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Optimising UK sheep breeding programmes by the inclusion of Genotype x Environment (GxE) interactions

Ann McLaren

A thesis submitted in fulfilment of the requirements for the degree of

Doctor of Philosophy

University of Edinburgh

2014
Declaration

I declare that this thesis is my own composition and that the research described in it is my own work, except where otherwise stated.

Ann McLaren        Date:
Thesis Abstract

Genotype by environment interactions (GxE) can form a potential source of inefficiency in animal breeding if selection decisions are made without accounting for their effects. The UK sheep industry covers an assorted range of farming systems and environments, with each flock having a unique and diverse set of resources and management styles. As a result, what may be the best performing genotype in one environment may not necessarily be the best performing genotype in another. This thesis reports on an investigation into the presence of GxE within the UK sheep industry.

Pedigree and performance data, available from both hill and terminal sire breeds, were analysed using a number of different methods. When environments were defined as 2 individual hill farms, genetic correlations were estimated between farms, for a range of Scottish Blackface ewe and lamb traits. Those found to be significantly different from 1 (P<0.05), and therefore indicating the presence of GxE, were lamb birth weight and ewe pre-mating weight.

Following on from this, fine-scale information obtained by a farmer questionnaire, from 79 different terminal sire flocks was combined with nationally-available climatic data and analysed using principle coordinate analysis and non-hierarchical clustering methods. Three distinct clusters of farm environments were identified, with grazing type, climatic conditions and the use of vitamin/mineral supplements proving to be the most distinguishing factors.

The presence of GxE was then investigated by estimating genetic correlations between the clusters identified, using performance data from Charollais lambs, for 21 week old weight (21WT), ultrasound back-fat (UFD) and muscle (UMD) depths. The correlations estimated between clusters 1 and 2, which had the highest number of common Charollais sires used, were all low and significantly different from 1 (P<0.05) suggesting GxE was evident in terms of both scaling and re-ranking.

Finally, the relationship between the level of concentrate feed used in each flock, as obtained from the questionnaire, and performance and climatic information available nationally for all flocks was estimated using canonical correlation analysis. This allowed the development of a farm environment scale, applicable to all flocks within the UK, and the use of reaction norm analyses to investigate the presence of GxE. The reaction norm describes the phenotype of an individual animal as a function of the environment. The environment scale developed, using data from Texel flocks only, went from low performance averages and poorer weather conditions to high performance averages and improved weather conditions. The slope of the reaction norm measures the sensitivity of an animal to a change in the environment. For each trait, (21WT, UMD and UFD), evidence of both re-ranking and scaling of sires were observed. A number of “robust” sires, with a low level of environmental sensitivity, were also identified.

The findings from these analyses may have implications for future sheep breeding programmes. Providing a suitable “measure of environment” can be agreed, the identification of sires that perform well in specific environments, as well as those who perform consistently across a number of different environments, would be beneficial for farmers. This would potentially remove any unwanted effects of GxE and allow the farmer to select animals best suited to their overall farm environment.
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During the course of this study a number of people have given me their time and valuable advice, to whom I am also grateful: Everyone involved in the Hill Sheep Breeding project, particularly those who were involved in the collection of the data used in Chapter 2 and Chapter 3; Claire and Justin Morgan-Davies for their input during the typology analysis in Chapter 4; Ian White and Sebastian Mucha for their statistical assistance in Chapter 5; Sam Boon at Signet Breeding Services and Kirsty Moore and her colleagues at EGENES for their help with providing the data used in Chapter 4 and Chapter 5 and Tony Waterhouse for his support, particularly during the final year.

In addition to those already mentioned, thanks also to all of my other colleagues at Kirkton (past and present) for their help and support (John, Christina, Harriet, Ewen, Zach, Meg, Gilly, Jenna as well as Ally, Tommy and Eoin). They helped keep me going during the tough spell in the early days and have worked extremely well in making sure I didn’t escape from the office during the latter stages!!

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Cheers everyone

😊
Publications

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Chapter 1: Introduction
1.1 Background

Sheep industries across the world encompass a diverse range of farming systems and environments. Over many generations producers have sought to exploit desirable traits whilst working within the constraints of the local topography and climate. As well as playing an important role in many rural economies, particularly in areas unsuitable for any other type of agricultural production, the benefits of sheep production in terms of biodiversity and landscape are well documented (Grime, 1979; Pollock et al., 2013). However, in countries well known for sheep production, such as Australia, New Zealand and the UK, the number of breeding ewes has been reducing steadily for several years (Renwick et al., 2008; Curtis, 2009; Bascand, 2012). Although there are a range of regional differences in the cause and level of reduction, the main catalysts for the decline have been unfavourably high costs of production and the poor prices received for the end product (Renwick et al., 2008; Bascand, 2012).

For the farmers and flocks remaining, it is increasingly important that breeding animals perform to their optimum potential. Some have opted to record pedigree and performance information from their flocks as part of specialised index selection programmes. Using the performance of the individual animal itself as well as that of its relatives, Best Linear Unbiased Prediction (BLUP) (Henderson, 1975) can be used to estimate breeding values (EBVs) for each trait. An overall index score can then be assigned to each animal, calculated as the sum of each trait EBV in the index, multiplied by the relative economic value assigned to each trait. The animals can then be ranked in order of their index value and selected for breeding accordingly.
Alternatively, farmers can identify and select animals with EBVs for the traits that they specifically want to maintain or improve in their flock. The traits recorded, as part of a selection programme, can be both ewe and lamb traits and can vary in terms of their economic weightings, often depending on the breed type.

Examples of selection indexes used in the UK sheep industry include the Terminal Sire Index and the Hill Index (Simm and Dingwall, 1989; Conington et al., 2001). The Terminal Sire Index has been developed for breeds such as the Charollais, Texel and Suffolk, and is designed to increase the yield of lean meat in the carcase, while attempting to reduce any associated rise in fatness (Simm and Dingwall, 1989). The Hill Index, on the other hand, attempts to simultaneously enhance the productivity of both the ewe and lamb, by taking into account a number of different traits. The index is commonly used for hill breeds such as the Scottish Blackface and the North Country Cheviot. Unlike the Terminal Sire Index which is very much growth and carcase orientated, the Hill Index includes traits such as the maternal ability of the ewe, the number of lambs reared to weaning as well as the performance of these lambs (Conington et al., 2001). To date, these programmes have proven to make considerable gains in terms of genetic improvement (Conington et al., 2006; Macfarlane and Simm, 2007).

However, if genes express themselves differently in different environments inconsistencies in animal performance can arise. Often, when animals are expected to perform in very different environments to where they have originated, the assumption commonly made is that they will respond the same, regardless of their location. Inevitably this is not always the case. The result of which can lead to
farmers being wary of using genetic selection as a tool to improve the performance of their flock. Overall, the association between environment and the phenotypic expression of a genotype constitutes a genotype by environment interaction (GxE), which can lead to the best genotype in one environment not necessarily being the best genotype in another environment (Falconer and Mackay, 1996).

1.2 Genotype by Environment Interactions

The presence of GxE can form a potential source of inefficiency in animal breeding if selection decisions are made without acknowledging its effects. Environmental factors that can impact on genotype performance can arise in many different ways, such as climatic conditions, nutrition levels, disease pressures or indeed general farm management decisions.

The effects of GxE can take two main forms (Figure 1.1). There may be a scaling effect which, although maintaining the rank of genotypes, causes the difference in performance between genotypes to be larger in one environment than in another. Alternatively, re-ranking can occur where the best genotype in one environment is not the best genotype in another environment (Falconer and Mackay, 1996). Namkoong (1985) also highlights that if a number of traits combined in an economic index differ in terms of scaling, the overall ranking of animals can change in different environments. The impact of GxE is stronger when there is a wide divergence between different genotypes as well as between different environments. The consequences can lead to the efficiency of index selection, economic performance and genetic gain all being inhibited (Mulder and Bijma, 2005; Dominik
and Kinghorn, 2008), with GxE that causes re-ranking being of most concern with respect to the selection of appropriate animals for future breeding.

![Figure 1.1. Estimated breeding values (EBVs) for two sires across three farms](image)

However, it should be noted that, although the presence of GxE is often regarded as a hindrance, it can, in some circumstances, provide an opportunity for breeders. Lynch and Walsh (2009) discuss three approaches available to breeders with which to deal with GxE. They can either ignore it, risking poor and somewhat unpredictable performance of selected individuals across different environments. Secondly, they can avoid it, by selecting lines with wide adaptability across different environments. Or thirdly, they can exploit it by developing locally-adapted lines suited to the environments in which they are to be based. The options open to breeders are however dependent on the predictability of the environmental factors. If predictable, there is the option to exploit, but if unpredictable, breeders can do no more than deal with the GxE present through the selection of “robust” stock that will perform relatively consistently across environments.
1.3 Methods for Identifying GxE

There are three different methods that can describe the extent of GxE, all of which rely on observations to be made on the same, or related, animals across at least two different environments. Although GxE can be estimated by including an interaction term in the traditional quantitative genetic model \( P = G + E \), the two most commonly used methods are the multi-trait and reaction-norm methods. Mulder (2007) discusses in depth the merits of each of these models concluding that, when compared with the multi-trait and reaction-norm models, the interaction model scores poorly for a number of criteria due to its limitations with unbalanced data and the presence of heterogeneity of variance among environments.

In most animal breeding situations it is unlikely that the same individual will be exposed to each of the different environments. Falconer (1952) realised that if a trait in various environments was considered as separate traits, their relationships could be described by calculating genetic correlations between them, giving rise to the multi-trait model. A high genetic correlation between environments indicates that the traits are being controlled by a similar set of genes, whereas a low correlation suggests that the phenotypic expression, across the environments, is not being controlled by the same genes, indicating the presence of GxE (Falconer and Mackay, 1996). The analysis also allows separate breeding values to be estimated for each different environment.

In terms of the level of correlation, there are differing views on what level represents GxE of practical importance. Robertson (1959) suggests a threshold of 0.80, however, further investigation to determine if this level is still relevant, or
appropriate to all livestock species, would be beneficial. Additionally, Mulder et al. (2006) suggested that in circumstances where correlations were below 0.61, separate breeding schemes, for environments of equal importance, would be warranted. An alternative option is to identify whether or not correlations estimated are significantly different to unity (Bryant et al., 2007).

As well as identifying the presence of GxE, the degree by which genotypes vary across environments is also of interest. This is often referred to as phenotypic plasticity (Bradshaw, 1965; de Jong and Bijma, 2002) or environmental sensitivity (Falconer, 1990; Kolmodin et al., 2002). Genotypes are considered “plastic” if they demonstrate highly variable phenotypes across environments or “robust” if they remain relatively constant (de Jong and Bijma, 2002; Bryant et al., 2005). Plasticity, or sensitivity, can be calculated by reaction norms, which are obtained by the random regression of genotype performance on environmental descriptors (Strandberg et al., 2000; Kolmodin et al., 2002; Fikse et al., 2003). In other words, the model describes the phenotype expressed by a certain genotype over a number of different environments. This can be particularly useful when environments are described along a continuous scale or gradient (de Jong and Bijma, 2002).
Examples of the different scenarios, with and without environmental sensitivity, are shown in Figure 1.2 (Strandberg, 2006). As discussed by Strandberg et al., (2000), the ideal situation regarding sire reaction norms is for each production trait to have a high level and a flat slope (for example Sire A, in Figure 1.2a). This would indicate that the sire performance would be high even if the environment changed. However, robust, high performing sires such as these may be rare. Figure 1.2a demonstrates a scenario where there is no environmental sensitivity, unlike Figure 1.2b, where environmental sensitivity is evident. However, in both cases, there is no variation in the level of difference between the sires, or in other words, no GxE as the sires respond similarly along the environment scale. Sire A remains the best sire across all environments, with Sires B and C also performing consistently. Figure 1.2c
demonstrates environmental sensitivity, as well as variation in the sensitivities, therefore indicating the presence of GxE due to scaling. Sire A remains the best performing sire, but the advantage that it had over Sire B has reduced. Finally, environmental sensitivity and GxE, in the form of re-ranking, are demonstrated in Figure 1.2d. Although Sire A is the best sire at one end of the environmental scale, Sire C proves to be superior at the other end. Overall, if different genotypes have different levels of reaction norms, then GxE exists (de Jong and Bijma, 2002).

