098
FD	0.719	1.574	0.763	**0.60**	0.001	0.00	0.379
LSB	0.067	0.118	0.020	0.001	**0.282**	0.200	-0.514
LSR	0.053	0.077	0.022	0.00	0.200	**0.250**	-0.397
LW	0.877	1.916	1.098	0.379	-0.514	-0.397	**11.11**

Table G.7 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait in the Welsh Mountain.

Weighting		EWW	SW	MD	FD	MW	LSB	LSR	LW
EWW	+1	6.76	2.48	0.91	1.14	3.51	7.34	5.50	4.23
SW	+1	3.79	4.41	1.37	2.24	1.66	3.48	2.22	2.18
MD	+1	1.95	1.91	3.15	2.24	1.26	2.13	1.26	2.07
FD	-1	-0.93	-1.20	-0.85	-8.24	-1.35	-0.59	-0.25	-1.78
MW	-1	-4.27	-1.32	-0.71	-2.00	-5.56	-4.50	-3.24	-2.68
LSB	+1	5.99	1.85	0.81	0.59	3.02	8.28	6.53	3.58
LSR	+1	5.61	1.48	0.60	0.31	2.72	8.17	6.62	3.38
LW	+1	6.09	2.04	1.38	3.12	3.18	6.32	4.77	4.69

Table G.8 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait with fat depth restricted in the Welsh Mountain.

Weighting		EWW	SW	MD	MW	LSB	LSR	LW
EWW	+1	6.69	2.33	0.80	3.36	7.33	5.51	4.02
SW	+1	3.68	4.24	1.18	1.34	3.45	2.23	1.76
MD	+1	1.76	1.65	3.03	0.93	2.05	1.24	1.64
MW	-1	-4.17	-1.06	-0.52	-5.39	-4.50	-3.28	-2.32
LSB	+1	5.94	1.77	0.75	2.93	8.26	6.53	3.46
LSR	+1	5.58	1.43	0.57	2.67	8.15	6.61	3.32
LW	+1	6.20	1.72	1.15	2.88	6.59	5.05	4.34

Table G.9 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait with mature weight restricted in the Welsh Mountain.

Weighting		EWW	SW	MD	FD	LSB	LSR	LW
EWW	+1	5.24	2.12	0.59	-0.17	5.80	4.45	3.27
SW	+1	2.64	4.21	1.21	1.72	2.23	1.31	1.44
MD	+1	1.01	1.66	3.06	1.83	1.14	0.54	1.49
FD	-1	0.11	-0.91	-0.70	-7.99	0.52	0.55	-1.16
LSB	+1	4.37	1.35	0.50	-0.60	6.94	5.68	2.53
LSR	+1	4.04	0.95	0.29	-0.77	6.83	5.77	2.37
LW	+1	4.45	1.57	1.19	2.41	4.57	3.55	3.85

Table G.10 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait in the Welsh Mountain (correlations with LW set at zero).

Weighting		EWW	SW	MD	FD	MW	LSB	LSR	LW
EWW	+1	6.32	1.66	0.37	-0.48	2.88	7.46	5.95	3.01
SW	+1	2.95	3.56	0.54	-0.49	0.38	3.57	2.89	-0.73
MD	+1	0.87	0.71	2.72	-0.01	0.12	1.87	1.58	0.01
FD	-1	0.38	0.22	0.00	0.00	-1.00	-0.04	0.36	-2.31
MW	-1	-3.40	-0.25	-0.06	-1.50	-5.35	-4.24	-3.45	-2.53
LSB	+1	5.74	1.54	0.62	0.04	2.76	8.21	6.60	2.85
LSR	+1	5.68	1.56	0.65	0.44	2.79	8.20	6.61	2.91
LW	+1	4.16	-0.57	0.00	4.07	2.96	5.14	4.23	4.56

Table G.11 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait when fat depth is restricted in the Welsh Mountain (correlations with LW set at zero).