1.4 Environment Descriptors

Across the literature, a range of different environmental descriptors have been used. For studies that have used the multi-trait method of analysis, distinct environments are required, which, for example, can be in the form of different geographical regions (Carabano et al., 1989; de Mattos et al., 2000; Lee and Bertrand, 2002; Jeyaruban et al., 2009), farming system (Nauta et al., 2006; Wallenbeck et al., 2009), feed types (Boettcher et al., 2003; Kearney et al., 2004a, 2004b) or feeding levels (Dominik et al., 2001).

In addition to the examples that have used specific environments, studies such as those by Weigel and Rekaya (1999), Zwald et al. (2003a), Neser et al. (2008) and Espasandin et al. (2013) went a step further by using clustering techniques in order to group farms with similar production environments, therefore allowing the removal of geographical borders and allowing similar farms in one country/region to be grouped together with similar farms in another. Alternatively, some have considered the extremes of certain environments, for example high and low quartiles or input levels (Cromie et al., 1998; Castillo-Juarez et al., 1999; Hayes et al., 2003). These have
often been used when some sort of underlying continuous scale exists and as a result are often found in studies alongside reaction norm analyses, such as those used by Calus et al. (2005), Strandberg et al. (2009) and Espasandin et al. (2013).

For those that have used reaction norm methods, the environments have often been based on continuous scales, allowing environments to be classed as more or less favourable for the trait, or traits, of interest. Examples include environments based on specific aspects such as production levels, for example herd levels of milk production, herd-year-season effects, contemporary group averages, feed levels and fertility descriptors (Kolmodin et al., 2002; Pollot and Greef, 2004; Bryant et al., 2007; Knap and Su, 2008; Strandberg et al., 2009; Santana et al., 2013a, 2013b). The use of weather variables have also been explored, such as rainfall and temperature (Fikse et al., 2003) and the development of a temperature-humidity scale (Ravagnolo and Misztal, 2002). Overall, taking into account a number of different environment variables, while trying to maintain a scale, is not easy. Methods that have been explored, in order to address this problem, have included the use of principal components to identify combinations of descriptors to form environmental scales (Windig et al., 2005, 2006; Haskell et al., 2007; Strandberg et al., 2009).

1.5 GxE in Livestock Species

1.5.1 Dairy Cattle

In terms of livestock species, the majority of literature available on the effects of GxE relate to the dairy cattle industry (Montaldo, 2001; Bryant et al., 2005; Mulder, 2007; Hammami et al., 2009). This has, in part, been due to the increasingly global
nature of the industry with technologies such as embryo transfer, artificial insemination (AI) and the use of a multiple-trait, across-country evaluation (MACE) procedure (Schaeffer, 1994). The International Bull Evaluation Service (Interbull) has been using the MACE procedure for a number of years, allowing the transfer of semen and embryos worldwide (Banos and Sigurdsson, 1996).

The assumption often made in global evaluations is that each country represents a different environment. However, as mentioned previously, this does not consider any potential within-country variation or the fact that some countries may share similar cross-border environments. Evidence of differing performance between countries has been found by Cienfuegos-Rivas et al. (1999) who identified significant GxE and re-ranking of sires for milk yield between the USA and Mexico and Peterson (1988) who also observed significant evidence of re-ranking for milk production traits between Canada and New Zealand. Hammami et al. (2008) identified low correlations and re-ranking for milk yields between Luxembourg and Tunisia, whereas Caranabo et al. (1989) observed low genetic correlations for fat yield between Spain and the USA.

A number of studies have, therefore, attempted to find alternative environment parameters by which different global environments can be distinguished. The use of clustering has been used by Weigel and Rekaya (2000) and Zwald et al. (2003a, 2003b) to define environments based on herd management, climatic and genetic descriptors. In most cases, high correlations were identified between clusters, therefore little GxE was observed. However, although the correlations identified in these studies were all relatively high, there are still benefits of using clustering
techniques. Zwald et al. (2003a) commented that the implementation of such a model would reduce the number of EBV’s generated, as part of the Interbull evaluation service, from 27 (due to there being 27 member countries) to 7, due to the creation of 7 unique production clusters, or environments, accounting for different parameters such as management and climatic differences.

Within countries, clustering techniques have also been used, such as those identified by Windig et al. (2006) and Huquet et al. (2012a, 2012b). In the Netherlands, Windig et al. (2006) investigated the relationship of milk yield with health and fertility across four different herd environments, based on four principal components. Correlations between clusters were all relatively high (0.84-1.00), but correlations between milk yield and the health and fertility traits changed over the different environments, resulting in changes in selection response. Similarly, in France, Huquet et al. (2012b) identified high correlations between environments that were defined by herd-test-day profiles. These were used to be representative of the overall herd management, or more specifically the level of feeding.

The identification of principal components allowed Haskell et al. (2007) to create an intensity scale, based on information gathered from a sample of UK dairy herds. The scale described the intensity of inputs into each sample herd, which was then applied to all herds in the UK, by predicting inputs per herd from information available for all herds in the population, such as production and climatic data. Haskell et al. (2007) then went on, using the scale developed and the reaction-norm model, to observe GxE for cow life span. The scale was further analysed by Strandberg et al. (2009), along with a production scale and a number of fertility descriptors. Overall, moderate
levels GxE were detected for fertility traits across both the production and intensity scales using both multi-trait and reaction-norm models.

Also using the reaction norm model, Bryant et al. (2006) identified that over a range of feeding levels, Holstein Friesians of overseas origin were more sensitive, or in other words their EBVs changed more, when their diet contained less concentrate feed than New Zealand Friesian and Jersey cattle. Environments defined by herd-by-year averages for protein production and days open (the number of days between calving and conception, used to assess reproductive performance) were used by Kolmodin et al. (2002). Scaling was observed in both the production and fertility environments. Sires with genetically high production and many days open tended to be more sensitive to changes in the production and fertility environments respectively. However, re-ranking was only observed between the extreme environments. In terms of weather variables, Ravagnolo and Misztal (2002) studied the environmental sensitivity to heat stress of Holstein cattle in the USA, using a temperature-humidity scale (Ravagnolo et al., 2000; Ravagnolo and Misztal, 2000). The genetic correlation between the extreme environments, for milk production, was 0.60. Annual rainfall was also identified by Fikse et al. (2003) as one of nine different environment descriptors that indicated GxE in terms of both re-ranking and scaling for milk production.

When different feeding regimes were classed as being high or low input, a number of studies found little evidence of re-ranking, but often the presence of scaling. Cromie et al. (1998) observed relatively high correlations between high input herds and low input herds in Ireland, but did observe substantial scaling between the different input
levels. Boettcher et al. (2003) also found little evidence of GxE interaction with correlations for production, reproduction and body conformation traits for two different feeding regimes all above 0.8. Similar results were identified by Kearney et al. (2004a) with correlations for milk, fat and protein all lying within the range of 0.88 – 0.91. Boettcher et al. (2003) did however observe a correlation of 0.64 for calving interval, although the standard errors associated were high. Scaling was also observed across environments with phenotypic differences for yield, in cows on conventional feeding systems, which the authors highlight were greater than what would have been predicted based on the EBVs of their respective sires.

1.5.2 Beef Cattle

Beef cattle studies have concentrated primarily on weaning weights, with few considering other traits such as birth and post-weaning data. Jeyaruban et al. (2009) investigated GxE interactions for production and reproductive traits between two geographical states within Australia. Correlations for growth traits ranged from 0.89 - 1.00, for reproductive traits between 0.97 - 1.00 and between 0.84 - 0.99 for carcass traits, with the exception of bull intramuscular fat, which was 0.65. This result however was said to be influenced by the measurement procedure and therefore not by true GxE effects. Meyer (1995) considered a number of traits for Angus cattle in Australia and New Zealand and reported genetic and maternal correlations, between the two countries, for weaning weight of 0.97 and 0.82 respectively and therefore concluded that there was little evidence of GxE. De Mattos et al. (2000) investigated the presence of GxE for weaning weights of Hereford cattle raised in three different countries (USA, Canada and Uruguay), as
well as across 4 regions within the USA. For the between-country analysis, correlations all lay within the region of 0.82 – 0.90. Similarly, correlations between USA regions were between 0.84 – 0.88, therefore the authors concluded that cattle from these three countries could be treated as a single population. Lee et al. (2002) observed similar results for birth and weaning weights in Herefords between Argentina, Canada, Uruguay and the USA. Low correlations were observed however for post weaning gain, with those between Argentina and either the USA or Canada (0.51 and 0.64 respectively) being the lowest. More recently, when weaning weights of American Angus cattle were studied across two different regions and calving seasons, within the USA, genetic correlations between 0.69 – 0.93 were observed by Williams et al., (2012), indicating some re-ranking of sires.

In terms of clustered environments, correlations observed by Noser et al. (2008) for Bonsmara cattle weaning weight records, between cluster environments, ranged between 0.51 and 1.00, although many were associated with high standard errors and therefore not significantly different from one. However, when Espasandin et al. (2013) used cluster analyses to define three different production environments across Uruguay and Brazil, low genetic correlations (between 0.27 – 0.33) were observed between clusters for weaning weight in Angus beef cattle. The clusters were based on different climatic conditions and management practices, therefore the results obtained indicated that across-country clusters could provide a better prediction of animal performance when compared to between country comparisons.
1.5.3 Sheep

Studies of GxE carried out using sheep are somewhat limited, perhaps due to the lack of globalisation in the industry, and the use of already locally-adapted breeds in many areas. However, interest is growing, in part due to technologies such as AI, as well as sire-reference and ram-circle schemes. Examples of sire-reference and ram-circle schemes, which aim to improve genetic links between flocks and aid the progeny testing of rams, are described by Macfarlane and Simm (2007) and Eikle et al. (2011). Although there is little between-country exchange of genotypes, within each country there remains a wide variation in environments in which genotypes are expected to perform.

Early studies often looked for evidence of GxE between breeds, such as those reviewed by Steane (1983), as well as those carried out by Carter et al. (1971a, 1971b, 1973). More recently, the effects of different planes of nutrition, as well as different geographical areas, have been investigated in terms of their effects on lamb growth and carcass characteristics (Bishop et al., 1996; Lewis et al., 2004; Macfarlane et al., 2004a, 2004b). Weather conditions during spring and summer months have also been found to significantly affect lamb weaning weights across a number of regions in Norway (Steinheim et al., 2004). Following on from this, when environments were characterized by flock x year effects, Steinhjem et al. (2008) observed a significant breed by environment interaction effect on lamb weaning weights. Two Norwegian breeds of sheep were monitored and the results found that the breeds differed in their environmental sensitivities to changing environments. However, when Valdez-Nava et al. (2011), investigated the presence of GxE
between three different Norwegian White Sheep ram-circle groups, all correlations estimated for lamb weaning weight were high and not significantly different to unity. Although the groups differed in aspects such as latitude and grazing type, all correlations estimated were 0.85 or above. However, Maniatis and Pollot (2002) observed GxE to be a significant source of variation in Suffolk lamb growth and carcass composition traits when using data available from the UK Suffolk sire-reference scheme. The effects of different nutrition levels on Merino wool production and quality traits were investigated by Dominik (1999). Correlations of 0.62 for clean fleece weight, 0.77 for fibre diameter and 0.80 for staple length were estimated between different nutrition levels, although some were associated with large standard errors. Environments based on flock milk yield were used by Sanna et al. (2002) to identify GxE for milk yield in Sardinian Sarda sheep. Pollot and Greef (2004) identified low levels of GxE associated with traits such as body weight, fleece weight and faecal egg count (FEC) in Merino sheep. The authors also observed that the heritabilities estimated for body weight, fleece weight and FEC varied with the environment, thus potentially causing inefficiency in selection. Santana et al. (2013b), also observed both “plastic” and “robust” individuals when investigating GxE in Santa Ines sheep.

Overall, it can be concluded that the subject of GxE interactions and their effect in livestock breeding can be complex and dependent on a number of different factors. For all species, there has been a high emphasis on traits associated with production. However, there has also been a growing interest in traits related to the health status and fertility of animals, allowing farmers to improve, or maintain, performance as
well as health and welfare within their herds/flocks. The range of environment classifications and scales used also emphasise the complexity of the subject.

1.6 GxE in the UK Sheep Industry

As can be seen from the literature available, relatively few studies have investigated GxE in sheep, with even fewer using sheep in the UK. In order to help optimise the current UK sheep breeding programmes, it is vital that an increased level of information is collected in order to investigate the presence of GxE. With a number of different breeding schemes in existence across the stratified UK sheep industry, as discussed by Macfarlane and Simm (2007), the choice of breeds included in this thesis attempts to provide an indication of what the situation may be in different levels of the UK sheep industry. Methods to define environments are also explored, allowing the use of both multi-trait and reaction norm analyses.

The overall aim of this thesis, therefore, is to explore the different methods used to identify GxE as well as investigate options to define environments, thus potentially allowing future breeding programmes to take the presence of GxE into account. This information can then be used by farmers to make more informed selection decisions, by identifying animals appropriate for their farm environment, in order to improve production efficiency and profitability.

Chapters 2 and 3 of this thesis describe the analyses carried out to identify potential GxE in Scottish Blackface ewes and lambs based in two contrasting hill farm environments. Because the Scottish Blackface is a maternal breed, and recorded as
part of the Hill Index as mentioned previously, a range of both ewe and lamb traits are investigated.

Chapter 4 extends the analyses from individual flock comparisons to include a number of different flock environments. In order to increase our knowledge of the many aspects that can potentially affect animal performance, information was gathered using a questionnaire sent to all members of the Signet Sheepbreeder programme (www.signetfbc.ac.uk). Principal coordinate analyses, followed by non-hierarchical clustering methods, were used to identify clusters of flocks that shared similar environments. The cluster environments were then investigated, using data available for the Charollais breed, in order to identify if GxE exists for lamb traits at weaning, between the different environment clusters.

Chapter 5 also utilises information collected from the questionnaire, primarily in terms of flock inputs, such as the use of concentrate feeding. Using the information provided by a sample of Texel flocks across the UK, together with information readily available for all Signet Sheepbreeder flocks, a canonical correlation analysis allowed the development of a farm environment (FE) index, which was then applied to all Texel Signet member flocks. The FE values estimated for each flock were used in genetic analyses of Texel lamb traits, from which reaction norms for each sire could be estimated and the presence of GxE identified. The reaction norms estimated provide information on the “sensitivity” of animals along the FE scale, allowing the identification of “robust” and “plastic” sires.
Chapter 2: Investigation into the presence of genotype by environment interactions (GxE) in Scottish Blackface lamb traits
2.1 Summary

Genotype by environment interactions (GxE) can form a potential source of inefficiency in animal breeding if selection decisions are made without acknowledging their effects. The presence of such interactions between two Scottish hill farms was investigated using performance data collected from 18459 Scottish Blackface lambs between 1997 and 2010. Pedigree information was available for 27548 animals and 30 out of 379 sires used during this time period were used on both farms. Farm A is located on the East Coast of Scotland, whereas Farm B is on the West Coast. The farms differ in a number of aspects including annual rainfall, topography, vegetation, temperature and altitude ranges, with Farm B representing a harsher environment overall.

Traits studied were birth weight, 8-week weight and weaning weight, ultrasound back-fat and muscle depths at weaning, carcass weight, carcass fat grade and carcass conformation score. Genetic correlations were estimated for each trait, between the two farms, with those significantly different to 1 (P<0.05) indicating the presence of GxE. The models used fitted relevant fixed effects as well as direct and maternal genetic and permanent environmental random effects.

Correlations estimated were not significantly different from 1 for all traits apart from birth weight, which had a correlation of 0.45 (s.e. 0.31). By taking GxE into account and comparing bivariate and univariate analyses, the maximum selection response observed for birth weight was 0.0016kg per generation. The lack of GxE observed for the majority of traits studied suggest that the common sire offspring have performed similarly across both farms. However, the presence of GxE associated with birth weight may have implications for lambing associated problems, or lamb survival, if sires produce lambs with unexpectedly high or low birth weights.
2.2 Introduction

Within the UK hill sheep production sector, a multi-trait selection index is currently available to producers, comprising of traits relevant for both maternal and lamb performance (Conington et al., 2006). Hill breeds have a complex role, providing breeding ewes for both pure and crossbred flocks as well as lambs for meat production. To date, the selection index and the commercial breeding programmes associated with it have made considerable gains in terms of both genetic and economic improvement (Conington et al., 2006). However, the selection index currently assumes that no variation exists in the performance of genotypes across different environments, or in other words, that no genotype by environment interactions (GxE) are present. With many of the farms who record their flocks as part of these breeding programmes varying greatly in environmental factors such as annual rainfall, topography, vegetation, temperature and altitude range, it is not unexpected that sire performance can be inconsistent. When sires fail to perform as expected over different environments, producers can become wary of the merits of using genetic evaluations in order to improve the performance of their flock.

The presence of GxE can therefore lead to reductions in the efficiency of index selection, economic performance and overall genetic gain (Montaldo, 2001; Dominik and Kinghorn, 2008). Any effects of GxE on the re-ranking of animals for future breeding selection are perhaps of most concern. The purpose of this study, therefore, was to identify possible GxE in Scottish Blackface lamb traits measured from birth to slaughter, between two contrasting hill farms, differing in topographical, climatic and environmental severity.
2.3 Materials and Methods

2.3.1 Farms and Flocks

Performance records were available for Scottish Blackface lambs based on two contrasting hill farms. Farm A is located in the Pentland Hills near Edinburgh and is typical of hill farms in the surrounding area. It is mainly south east facing, covering an area of 426ha, of which 287ha is unimproved hill ground comprised mainly of heather (*Calluna vulgaris*), and acid grasslands such as *Nardus stricta*, *Agrostis* and *Festuca*, 79ha is semi improved grassland and 68ha is improved grassland. The land rises from 305 to 488 metres above sea level and the area has an average yearly rainfall of approximately 1000mm. Farm B is located in the Western Highlands near Crianlarich, and is typical of a more extensive hill farming system. It is mainly south west facing and covers an area of 374ha, of which 266ha is unimproved hill ground comprised mainly of acid grasslands (*Nardus stricta*, *Agrostis* and *Festuca*) as well as heath rush, wet heath and sedge mire. Twelve ha is unimproved grassland, 14ha is semi-improved grassland and 52ha is improved grassland/silage fields. In contrast to Farm A, the land rises from 180 to 1034 metres above sea level, and the average yearly rainfall is approximately 2500mm. Using weather data from 1996 to 2009, Farm B had significantly higher rainfall levels (*P*<0.05) and significantly lower minimum temperatures (*P*<0.05) compared to Farm A, throughout the year (examining each month separately using paired student’s t-tests, with one record per farm per year). The only exception was the minimum temperatures recorded in April, which showed no significant difference between the farms. During the winter months (December to February) Farm B was significantly warmer (*P*<0.05), whereas during
the summer months (July to September) Farm A was significantly warmer ($P<0.05$), (UK Meteorological Office. 2006).

The flocks include around 600 (Farm A) and 530 (Farm B) breeding ewes and have been pedigree and performance recorded since 1991 (Farm A) and 1996 (Farm B). Within each flock, three genetic lines were run together, consisting of a Selection line, a Control line and an Industry line, with approximately one third of all ewes in each line. Both Selection and Control line animals were kept as breeding stock according to their multi-trait selection index score, as developed by Conington et al. (2001, 2004). Animals in the Selection line with the highest index score were selected, while the Control line animals were selected to try to maintain an average index score. Industry line animals were selected on appearance only, which is currently the common practice used by many commercial farmers.

2.3.2 Flock Management

Ewes were mated in single-sire mating groups from mid-November, until early January, on both farms. The majority of ewes were mated naturally, although a small proportion, (around 40 at each farm), were artificially inseminated each year using semen from two sires that were selected as part of the Blackface Sire Reference Scheme (http://www.maternalsheep.co.uk). The purpose of using common sires is to provide genetic links across farms in order to improve the connectedness between flocks and thus decrease any bias when estimated breeding values (EBVs) of animals are compared across different flocks (Lewis et al., 1999; Kuehn et al., 2009). Since November 1996, a total of 379 different Scottish Blackface sires have been used on the two farms, of which 30 have been used on both (Figure 2.1). Twenty two of these
common sires were used via artificial insemination (AI), while 8 have been used naturally (sires aa, bb, cc, dd, n, p, u and v), spending 1-2 years at Farm A then 1-2 years at Farm B (or vice-versa). Sire w was originally chosen as an AI sire and used for one year, but was then used again naturally at Farm A for an additional two years. Unlike the AI sires, the eight naturally used rams were not used in both flocks in the same year. The mating ratio for natural mating was around 1 ram to 45 ewes, whereas each AI sire was only used to inseminate around 20 ewes per farm per year. Overall, using the connectedness correlation proposed by Lewis et al (1999), this has achieved a good level of connectedness between the two farms. Kuehn et al. (2009) comment that a reduction in the bias of EBV estimates has a strong relationship with the connectedness correlation ($r_{ij}$). Correlations of 0.05 and 0.10 would correspond with an approximate 80% and 90% reduction in bias respectively. If flocks were not well connected, and the animals within these flocks had different genetic means, the risk of bias affecting the EBV estimates could be substantial. The degree of connectedness, expressed as a correlation, using the farms in this study was 0.11 (K. Moore, pers. communication), suggesting the EBVs estimated on both farms were subject to a very low level of bias and were therefore comparable.

After approximately 35 days in the single-sire mating groups, the Scottish Blackface rams were removed and white-faced rams (e.g. Texel, Lleyn or Cheviot) were added for a further 17 days, in case there were any problems of infertility with the Scottish Blackface rams. The majority of ewes were then returned to their hill grazing. At Farm B, younger ewes (2 year olds), as well as those classed as being below target condition score of 2.5, were kept in unimproved/semi-improved fields after mating in order to receive supplementary feeding.
The ewes were then ultrasonically-scanned for pregnancy in mid-February. Based on scan results, ewes at Farm B were split into different management groups consisting of ewes that were barren, ewes bearing single lambs and ewes bearing multiple lambs (twins and triplets). Those that were barren or bearing singles were returned to the hill, where they were given supplementary feed until lambing time. The multiple bearing ewes did not return to the hill and were kept on improved/semi-improved fields where they also received supplementary feeding until lambing time. At Farm A, all ewes were returned to the hill following scanning, apart from any that were in poor condition. After approximately two weeks, all twin-bearing ewes were brought onto lower ground and provided with supplementary feeding.

At approximately 1 week before lambing (early April), all pregnant ewes were brought onto the fields to aid pedigree recording, as well as to allow the shepherds to closely monitor the animals during this period. Throughout lambing, all single-
bearing ewes at both farms remained outside in unimproved/semi-improved fields, with only those requiring extra care being brought inside. Multiple bearing ewes at Farm B were kept on improved pasture during the day and brought inside at night, whereas at Farm A they remained outside, apart from individuals requiring extra care and attention. Ewes at Farm B rearing single ewe lambs were returned to the hill with their lambs around mid-July until weaning in mid-August. However, those rearing multiple lambs, or single male lambs, remained in the fields of both improved and unimproved pasture until weaning. This is because the hill grazing at Farm B is generally unsuitable for rearing multiple lambs and rearing them in this environment would be likely to compromise their growth. At Farm A, all single-reared lambs went straight to the hill grazing after lambing and all lambs that were reared as multiples remained on improved pasture until mid-lactation (late June), after which they also had access to hill grazing.

After weaning (mid-August), all lambs were managed in separate sex groups in improved/unimproved fields and ewes were returned to the hill until pre-mating. The ewe lambs that were selected for future breeding stock were sent away from the farm and grazed on surplus grass on lowland farms, from October until April. Although the management has differed slightly over the years, in recent years the male lambs have remained on improved pasture until October (depending on grass availability), after which they were then moved into a shed for finishing.