Weighting		EWW	SW	MD	MW	LSB	LSR	LW
EWW	+1	6.31	1.65	0.37	2.95	7.48	5.99	3.15
SW	+1	2.93	3.55	0.54	0.44	3.57	2.92	-0.59
MD	+1	0.87	0.70	2.72	0.12	1.87	1.58	0.01
MW	-1	-3.53	-0.30	-0.06	-5.26	-4.30	-3.45	-2.13
LSB	+1	5.74	1.55	0.62	2.76	8.21	6.60	2.84
LSR	+1	5.71	1.57	0.65	2.74	8.21	6.61	2.79
LW	+1	5.05	-0.53	0.01	2.85	5.94	4.69	3.93

Table G.12 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait when mature weight is restricted in the Welsh Mountain (correlations with LW set at zero).

Weighting		EWW	SW	MD	FD	LSB	LSR	LW
EWW	+1	5.32	1.81	0.40	-1.53	6.15	4.85	1.95
SW	+1	2.72	3.55	0.54	-0.59	3.28	2.65	-0.90
MD	+1	0.79	0.70	2.72	-0.04	1.77	1.50	-0.05
FD	-1	1.03	0.27	0.01	-7.89	0.77	0.28	-1.87
LSB	+1	4.65	1.65	0.69	-0.86	7.04	5.63	1.81
LSR	+1	4.58	1.67	0.72	-0.39	7.02	5.64	1.87
LW	+1	2.74	-0.85	-0.04	3.89	3.35	2.78	3.80

Table G.13 Percentage gain in selection criteria using the two indexes derived by Roden (1999) for the Welsh Mountain breed (correlations with litter weight (LW) are set at zero).

INDEX	EWW	SW	MD	FD	MW	LSB	LSR	LW
1	5.30	1.45	1.69	0.91	2.43	6.79	5.49	2.87
2	4.87	2.09	1.92	-0.85	1.78	6.51	5.23	1.56

Table G.14 Percentage gain in selection criteria using the index employed for CAMDA flock of the Welsh Mountain breed (correlations with litter weight (LW) are set at zero).

INDEX	EWW	SW	MD	FD	MW	LSB	LSR	LW
1	4.85	3.13	0.52	1.45	1.96	5.91	4.82	1.50
2	6.14	1.10	0.29	0.90	3.24	7.33	5.88	3.72

INDEX 1 – uses scan weight for growth rate weighting ; INDEX 2 – uses eight-week weight for growth rate weighting.

Table G.15 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait in the Beulah Speckled Face.

Weighting		EWW	SW	MD	FD	LSB	LSR	LW
EWW	+1	2.38	2.41	0.79	3.71	2.86	2.48	1.90
SW	+1	1.73	3.33	1.15	4.79	2.65	2.05	2.00
MD	+1	0.73	1.50	2.55	1.79	0.83	1.06	1.78
FD	-1	-1.08	-1.95	-0.56	-8.18	-0.42	-0.19	-1.84
LSB	+1	1.46	1.89	0.45	0.75	4.68	3.76	0.67
LSR	+1	1.54	1.77	0.70	0.40	4.58	3.85	0.79
LW	+1	1.73	2.53	1.73	5.74	1.19	1.16	2.63

Table G.16 Analysis 1: Percentage gain in selection criteria with change of economic weighting on one trait when fat depth is restricted in the Beulah Speckled Face.

Weighting		EWW	SW	MD	LSB	LSR	LW
EWW	+1	2.12	1.72	0.60	3.00	2.69	1.20
SW	+1	1.35	2.70	1.01	2.96	2.39	1.13
MD	+1	0.51	1.10	2.49	0.76	1.05	1.41
LSB	+1	1.37	1.72	0.40	4.65	3.76	0.50
LSR	+1	1.49	1.68	0.68	4.57	3.84	0.70
LW	+1	1.36	1.63	1.88	1.25	1.44	1.87

Table G.17 Percentage gain in selection criteria using the two indexes derived by Roden (1999) for the Beulah Speckled Face when fat is restricted.

INDEX	EWW	SW	MD	FD	LSB	LSR	LW
1	1.51	2.62	2.24	3.29	1.82	1.74	2.31
2	1.49	2.63	2.22	2.44	2.39	2.19	2.09