### 2.3.3 Dataset

A summary of the traits included in the study, and the data available for each, are shown in Table 2.1. Birth weights were recorded on each lamb within 24 hours of
birth. The average age of the lambs when weighed at 8 weeks (8WT) and weaning (WWT) were 52 days (Farm A: 3 – 70, Farm B: 10 – 91) and 109 days (Farm A: 56 - 138, Farm B: 73 - 138) respectively. Ultrasound measurements (UFD and UMD) were taken at the third lumbar vertebra on the same day as weaning live weight (WWT) was recorded. Slaughter data were only collected from entire male lambs that were slaughtered at a commercial abattoir upon reaching the appropriate slaughter criteria. The criteria differed slightly depending on abattoir specifications in a given year or season, but in general, were a minimum live weight of 37kg and a target condition score of 3 (based on the subjective scale of 0 to 5; Jefferies, 1961).

Table 2.1. Summary of traits included in the data set

<table>
<thead>
<tr>
<th>Trait</th>
<th>Farm</th>
<th>Count</th>
<th>Mean</th>
<th>s.d.</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT - Birth Weight (kg)</td>
<td>A</td>
<td>10688</td>
<td>3.95</td>
<td>0.7</td>
<td>1</td>
<td>7.3</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>7771</td>
<td>3.64</td>
<td>0.76</td>
<td>0.6</td>
<td>6.4</td>
</tr>
<tr>
<td>8WT - 8 Week Weight (kg)</td>
<td>A</td>
<td>10876</td>
<td>16.95</td>
<td>3.45</td>
<td>4.4</td>
<td>30.1</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>7464</td>
<td>18.01</td>
<td>4.08</td>
<td>5</td>
<td>33</td>
</tr>
<tr>
<td>WWT - Weaning Live Weight (kg)</td>
<td>A</td>
<td>10662</td>
<td>28.09</td>
<td>5.18</td>
<td>9</td>
<td>49.5</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>7445</td>
<td>26.82</td>
<td>4.66</td>
<td>10.4</td>
<td>46.3</td>
</tr>
<tr>
<td>UFD - Ultrasound Fat Depth (cm)</td>
<td>A</td>
<td>10277</td>
<td>0.17</td>
<td>0.11</td>
<td>0.01</td>
<td>1.02</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>7372</td>
<td>0.16</td>
<td>0.09</td>
<td>0.01</td>
<td>0.84</td>
</tr>
<tr>
<td>UMD - Ultrasound Muscle Depth (cm)</td>
<td>A</td>
<td>10277</td>
<td>2.02</td>
<td>0.25</td>
<td>0.83</td>
<td>2.95</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>7372</td>
<td>2.01</td>
<td>0.26</td>
<td>0.92</td>
<td>2.91</td>
</tr>
<tr>
<td>DCWT - Carcass Weight (kg)</td>
<td>A</td>
<td>3164</td>
<td>18.68</td>
<td>2.28</td>
<td>9.5</td>
<td>29.3</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>2228</td>
<td>16.57</td>
<td>2.57</td>
<td>9.8</td>
<td>25.6</td>
</tr>
<tr>
<td>MLCF - MLC Fat Grade*</td>
<td>A</td>
<td>3090</td>
<td>11.12</td>
<td>1.46</td>
<td>4</td>
<td>20</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>2214</td>
<td>10.15</td>
<td>1.64</td>
<td>4</td>
<td>17</td>
</tr>
<tr>
<td>MLCC - MLC Conformation Grade**</td>
<td>A</td>
<td>3110</td>
<td>3.07</td>
<td>0.6</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>2217</td>
<td>2.54</td>
<td>0.61</td>
<td>1</td>
<td>5</td>
</tr>
</tbody>
</table>

* Converted to numerical scale as described by Kempster et al. (1986)
** Converted to numerical scale as described by Conington et al. (2001)
MLC – Meat and Livestock Commission
2.3.4 Data Analysis

The pedigree file used in the analyses contained sire and dam information for a total of 27,548 animals. Heritability estimates for each trait were estimated using univariate analyses in ASReml (Gilmour et al., 2002), within-farm. Random effects in the models included a direct genetic effect (animal), maternal genetic effect (dam) and a maternal permanent environment effect (pe). The dam has an influence on the lamb traits both genetically and environmentally, which if ignored, can bias the estimate of the direct genetic effect. The maternal genetic effect describes the amount of variation in the trait due to the genotype of the dam. The maternal permanent environment effects describe the amount of variation caused by the environment which the ewe provides for the lamb, for example in utero or on a certain area of grazing on the hill. All univariate models converged with the exception of MLCF. The random effects fitted for this trait were therefore reduced and included the direct genetic effect (animal) and the maternal permanent environment effect ($c^2$) only. The $c^2$ component comprised both the maternal genetic effect (dam) and a permanent environment effect (pe).

All biologically-sensible effects and interactions were tested in order to find an appropriate fixed effects model, resulting in the following model that was fitted for each separate trait:

\[
\text{Lamb Trait} = \text{mean} + \text{age} + \text{birth year} + \text{sex} + \text{rearing rank at 1 week} + \text{dam age} + \text{grazing} + (\text{sex x age}) + (\text{sex x birth year}) + \text{animal} + \text{dam} + \text{pe} + \text{error}
\]
Lamb age was the age of the lamb (in days) at which the relevant measurement was taken and was treated as a covariate. Dam age, however, was a factor and measured in years (6 levels: 1 to ≥ 6 years old). Other factors in the model included birth year (14 levels: 1997 to 2010) and sex (2 levels: entire males and females). Rearing rank at 1 week, or in other words the litter size in which the animal was actually reared, (3 levels: single, twin and triplet) was chosen over litter size at birth for all traits, as this was considered likely to have a larger impact on the early growth and development of the lamb. The grazing factor represented the area or field that the lamb had been grazing at 8 weeks (13 levels: Farm A, 18 levels: Farm B) and weaning (9 levels: Farm A, 16 levels: Farm B). Overall, each fixed effect or interaction was significant for the majority of traits. Effects that were not significant for all traits were still included in the model to keep consistency over all traits.

The only exceptions to this were for the carcass traits (DCWT, MLCF & MLCC), where all sex-related factors and interactions were removed as measurements were from entire male lambs only. For BWT, rearing rank at 1 week was replaced with litter size at birth (4 levels: single, twin, triplet and quad), grazing and lamb age were removed and the only interaction included in the model was (dam age x birth year). The weight of the dam prior to mating was found to cause a significant effect and was therefore included as a covariate. The inclusion of line (Selection, Control or Industry) did not significantly improve the models.

In order to investigate the presence of GxE interactions, genetic correlations between the same traits expressed on the two farms were estimated using bivariate analyses in ASReml, similar to the method originally proposed by Falconer (1952). High
correlations would indicate that no, or little, GxE was evident whereas low correlations would suggest that GxE was present. The models were similar to those used for the univariate analyses. The correlations estimated were also tested using a likelihood ratio test. For each trait, the log-likelihood for the original bivariate analysis (logL₀) was taken from an analysis where all parameters were estimated. The genetic correlation between farms was then fixed close to unity (0.999) and the log-likelihood recalculated (logL₁). This analysis required one less parameter to be estimated than the full analysis. The test statistic, \( LR = 2(\text{log}L₀ - \text{log}L₁) \), therefore had a \( \chi^2 \) distribution with one degree of freedom, from which any significant genotype by farm difference, although providing a conservative cut-off point, could be determined (Morrell. 1998, Steinheim et al., 2008).

In an attempt to investigate the impact of GxE on the response to selection (\( R \)), \( R \) was computed for traits where the genetic correlation was found to be significantly different from unity. For each farm, \( R \) was calculated as \( i h^2 \sigma_p \) where \( h^2 \) is the heritability and \( \sigma_p \) is the phenotypic standard deviation. The selection intensity \( i \) was calculated by subtracting the mean of all sires (\( \mu \)) from the selection differential (\( S \)), and then dividing by \( \sigma_p \). \( S \) was calculated, for both farms, as the difference in EBVs between the top 50 performing sires and all sires (n=214 sires at Farm A, n=148 sires at Farm B) used over the time period. The top 50 performing sires were selected from those with at least 30 progeny at each farm, while the overall mean was based on all sires with at least 5 progeny. Overall \( S \), \( \mu \) and \( h^2 \) were calculated as the weighted average of the appropriate within-farm figures (weighted by the number of sires at each farm), allowing a pooled \( R \) to be estimated.
A univariate analysis was also used, across both farms, from which $R$ could be calculated using (1) the same sires identified from the bivariate analysis ($n=99$) as well as (2) the top 100 performing sires identified using the univariate analysis only. The number of sires chosen for (1) was 99 and not 100 because one sire appeared in the top 50 at both farms. By comparing $R$ from a univariate analysis, which assumes a genetic correlation of 1.0 between traits on different farms, to the $R$ from a bivariate, where the genetic correlation is significantly different to unity, the value of including GxE in future genetic analyses can be quantified.

2.4 Results

2.4.1 Genetic Parameters and Correlations

Heritabilities were similar on both farms, with a tendency for higher values on Farm B (Table 2.2). In general they were low to moderate, ranging from 0.10 to 0.32, with the highest estimated for UMD at both farms. Maternal heritabilities ranged from 0.02 to 0.16 with the lowest being estimated for MLCC and the highest for BWT, at both farms. Permanent environmental effect sizes (permanent environmental variance divided by the phenotypic variance) were also low, ranging from 0.01 to 0.13, with the carcass grade traits (MLCC and MLCF) having the lowest and the live weight traits (BWT, 8WT and WWT) having the highest.
Table 2.2. Univariate direct ($h^2_d$) and maternal ($h^2_m$) heritabilities, permanent environmental effect ($pe$) and phenotypic variances ($\sigma^2_p$) between farms for each trait (s.e. in parenthesis)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Farm</th>
<th>$h^2_d$</th>
<th>$h^2_m$</th>
<th>pe</th>
<th>$\sigma^2_p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>BWT (kg)</td>
<td>A</td>
<td>0.13 (0.02)</td>
<td>0.15 (0.02)</td>
<td>0.11 (0.02)</td>
<td>0.33 (0.01)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.15 (0.02)</td>
<td>0.16 (0.02)</td>
<td>0.12 (0.02)</td>
<td>0.38 (0.01)</td>
</tr>
<tr>
<td>8WT (kg)</td>
<td>A</td>
<td>0.12 (0.02)</td>
<td>0.10 (0.02)</td>
<td>0.10 (0.02)</td>
<td>5.54 (0.09)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.16 (0.02)</td>
<td>0.08 (0.02)</td>
<td>0.13 (0.02)</td>
<td>6.95 (0.14)</td>
</tr>
<tr>
<td>WWT (kg)</td>
<td>A</td>
<td>0.15 (0.02)</td>
<td>0.11 (0.02)</td>
<td>0.08 (0.02)</td>
<td>13.16 (0.22)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.19 (0.03)</td>
<td>0.08 (0.02)</td>
<td>0.12 (0.02)</td>
<td>12.57 (0.25)</td>
</tr>
<tr>
<td>UFD (cm)</td>
<td>A</td>
<td>0.16 (0.02)</td>
<td>0.06 (0.01)</td>
<td>0.05 (0.01)</td>
<td>0.01 (0.0001)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.20 (0.03)</td>
<td>0.07 (0.02)</td>
<td>0.06 (0.02)</td>
<td>0.01 (0.0001)</td>
</tr>
<tr>
<td>UMD (cm)</td>
<td>A</td>
<td>0.26 (0.03)</td>
<td>0.08 (0.02)</td>
<td>0.03 (0.01)</td>
<td>0.05 (0.001)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.32 (0.03)</td>
<td>0.06 (0.02)</td>
<td>0.06 (0.02)</td>
<td>0.05 (0.001)</td>
</tr>
<tr>
<td>DCWT (kg)</td>
<td>A</td>
<td>0.17 (0.04)</td>
<td>0.06 (0.03)</td>
<td>0.07 (0.03)</td>
<td>3.26 (0.09)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.20 (0.05)</td>
<td>0.07 (0.04)</td>
<td>0.05 (0.04)</td>
<td>3.56 (0.12)</td>
</tr>
<tr>
<td>MLCF</td>
<td>A</td>
<td>0.20 (0.04)</td>
<td>-</td>
<td>0.01 (0.02)</td>
<td>1.86 (0.05)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.15 (0.04)</td>
<td>-</td>
<td>0.02 (0.03)</td>
<td>2.27 (0.07)</td>
</tr>
<tr>
<td>MLCC</td>
<td>A</td>
<td>0.19 (0.05)</td>
<td>0.02 (0.02)</td>
<td>0.01 (0.03)</td>
<td>0.81 (0.02)</td>
</tr>
<tr>
<td></td>
<td>B</td>
<td>0.10 (0.04)</td>
<td>0.02 (0.03)</td>
<td>0.03 (0.04)</td>
<td>0.45 (0.01)</td>
</tr>
</tbody>
</table>

Birth Weight (BWT); 8 Week Weight (8WT); Weaning Weight (WWT); Ultrasound Fat Depth (UFD); Ultrasound Muscle Depth (UMD); Carcass Weight (DCWT); MLC Fat Grade (MLCF); MLC Conformation Grade (MLCC).

The correlations estimated are shown in Table 2.3. High correlations were estimated for 8WT, UMD, UFD and DCWT, however, problems arose with the convergence for these traits, which is perhaps not unexpected when the underlying correlation is close to, or equal to, one. As a result, the standard errors were therefore not estimable. Low correlations were estimated for BWT, MLCF and MLCC, but the standard errors associated with MLCF and MLCC were very high. Using the likelihood ratio test ($LR$), the genetic correlations estimated were found to be
significantly different from 1 ($P<0.05$) for BWT suggesting that GxE was only present for this trait (Table 2.3). Re-ranking was observed, as shown in Figure 2.2.

**Table 2.3.** Genetic correlations ($r_g$) and Likelihood ratios ($LR$) between farms for each trait.

<table>
<thead>
<tr>
<th></th>
<th>BWT</th>
<th>8WT</th>
<th>WWT</th>
<th>UMD</th>
<th>UFD</th>
<th>CWT</th>
<th>MLCF</th>
<th>MLCC</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_g$</td>
<td>0.45</td>
<td>0.98</td>
<td>0.9</td>
<td>0.99</td>
<td>0.99</td>
<td>0.99</td>
<td>0.38</td>
<td>0.03</td>
</tr>
<tr>
<td>s.e.</td>
<td>0.31</td>
<td>†</td>
<td>†</td>
<td>†</td>
<td>†</td>
<td>†</td>
<td>0.71</td>
<td>0.96</td>
</tr>
<tr>
<td>$LR$</td>
<td>6.52</td>
<td>0.48</td>
<td>0.58</td>
<td>3.66</td>
<td>0.38</td>
<td>0.6</td>
<td>1.12</td>
<td>0.58</td>
</tr>
<tr>
<td>$P$-value</td>
<td>0.011</td>
<td>0.488</td>
<td>0.446</td>
<td>0.06</td>
<td>0.538</td>
<td>0.439</td>
<td>0.29</td>
<td>0.446</td>
</tr>
</tbody>
</table>

Birth Weight (BWT); 8 Week Weight (8WT); Weaning Weight (WWT); Ultrasound Fat Depth (UFD); Ultrasound Muscle Depth (UMD); Carcass Weight (CWT); MLC Fat Grade (MLCF); MLC Conformation Grade (MLCC).

† Standard error not estimable.

**Figure 2.2.** Rankings of common sires (a-dd) according to their estimated breeding value (EBV) for Birth Weight, calculated at Farm A and Farm B (using the bivariate analysis).
The $R$ calculated for BWT (expressed as kg), from the bivariate analysis, was 0.0234kg and 0.0373kg for Farm A and Farm B respectively, and 0.0288 when the analyses were pooled (Table 2.4). In the univariate analyses the $R$ equivalent for selecting the top 100 performing sires identified by the bivariate was 0.0279kg, whereas the $R$ for the same individual sires, as identified by the original bivariate analysis, was 0.0272kg (Table 2.4). The maximum increase in response observed between the pooled bivariate and the two univariate analyses was therefore 0.0016kg.

<table>
<thead>
<tr>
<th>Table 2.4. Birth Weight estimated breeding value (EBV) responses calculated from bivariate and univariate analyses</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bivariate</strong></td>
</tr>
<tr>
<td>Selection Differential - $S$</td>
</tr>
<tr>
<td>Mean of all sires - $\mu$</td>
</tr>
<tr>
<td>Heritability - $h^2$</td>
</tr>
<tr>
<td>Phenotypic Variance - $\sigma_p$</td>
</tr>
<tr>
<td>Selection intensity - $i$</td>
</tr>
<tr>
<td>Selection Response - $R$</td>
</tr>
</tbody>
</table>

2.5 Discussion

Overall, literature available regarding the effects of GxE in the sheep industry is rare, perhaps due to the lack of globalisation in the industry, the use of already locally-adapted breeds in many areas and the lack of suitable data available. However, interest is growing in GxE effects, in part due to the increasing use of selection indices and technologies such as AI and sire-reference schemes. Although there is
little across-country exchange of genotypes, within many countries (e.g. the UK lowlands and highlands) there remains a wide variation in environments within which many individual animals are expected to perform.

The current multi-trait selection index for hill sheep such as the Scottish Blackface includes all of the lamb traits analysed in the present study as breeding goals, with the exception of BWT and 8WT. The heritabilities estimated for the traits, although calculated within-farm, were in general agreement with a number of different studies available in the literature also using Scottish Blackface lambs (differences of <0.09 for the majority of traits) (Bishop et al., 1996; Conington et al., 2001; Lambe et al., 2008; Riggio et al., 2008). The only exception was a heritability of 0.33 for DCWT reported by Conington et al. (2001). The studies carried out by Conington et al. (2001) and Lambe et al. (2008) used data from the same Scottish Blackface flocks as are used here, but estimated heritabilities across both farms rather within each farm, which therefore may explain the slightly lower heritabilities estimated in the present study. The models used in the present study were similar to those of Lambe et al. (2008), but differed slightly to the model used by Conington et al. (2001) which may also account for the differences observed, particularly for CWT.

Bishop et al. (1996) investigated a number of possible GxE interactions in relation to the performance of Scottish Blackface lambs at weaning (WWT, UMD and UFD), using older data collected on one of the same flocks used in the current study (Farm A) and another flock located on an adjacent hill to what is termed Farm B in the current study (Farm C). For many producers, particularly of hill lambs, these traits are extremely important. They have a key role in terms of the quality of the lambs
produced for finishing, as well as the quality of lambs retained for future breeding stock. Bishop et al. (1996) found that to maximise genetic gain, when considering the improvement of traits in extensive environments, selection in an intensive environment would not be beneficial, particularly in terms of WWT and UFD. This agrees with the theory discussed by Falconer and MacKay (1996) in that selection is most effective when carried out in the environment in which the improvement is sought. In other words, the offspring of animals reared in favourable, high quality resource systems may not perform well when tested in poorer resource systems, such as those found in extensive grazing situations. Unfortunately, for the 30 common sires used in the present study, no information was available as to what the original selection environments were like, in terms of factors such as feeding regime, management conditions etc.

Correlations estimated by Bishop et al. (1996), combining data from both farms (1,984 lambs sired by 32 common rams), but splitting the data between hill reared lambs and lambs reared on improved pasture, were 1.00, 0.71 and 0.70 for WWT, UMD and UFD respectively. However these results were associated with high standard errors and were not significant \((P>0.05)\). The correlations for the same traits, between Farm A and Farm B in the present study were 0.90, 0.99 and 0.99 respectively. It should also be noted that, in the study by Bishop et al. (1996), the lambs reared on hill ground were mainly single lambs, while those reared on improved pasture were mainly reared as twins, therefore there would be some confounding with birth type. The authors also acknowledge the hill lambs at Farm C performed much poorer than the hill lambs on Farm A. During the present study, however, the lambs (both singles and twins) reared at Farm B spent longer on the
improved pasture, between birth and weaning, when compared to both of the Farm A and Farm C flocks used in the study by Bishop et al. (1996). This may therefore explain the improved performance of the flock as well as the slightly higher heritabilities and correlations estimated. The results observed in the current study for the other remaining index traits, DCWT, MLCF and MLCC, did not provide any significant evidence of GxE interactions. The correlations estimated for MLCF and MLCC were 0.38 and 0.03 respectively, but were associated with extremely high standard errors, and were found not to be significantly different to one ($P>0.05$).

The lack of GxE observed for the weaning and carcass traits, which are breeding goals in the current selection index, could be due to a number of reasons. It is possible that the common sires used in the study were “robust”, and therefore had offspring that were well adapted to both farm environments. However, although both farms are well connected genetically, the number of lambs sired by a common sire may have been too low to fully test this theory. Each AI sire was normally only used for one year, with only 20 ewes, thus producing a relatively low number of offspring. The naturally used sires, on the other hand, were used for up to four years (two years at each farm) with around 45 ewes each year, producing a much larger number of offspring. It may therefore be the case that if the study was to continue using sires naturally in a similar fashion, or increase the number of ewes artificially inseminated, the greater number of offspring of common sires would increase the accuracy of the results. Alternatively, although Farm B is generally considered the harsher of the two farms, it could be that the farms, as well as the actual flocks, may not have been divergent enough to identify GxE. The Scottish Blackface breed is already well known for being adapted to harsher farming systems. It is likely that if breeds such as
the Texel or Suffolk were studied on these farms more evidence of GxE may have been observed. In studies that compared breed performance, Osoro et al. (1999), found that breeds with smaller body sizes were likely to be better suited to environments where the land resources were poorer. Larger sized breeds would require an increased level of resources to maintain growth and production. Similarly, Steinheim et al. (2004; 2008) identified differences in weaning weights between two contrasting breeds of Norwegian sheep, with the small breed, originating from old Scandinavian breeds, being less sensitive to environmental variation compared to the large cross breed, which originated mainly from British breeds. Macfarlane et al. (2004b) also found similar results when comparing the growth rate of terminal sire lambs (Suffolk) with hill lambs (Scottish Blackface) raised together on different qualities of pasture.

Although the current multi-trait selection index for hill sheep does not include the traits BWT and 8WT directly as breeding goals, they are important traits to consider in terms of GxE. The low genetic correlation of 0.45 observed for BWT (Table 2.3), between Farm A and Farm B indicates the presence of GxE and allows the effect of GxE on selection responses to be calculated using univariate and bivariate approaches. The univariate assumes the trait is affected by the same genes and can therefore be considered as the same trait across both farms. The bivariate assumes that the trait is affected, on both farms, by different genes and should therefore be considered as two different traits on the two farms. In terms of the bivariate analysis, the difference in R observed between the two farms (0.0139kg) suggests that GxE had more of an impact at Farm B than at Farm A. This is perhaps not unexpected, given that Farm B is considered the harsher and somewhat more variable of the two.
Farm B was also associated with a higher standard deviation and heritability for BWT (Table 1). When the pooled bivariate data was compared to the two univariate analyses (Table 4), although an overall increase in $R$ was observed, the level of increase was relatively low, with a maximum gain of 0.0016kg per generation. It would therefore take some time for any significant gains to be made in terms of BWT, should GxE be accounted for in future analyses.

However, although the overall changes in $R$ were low, the presence of GxE for BWT is still of interest and may have implications in terms of lambing difficulties and lamb survival. With a number of sires re-ranking between the two farms in the study in terms of the BWT of their progeny, if offspring were to deviate below or above the optimum birth weight in different environments, it could prove problematic for lamb survival. Sawalha et al. (2007), using a similar dataset as that of the present study, found that lambs born of average weight (3.5 to 4.0 kg) had the highest survival potential compared to heavier or lighter lambs. Heavier lambs are at risk of dystocia, while smaller, lighter ones, are often more prone to mis-mothering and starvation. Similar results were found by Morris et al. (2000) using Romney sheep. In terms of breeding values, care must be taken, as Sawalha et al. (2007) found an unfavourable relationship between EBVs for birth weight and mortality rate. Lambs that had high EBVs for birth weight also had higher mortality rates. The selection responses calculated in the present study were using sires with the highest EBVs for BWT, which would imply that the offspring of these sires may therefore be prone to a higher level of mortality. If this trait was to be included in future selection indexes, selection for an optimum weight would be more beneficial than maximum birth weight.
2.6 Conclusions

The lack of GxE observed for traits currently included in the hill sheep index suggest that the common sire offspring have performed similarly across both farms. Although Farm B is generally considered the harsher of the two farms, either the sires selected were suitable for both farms, or the farms did not differ sufficiently for any GxE to be present. The commercial breeding programme under which the majority of these common sires were selected, have therefore chosen “robust” reference sires. However, it is also possible that the flocks were not divergent enough when the study began. The GxE observed for BWT could have implications for lambing associated problems if sires produce lambs with unexpectedly high or low birth weights. Overall, as well as providing reassuring evidence of the robustness of the current hill sheep index, the study also highlights that BWT, and to a lesser extent possibly MLCF and MLCC, are traits that may have to be monitored closely in the future.
Chapter 3: Do Genotype by Environment Interactions (GxE) exist in Scottish Blackface Ewes?
3.1 Summary

The presence of genotype by environment interactions (GxE) between two Scottish hill farms was investigated using performance data collected from 6,465 Scottish Blackface ewes between 1991 and 2011. Pedigree information was available for 27,548 animals and 25 out of 398 sires used during this time period had daughters on both farms. Farm A is located on the East Coast of Scotland, whereas Farm B is on the West Coast. The farms differ in a number of aspects including annual rainfall, topography, vegetation, temperature and altitude ranges, with Farm B representing a harsher environment overall.

The traits studied were pre-mating weight, total weight of lamb weaned, number of lambs weaned, number of lambs lost, longevity and fleece weight. Heritability estimates for these traits were found to be similar at each farm. In addition to these traits, which form the maternal part of the hill sheep selection index, ewe efficiency was also studied, in terms of total weight of lamb weaned per kilogram of ewe body weight at mating. Heritability estimates for this trait ranged between 0.08-0.13 (±0.02).

The majority of genetic correlations estimated between the two farms were high and not significantly different to 1 (P<0.05), indicating little evidence of GxE for Scottish Blackface ewe traits. A significant correlation of 0.48 (±0.32) was observed for pre-mating weight. Overall the similarities between the heritability estimates at each farm, and the high genetic correlations estimated between farms, suggests the environments did not differ sufficiently for GxE to be observed. However, the GxE associated with pre-mating weight could have implications in terms of ewe maintenance, prolificacy, lambing rate and lamb weaning weights.
3.2 Introduction

As discussed in the previous chapter, hill breeds, such as the Scottish Blackface, have an important and complex role within the UK sheep industry, providing lamb for meat production as well as breeding ewes for both pure and crossbred flocks. Many hill ewes are found in often harsh and extensive environments where weather conditions can be severe and food resources scarce. As a result, hill farmers, over many generations and whilst working within the constraints of the local climate and topography, have sought to exploit desirable traits such as good maternal and survival characteristics, whilst also considering the quality of lambs produced.

With an increasing emphasis to enhance the efficiency, productivity and profitability of flocks, a number of UK farmers have opted to use genetic selection programmes to help achieve this. In terms of hill breeds, a multi-trait selection index has been commercially available since the early 2000s, combining both maternal and lamb performance traits, to improve the overall economic productivity of hill sheep flocks (Conington et al., 2001; 2004). As well as the lamb traits discussed in Chapter 2, the selection index includes maternal traits associated with ewe performance in terms of the number and weight of lamb reared as well those associated with longevity, wool and mature size.

However, with many of the farms who record their flocks as part of these breeding programmes varying greatly in environmental factors such as annual rainfall, topography, vegetation, temperature and altitude range, it is unlikely that performance across environments will be consistent. Selection indices currently used
for sheep assume that there is no variation in the performance of genotypes across
different environments, or in other words, that no genotype by environment
interactions (GxE) exists. Therefore the purpose of this study was to identify possible
GxE in Scottish Blackface ewe traits, between two contrasting hill farms, differing in
topographical, climatic and environmental severity.

3.3 Materials and Methods

3.3.1 Farms and Flocks

Performance records were available for Scottish Blackface ewes based on two
contrasting hill farm environments. Farm A is located in the Pentland Hills near
Edinburgh and Farm B located in the Western Highlands near Crianlarich. A detailed
description of both farm environments, and flock management throughout the year, is
given in Chapter 2, with Farm B representing a harsher environment overall. The
flocks include around 600 (Farm A) and 530 (Farm B) breeding ewes, which have
been pedigree and performance recorded since 1991 (Farm A) and 1996 (Farm B).

Performance data were available from ewes born between 1988 and 2009, combined
with lamb performance data available between 1991 and 2011. During this time
period, a total of 398 different Scottish Blackface rams had sired the ewes that were
retained for stock, with 30 being used on both farms. Only 25 of these common sires,
however, sired ewes that have been used in this study, with the remaining 5 being the
sire of younger female offspring (those born in 2010 and 2011). Twenty one
common sires were used via artificial insemination (AI), while 4 were used naturally,
spending 1-2 years at Farm A then 1-2 years at Farm B (or vice-versa). Unlike the AI
sires, the 4 naturally used rams were not used in both flocks in the same year. The mating ratio for natural mating was around 1 ram to 45 ewes, whereas each AI sire was used to inseminate around 20 ewes per farm per year. Ewes were first mated when they were approximately 18 months old, therefore lambing when they were 2 years old. They remained in the flock until they either died, were no longer fit for breeding or they were 6 (Farm A) or 5 (Farm B) years old.

### 3.3.2 Dataset

A summary of the traits included in the study, and the data available for each, are shown in Table 3.1. For the pre-mating weight (PMWT), all ewes, at both farms, were weighed in November each year, just before going into single-sire mating groups. The PMWT dataset, which was the largest of all the traits included in the study (18,524 records in total) included data from 6,465 individual ewes, ranging from 1 weight record to 5 weight records, depending on how many years the ewes remained in the flocks. Of the 6,465 ewes, 404 (6%) were sired by one of the 25 common sires.

The total litter weight weaned (TOTWWT) included the weight of all lambs that the ewe reared to weaning (including any lambs that were fostered on) and was adjusted for the number and sex of the lambs reared. The production efficiency of the ewe (EEFF), each year, was tested by dividing the total weight of lamb reared by the ewe to weaning, by the live weight of the ewe at pre-mating. An alternative measure of efficiency (EEFF$^{0.75}$), was also used which measured the lamb output per kilogram of the ewe metabolic weight at pre-mating (PMWT$^{0.75}$) (McDonald et al., 1995; Annett et al., 2011). The datasets for both EEFF and EEFF$^{0.75}$ only included ewes that had
reared a lamb. Similarly for the number of lambs lost (LLOST), only ewes that had given birth to a lamb were included. The number of lambs weaned by the ewe (LWEAN) included the ewes own lambs only and not any that were fostered on.

Longevity (LONGV) was the age of the ewe at culling, or death, measured in years. The fleece weight (FLWT) was measured on 1 year old sheep only, and was recorded between 1991 and 2005.

Table 3.1. Summary of traits included in the data set

<table>
<thead>
<tr>
<th>Trait</th>
<th>Farm</th>
<th>Count</th>
<th>Mean</th>
<th>s.d.</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>PMWT – Pre-mating Weight (kg)</td>
<td>Farm A</td>
<td>10542</td>
<td>55.26</td>
<td>6.76</td>
<td>31.7</td>
<td>83</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>7982</td>
<td>49.19</td>
<td>6.19</td>
<td>29</td>
<td>75</td>
</tr>
<tr>
<td>TOTWWT – Litter Weight Weaned (kg)</td>
<td>Farm A</td>
<td>9529</td>
<td>39.48</td>
<td>13.45</td>
<td>12.4</td>
<td>104.6</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>6327</td>
<td>34.69</td>
<td>11.82</td>
<td>10.4</td>
<td>85</td>
</tr>
<tr>
<td>EEFF – Ewe Efficiency:</td>
<td>Farm A</td>
<td>7658</td>
<td>0.71</td>
<td>0.23</td>
<td>0.21</td>
<td>1.57</td>
</tr>
<tr>
<td>TOTWWT/(PMWT)</td>
<td>Farm B</td>
<td>4766</td>
<td>0.69</td>
<td>0.21</td>
<td>0.21</td>
<td>1.85</td>
</tr>
<tr>
<td>EEFF&lt;sup&gt;0.75&lt;/sup&gt; – Ewe Efficiency:</td>
<td>Farm A</td>
<td>7658</td>
<td>1.94</td>
<td>0.63</td>
<td>0.6</td>
<td>4.31</td>
</tr>
<tr>
<td>TOTWWT/(PMWT&lt;sup&gt;0.75&lt;/sup&gt;)</td>
<td>Farm B</td>
<td>4766</td>
<td>1.82</td>
<td>0.57</td>
<td>0.56</td>
<td>4.81</td>
</tr>
<tr>
<td>LWEAN – No. of Lambs reared to weaning</td>
<td>Farm A</td>
<td>10484</td>
<td>1.2</td>
<td>0.69</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>7951</td>
<td>0.98</td>
<td>0.69</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>LLOST – No. of Lambs lost by weaning</td>
<td>Farm A</td>
<td>9583</td>
<td>0.22</td>
<td>0.46</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>6566</td>
<td>0.22</td>
<td>0.47</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>LONGV – Age at culling/death (years)</td>
<td>Farm A</td>
<td>2622</td>
<td>4.37</td>
<td>1.12</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>1830</td>
<td>4.4</td>
<td>0.93</td>
<td>2</td>
<td>5</td>
</tr>
<tr>
<td>FLWT – Fleece Weight at 1 year old (kg)</td>
<td>Farm A</td>
<td>2160</td>
<td>2.1</td>
<td>0.44</td>
<td>0.62</td>
<td>3.71</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>1979</td>
<td>1.95</td>
<td>0.41</td>
<td>0.39</td>
<td>3.27</td>
</tr>
</tbody>
</table>

3.3.3 Data Analysis

The pedigree file used in the analyses contained sire and dam information for a total of 27,548 animals. Heritability estimates for each trait were estimated using univariate analyses in ASReml (Gilmour et al., 2002), within-farm. Random effects in the models included a direct genetic effect (animal) and a permanent environment.
effect (pe). Only animal was fitted for LWEAN and LLOST due to the problems with the convergence of the models when both animal and pe were fitted. Similarly, pe was removed for LONGV and FLWT as it was not appropriate due to the nature of these traits only being recorded once in the animals lifetime.

All biologically-sensible effects and interactions were tested in order to find an appropriate fixed effects model, resulting in the following model that was fitted for each trait:

\[
\text{Ewe Trait} = \text{mean} + \text{ewe age} + \text{year} + \text{grazing} + (\text{lamb breed} + \text{weaning category}) + \text{animal} + \text{pe} + \text{error}
\]

Factors included in the fixed effects model included ewe age, which was measured in years (5 levels: 2 year old to 6 years old and over), and year, which represented the year in which the trait was measured (21 levels: 1991 to 2011). The grazing factor represented the area or field where the ewe had been grazing prior to the trait being recorded, i.e., at pre-tupping for PMWT, EEFF and EEFF\(^{0.75}\), (5 levels: Farm A; 9 levels: Farm B) and at weaning for TOTWWT, LLOST and LWEAN (9 levels: Farm A; 16 levels: Farm B).

Lamb breed, to account for a proportion of cross-bred lambs, was fitted as a factor for TOTWWT, EEFF, EEFF\(^{0.75}\), LWEAN and LLOST (purebred Scottish Blackface lamb (~95% of records), or crossbred sired by a Texel (1%), Cheviot (0.5%), Lleyn (0.5%) or a white-faced ram of unspecified breed (3%). Weaning category (i.e. a combination of lamb sex and litter size; 6 levels: single male, single female, twin males, twin females, mixed twin, and multiple) was fitted for TOTWWT, EEFF and EEFF\(^{0.75}\). Overall, each fixed effect or interaction was significant for the majority of
traits. Effects that were not significant for all traits were still included in the model to keep consistency over all traits.

The exceptions to this general model were for LONGV and FLWT, where only year was fitted as a fixed effect in the model. Ewe age was removed, as these traits were only measured once in the ewe’s lifetime. Grazing was also removed as it was not significant at either farm. For LONGV the factor year represented the ewes’ year of birth rather than the year in which the trait was recorded. For LLOST, the number of lambs originally born was also included in the model and a binomial version of this trait was also analysed.

In order to investigate the presence of GxE interactions, genetic correlations between the same traits expressed on the two farms were estimated using bivariate analyses in ASReml (Gilmour et al., 2002), similar to the methods used in Chapter 2. The correlations estimated for PMWT, EEFF, EEFF^{0.75} and TOTWWT were then tested using a likelihood ratio test ($LR$) similar to that used in the previous chapter. This analysis required one less parameter to be estimated than the full analysis. The test statistic, $LR = 2(\log L_0 - \log L_1)$, therefore had a $X^2$ distribution with one degree of freedom. The estimated breeding values (EBVs) at each farm, for each common sire, were also used to calculate Pearson’s and Spearman’s Rank correlations.

Unfortunately problems arose with the convergence of the bivariate analyses for FLWT and LONGV due to the relatively small datasets and lack of fixed effects that could be fitted in the models. As a result these traits were not analysed further.
3.4 Results

3.4.1 Genetic Parameters and Correlations

Heritabilities estimated were generally similar on both farms, with a tendency for higher values on Farm A (PMWT, EEFF, LWEAN, LLOST and LONGV) (Table 3.2). The only trait for which Farm B had a higher estimate was TOTWWT. Low to moderate heritabilities were estimated for PMWT, FLWT, TOTWWT and EEFF, ranging from 0.08 to 0.42. The highest were estimated for FLWT at both farms (0.51). Very low estimates are found for LLOST and LWEAN, ranging from 0.01 to 0.08. Permanent environmental effects were low to moderate, ranging from 0.03 to 0.24 for all traits.

The genetic correlations estimated between the same trait on each farm are shown in Table 3.3. High correlations ($r > 0.90$) were estimated for TOTWWT, LWEAN, EEFF and $EEFF^{0.75}$. The standard errors associated with these correlations were also relatively high, particularly for LWEAN. Low correlations were estimated for PMWT, LLOST and LLOST Binomial. Using the $LR$ test, only the genetic correlations estimated for PMWT and LWEAN were found to be significantly different from one ($P<0.05$). However, due to the high standard errors estimated for LWEAN, LLOST and LLOST Binomial, the results for these traits were deemed unreliable, most likely due to the distribution of the data and the high number of zero values, therefore they were not analysed further.
Table 3.2. Univariate direct ($h^2_d$) and maternal ($h^2_m$) heritabilities, permanent environmental effect (pe) and phenotypic variances ($\sigma^2_p$) between farms for each trait (s.e. in parenthesis)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Farm</th>
<th>$h^2_d$</th>
<th>pe</th>
<th>$\sigma^2_p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>PMWT (kg)</td>
<td>Farm A</td>
<td>0.42 (0.03)</td>
<td>0.20 (0.02)</td>
<td>30.56 (0.67)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.36 (0.03)</td>
<td>0.24 (0.03)</td>
<td>26.30 (0.64)</td>
</tr>
<tr>
<td>TOTWWT (kg)</td>
<td>Farm A</td>
<td>0.14 (0.02)</td>
<td>0.03 (0.02)</td>
<td>27.76 (0.44)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.18 (0.02)</td>
<td>0.05 (0.02)</td>
<td>24.41 (0.49)</td>
</tr>
<tr>
<td>EEFF</td>
<td>Farm A</td>
<td>0.13 (0.02)</td>
<td>0.13 (0.02)</td>
<td>0.012 (0.0002)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.09 (0.02)</td>
<td>0.16 (0.02)</td>
<td>0.012 (0.0003)</td>
</tr>
<tr>
<td>EEFF$^{0.75}$</td>
<td>Farm A</td>
<td>0.11 (0.02)</td>
<td>0.10 (0.02)</td>
<td>0.075 (0.001)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.08 (0.02)</td>
<td>0.13 (0.02)</td>
<td>0.074 (0.002)</td>
</tr>
<tr>
<td>LWEAN</td>
<td>Farm A</td>
<td>0.08 (0.01)</td>
<td>-</td>
<td>0.26 (0.004)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.01 (0.01)</td>
<td>-</td>
<td>0.13 (0.002)</td>
</tr>
<tr>
<td>LLOST Original</td>
<td>Farm A</td>
<td>0.02 (0.01)</td>
<td>-</td>
<td>0.18 (0.003)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.01 (0.01)</td>
<td>-</td>
<td>0.16 (0.003)</td>
</tr>
<tr>
<td>LLOST Binomial</td>
<td>Farm A</td>
<td>0.03 (0.01)</td>
<td>-</td>
<td>0.14 (0.002)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.01 (0.01)</td>
<td>-</td>
<td>0.12 (0.002)</td>
</tr>
<tr>
<td>LONGV</td>
<td>Farm A</td>
<td>0.12 (0.03)</td>
<td>-</td>
<td>1.06 (0.03)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.05 (0.03)</td>
<td>-</td>
<td>0.82 (0.03)</td>
</tr>
<tr>
<td>FLWT</td>
<td>Farm A</td>
<td>0.51 (0.05)</td>
<td>-</td>
<td>0.17 (0.01)</td>
</tr>
<tr>
<td></td>
<td>Farm B</td>
<td>0.51 (0.05)</td>
<td>-</td>
<td>0.16 (0.01)</td>
</tr>
</tbody>
</table>

Table 3.3. Genetic correlations ($r_g$) and Likelihood ratios ($LR$) between farms for each trait.

<table>
<thead>
<tr>
<th></th>
<th>PMWT</th>
<th>TOTWWT</th>
<th>LWEAN</th>
<th>EEFF</th>
<th>EEFF$^{0.75}$</th>
<th>LLOST</th>
<th>LLOST Binomial</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r_g$</td>
<td>0.48</td>
<td>0.93</td>
<td>0.98</td>
<td>0.94</td>
<td>0.97</td>
<td>0.21</td>
<td>0.17</td>
</tr>
<tr>
<td>s.e.</td>
<td>0.32</td>
<td>0.53</td>
<td>1.09</td>
<td>0.63</td>
<td>0.75</td>
<td>2.24</td>
<td>1.94</td>
</tr>
<tr>
<td>$LR$</td>
<td>7.28</td>
<td>1</td>
<td>11.68</td>
<td>0.38</td>
<td>3.08</td>
<td>0.14</td>
<td>0.22</td>
</tr>
<tr>
<td>P-value</td>
<td>0.007</td>
<td>0.32</td>
<td>0.001</td>
<td>0.42</td>
<td>0.08</td>
<td>0.71</td>
<td>0.64</td>
</tr>
</tbody>
</table>

51
Pearson and Spearman’s rank correlations for sire PMWT EBVs, between farms, were the only estimates significantly different to one (0.68 and 0.62 respectively) (Table 3.4).

**Table 3.4.** Pearson (PR) and Spearman’s Rank (SpR) Correlations between farms for sire EBVs

<table>
<thead>
<tr>
<th>Farm A</th>
<th>Farm B</th>
<th>PMWT</th>
<th>EEFF</th>
<th>EEFF(^{0.75})</th>
<th>TOTWWT</th>
</tr>
</thead>
<tbody>
<tr>
<td>PMWT</td>
<td>PR</td>
<td>0.68</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>SpR</td>
<td>0.62</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>EEFF</td>
<td>PR</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>SpR</td>
<td></td>
<td>0.98</td>
<td></td>
<td></td>
</tr>
<tr>
<td>EEFF(^{0.75})</td>
<td>PR</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>SpR</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>TOTWWT</td>
<td>PR</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SpR</td>
<td></td>
<td></td>
<td>1</td>
<td></td>
</tr>
</tbody>
</table>

### 3.5 Discussion

#### 3.5.1 Hill Sheep Selection Index and Ewe Efficiency Trait

With the increasing interest in the effects of GxE in the sheep industry, it is important to consider their effects, not only in lamb production, but also in terms of ewe survival and performance, particularly in breeds which are classed as being dual-purpose, such as hill breeds like the Scottish Blackface. In 2003, Pollot & Stone (2006) comment that almost 67% of slaughter lambs in the UK were produced from ewes that contained substantial levels of hill breed genetics. The two main providers overall were Longwool x Hill breed type ewes (32.7%) and pure Hill breed ewes (23.9%). Although these levels may have changed slightly over recent years, the influence of hill breed genetics, in terms of the ewe, throughout the sheep industry remains high.
The current multi-trait selection index for hill breeds includes all the ewe traits analysed in the present study as breeding goals, with the exception of EEFF, EEFF$^{0.75}$ and LLOST Binomial. The similarities between the heritabilities estimated at both farms suggest that the environments were perhaps too alike, similar to the findings from Chapter 2. When compared with two previous studies that also used data from the same Scottish Blackface flocks (Conington *et al.*, 2001; Lambe *et al.*, 2008), the estimates were in general agreement. However, it should be noted that they estimated heritabilities across both farms rather than within each farm. The models used in the present study also differed slightly to the models used by Conington *et al.* (2001) and Lambe *et al.* (2008) which, combined with the increased number of records available for the present study, may account for some of the differences observed.

The current hill sheep index aims to improve the sustainability of flocks, or in other words improve the efficiency, through the combination of both ewe and lamb traits (Conington *et al.* 2001). The traits EEFF and EEFF$^{0.75}$ aim in a similar direction but are more detailed, by describing the efficiency of the individual ewe, which is a trait that has been growing in interest in recent years. There are a number of different ways in which the trait has been measured, ranging from simple ewe weight/lamb weight ratios, (Iman & Slyter, 1996; Abegaz and Van Wyk, 2002; Carson *et al.*, 2001; Annett *et al.*, 2011; Lobo *et al.*, 2012) to complex models that concentrate on the cost:benefit aspects involving production costs compared with what is produced (Sise *et al.*, 2009).
Unfortunately, very few genetic parameters have been estimated, or published, for this type of trait in sheep. Abegaz and Van Wyk (2002) estimated heritabilities of 0.03 for both EEFF and EEFF\(^{0.75}\) when studying Horro sheep in Ethiopia, whereas in Brazil, Lobo et al. (2012), using the metabolic weight of crossbred ewes at weaning, rather than pre-mating, estimated a heritability of 0.10. The heritabilities estimated for EEFF and EEFF\(^{0.75}\) in the present study ranged from 0.09 to 0.13, providing evidence that future selection, based on this trait, could be achieved.

The methods used in the present study calculated the ratio of the ewes’ actual live weight, as well as the metabolic weight, at pre-mating, with that of the total weight of lamb reared to weaning. According to Lobo et al. (2012) the use of the metabolic weight could provide a fairer comparison of animals of different size. Indeed, although large ewes may produce heavy lambs, this does not necessarily mean they are the most efficient. Annett et al. (2011), similar to the present study, used both methods when evaluating the performance of both pure- and cross-bred Scottish Blackface ewes in Northern Ireland. The average values that they reported for EEFF and EEFF\(^{0.75}\), using only ewes that had lambed (i.e. a litter size > 0), ranged between 0.74 – 0.83 and 2.00 – 2.26 for each trait respectively. The estimates for EEFF and EEFF\(^{0.75}\) for the pure Scottish Blackface ewes were 0.75 and 2.00, therefore slightly higher than the averages observed in the present study, for both traits, at both farms. Carson et al. (2001), also using the metabolic weight of Scottish Blackface ewes, estimated averages per ewe lambed, and per ewe mated, ranging from 1.69 – 2.00 and 1.46 - 1.79 respectively, depending on the breed of the sire used to mate the ewes. The results for Scottish Blackface ewes mated with a Scottish Blackface ram, were 1.69 and 1.46 per ewe lambed and per ewe mated respectively. Finally, Iman
and Slyter (1996), while comparing pure and cross-bred Targhee ewes in the United States, estimated efficiency averages ranging from 1.47 to 1.65, also based on the metabolic weight of ewes mated.

There therefore seems to be different interpretations of ewe efficiency across studies. In the present study, only data from ewes that had reared a lamb(s) to weaning were used, whereas both Annett et al. (2011) and Carson et al. (2001) used data from ewes that had lambed. Carson et al. (2001) and Iman and Slyter (1996), also used data from all ewes mated. This will therefore explain the difference between the estimated efficiency averages, with the studies that estimated averages per ewe mated being the lowest. In theory, therefore, the estimates observed in the present study should be the highest as only data from ewes that reared a lamb(s) to weaning were used. However, the results obtained by Annett et al. (2011) were in fact the higher. This is likely to have in part been influenced by the different environments and the fact that the sires used by Annett et al. (2011) were within the top 25% of their respective breeding programmes, compared with the sires that were used in the present study, which had a range of index values. Another point to note is that the Scottish Blackface dataset used in the present study was the largest (12,424 in total), and recorded over an 18 year period, compared with 767 (over a 5 year period) used by Annett et al. (2011), and 1,440 (over a 2 year period) used by Carson et al. (2001). Therefore this may also account for some of the differences observed.

Should this trait be used in future selection programmes, a method of determining ewe efficiency would have to be agreed upon. As can be seen from the sample of studies discussed above, there are a number of potential options. Vatankha and
Salehi (2010) suggest that the metabolic weight of all ewes mated, combined with total weight of lambs weaned, should be considered as this provides the most conclusive measurement of efficiency based on a range of factors including conception rate, lambing rate, mothering ability and weaning weight.

3.5.2 GxE Observations

The problems that arose when calculating genetic correlations between farms, particularly for LWEAN, LLOST and LLOST Binomial were mainly associated with the high standard errors estimated. This could be due to the fact that these traits have very low heritabilities, particularly in Farm B, and that the data is not normally distributed. It may be that much more data would be needed for these traits to improve the reliability of results.

The GxE observed for PMWT could have implications for the future maintenance of the ewes. Although mature weight of the ewe is positively correlated with lamb weaning weight (Conington et al., 2004), it also has a strong linear relationship with the amount of energy required for maintenance (Garrett et al., 1959). In order to maintain performance, ewes with high mature weights require higher levels of inputs (e.g. feed, grazing, health treatments). Indeed, in the current hill sheep index there is a negative weighting placed on ewe mature weight, as the costs of increasing the mature weight of the ewe were deemed to outweigh the benefits (Conington et al., 2004). The high number of sires that re-ranked across farms is a concern. If ewes born in a certain environment from sires with a given EBV for mature weight have unexpectedly high mature weights, they will require a higher level of inputs in order to achieve their optimum level of performance. Alternatively, if ewes are
unexpectedly small, the correlated relationship with lamb weaning weight could result in smaller lambs which take longer to finish or are worth less when sold at market.

Some early studies have also shown that the body weight of ewes at pre-mating can influence ovulation rates. Morley et al. (1978) observed, across different breeds, a parallel increase of approximately 2% in ovulation rate for each additional kilo of live weight. The response of the Scottish Blackface in that study was with 6.7% and curvilinear in nature, with the optimum, in the population studied, being around 57kg. Michels et al. (2000) reviewed a number of studies that have observed increases in ovulation rate when different ranges of ewe weights were considered such as those by Edey (1968) and Guerra et al. (1972). Therefore the presence of GxE for PMWT could also affect prolificacy and potentially lambing rate.

An interesting point also observed by Lobo et al. (2012), relating to both the use of a ewe efficiency trait and the potential problems observed with the presence of GxE for PMWT, was a negative correlation (-0.25) estimated between the weight of the ewe at weaning and the efficiency of the ewe. Lobo et al. (2012) suggest, therefore, that their results provide evidence that, should a ewe efficiency trait be included in future breeding programmes, it could improve efficiency without increasing the mature weight of ewes. This aspect certainly deserves more attention in future studies especially for Scottish Blackface ewes.
3.6 Conclusions

Overall, the results have demonstrated little evidence of GxE in Scottish Blackface ewe traits, between the two farm environments studied. The heritability estimates observed at both farms, combined with the fact that the majority of genetic correlations estimated did not differ significantly from one, may suggest that the two farm environments were not divergent enough for GxE to be observed. The results also provide evidence that the common sires, used across both farms, were relatively “robust” with little variation in the performance of their daughters in each environment. Only the result obtained for PMWT ($r_g$ 0.48) provided a reliable indication of GxE. This could have implications in terms of ewe maintenance, prolificacy, lambing rate and lamb weaning weights. The study also identified the potential for selection based on a ewe efficiency trait, calculated using the total weight of lamb weaned per kilogram of ewe body weight at mating. Heritability estimates, at each farm, ranged from 0.09-0.13 (+0.02), however further work would be required to investigate this trait further before it could be considered for inclusion into future breeding programmes.
Chapter 4: Characterisation of terminal sire sheep farm systems in the context of genotype by environment interactions
4.1 Summary

The objective of this study was to define different terminal sire flock environments in the UK and then investigate the presence of genotype by environment interactions (GxE). Using data available from 79 different terminal sire flocks (40 Texel, 21 Charollais and 18 Suffolk), principal coordinate analysis, followed by a non-hierarchical cluster analysis, identified three distinct environmental cluster groups. The type of grazing, climatic conditions and the use of vitamins and mineral supplements were identified as the most important factors in the clustering of flocks.

The presence of GxE was further investigated using data from the Charollais flocks only. Performance data were collected for 12,181 lambs, between 1990 and 2010, sired by 515 different sires. Fifty six of the sires had offspring in at least two of the three different cluster groups and pedigree information was available for a total of 161,431 animals. Traits studied were the 21 week old weight (21WT), ultrasound muscle depth (UMD) and log-transformed back-fat depth (LogUFD). Heritability estimates for each cluster, for each trait, ranged from 0.32 – 0.45. Genetic correlations were estimated for each trait, between each cluster. The correlations estimated between clusters 1 and 2 were all found to be significantly lower than unity, indicating the presence of GxE. They were 0.23 (±0.17), 0.67 (±0.14) and 0.16 (±0.20) for 21WT, UMD and LogUFD, respectively. Significantly low correlations, of 0.25 (+0.45) and -0.08 (+0.54), were also estimated for 21WT and LogUFD, respectively, between Cluster 1 and Cluster 3. Evidence of sires re-ranking across clusters was also observed. Providing a suitable strategy can be identified, there is potential for the optimisation of future breeding programmes, by taking into account the GxE observed. This would allow farmers to identify and select animals with an increased knowledge as to how they will perform in a specific farm environment therefore reducing any unexpected differences in performance.
4.2 Introduction

Genetic evaluations currently carried out for livestock use best linear unbiased prediction (BLUP) technology (Henderson, 1975). In sheep breeding, providing there are suitable levels of genetic linkage between flocks, BLUP allows estimated breeding values (EBVs) to be expressed relative to a common base, from which direct comparisons can be made across flocks. However, a problem that farmers can encounter is that having selected to use an individual animal based on their predicted performance, they obtain somewhat unexpected and inconsistent results when they are used in another location (Peterson, 1988; Cienfuegos-Rivas et al., 1999).

As discussed in Chapter 1, studies into the effects of GxE in sheep are somewhat limited, particularly when compared to the dairy industry. The sheep studies discussed in Chapter 1, as well as similar ones carried out in the dairy and beef industries, demonstrate that a variety of different environment classifications have been used when researching GxE. Within the UK, the extensive nature of the sheep industry means that each flock has its own unique and diverse set of resources and management styles. In order to gain a deeper insight into the effects of GxE, it may be valuable to classify individual flocks into different groupings, thus combining flocks based on a wide range of variables such as climatic conditions, nutrition and overall flock management. One option available is to consider farm typologies, which use multivariate statistical methods and cluster analysis to identify homogeneous groups of farms (Kobrich et al., 2003; Gasper et al., 2007; Gelasakis et al., 2012; Morgan-Davies et al., 2012). The use of such an approach allows homogeneous clusters, or groupings, to be defined from large datasets that include a
number of unrelated variables. In the dairy industry, Weigel and Rekaya (2000), Zwald et al. (2003a) and Huquet et al. (2012a) have used cluster analysis in order to group countries, or individual herds, according to common factors so that the number of production environments could be reduced. Similar methods have also been used by Nesser et al. (2008) and Espasandin et al. (2013) when investigating GxE in beef cattle systems.

The purpose of this study therefore was, initially develop a terminal sire sheep farm typology, exploring the differences and similarities of the farms who record as part of the Signet Sheepbreeder programme (www.signetfbc.co.uk). Then, using the clusters identified, the presence of GxE, for traits important for the genetic improvement of terminal sire lambs, was investigated using data available for Charollais lambs as a case-study.

4.3 Materials and Methods

4.3.1 Farm Questionnaire

A questionnaire was developed, which adhered to the principles of Fowler (2002), and was sent to all 515 members of the Signet Sheepbreeder programme. A copy of the questionnaire can be found in Appendix 1. It contained 33 questions covering aspects such as the farm location and land cover; sheep numbers and breed; the management of the flock at mating, ultrasound pregnancy scanning, lambing, weaning and post weaning; grazing and feeding throughout the year (Grazing options provided were; hill/rough grazing, in-byre/improved pasture; any other crop field. Feeding options provided were; feed blocks; hay; silage; concentrate feed); the use of
vitamins and mineral supplements (as well as other health treatments) and labour use. A glossary of grazing and production terms can be found in Appendix 4. For the purpose of the present study, 22 of the original 33 questions were used, after excluding those that were not relevant or answered incorrectly. The questions posed varied in format. Some required a numerical answer (e.g. ewe numbers, ram to ewe ratios at mating, land areas); some a tick-box answer (e.g. the months concentrate feed was available, grazing locations throughout the year); some were scaled questions (e.g. grade the quality of grazing available between weaning and mating on a scale of 1 (poor quality) to 5 (high quality)) and some questions could be answered yes or no (e.g. organic or nonorganic, has any chemical resistance been identified on your farm).

The questionnaire attempted to characterise the specific management of each recorded sheep flock, relevant to the production data, and disregarded information on other enterprises on the farm. Where more than one breed was performance recorded on the same farm, respondents were asked to select one breed and answer the remaining questions based on the management of that breed only. A total of 200 questionnaires were returned, from a possible 515, achieving a 39% response rate. The questionnaires returned provided information for 28 different breeds, with the main terminal sire breeds (Charollais, Texel and Suffolk) providing 45% of the questionnaire respondents. Due to the high percentage of terminal sire breeders replying, the analysis concentrated on these breeds only. A number of questionnaires returned (n=11) were not complete, therefore 79 questionnaires from terminal sire flocks, across the UK, were used in the final analysis (consisting of 21 Charollais flocks, 18 Suffolk flocks and 40 Texel flocks). Terminal sire breeders record their
animals for genetic analysis using the Terminal Sire Index, which is used to help select individuals with increased lean meat yield in the carcass, but without increased levels of fatness (Simm and Dingwall, 1989; Macfarlane and Simm, 2007).

4.3.2 Weather and Lambing Data

The farm postcode was used to identify a longitude and latitude value for each farm location, using Bing Maps (http://www.bing.com/maps/). The postcode was also used to locate regional monthly rainfall (mm), average temperature (°C) and hours of sunshine data, across the UK (http://www.metoffice.gov.uk/climate/uk/datasets/). Overall means for each season were calculated over a 5-year period (2005-2009), with the seasons being classified as: Winter (Dec-Feb), Spring (Mar-May), Summer (Jun-Aug) and Autumn (Sept-Nov). Lambing dates were also available from Signet, via the Basco Database website (http://www.egenes.co.uk/bascosearchsheep/). The percentage of lamb births recorded during Winter and Spring, for each flock between the 2005 and 2009 breeding seasons, were then used in the analysis.

4.3.3 Typology Analysis

The analysis was carried out by a series of steps using Genstat (11th edition, VSN International Ltd, 2008). Where pairs of variables were found to be highly correlated \((r \geq 0.90\) or \(r \leq -0.90\)), one variable from each pair was removed. Variables that did not show any variation were also removed, as they provided little assistance to the development of the clusters (Köbrich et al., 2003). A similarity matrix was created between each variable included in the analysis, using simple matching and Euclidean methods for the discrete and quantitative variables respectively, as described by
Gower (1971). The similarity coefficients calculated ranged from zero (completely different) to one (absolutely identical). These data were then used in a subsequent principal coordinate (PCO) analysis. A non-hierarchical cluster analysis was then carried out on the PCO scores, using the between-group sum of squares criterion, in order to maximise Euclidean distance between groups. To assess the overall differences between the identified clusters, a one-way analysis of variance (ANOVA) was used for the quantitative variables, whilst a Kruskal-Wallis analysis was used for the discrete variables, similar to the methods used by Morgan-Davies et al. (2012).

In order to establish significant differences between each cluster, least significant difference (LSD) tests and Bonferroni corrected Mann-Whitney U tests were used as post-hoc tests for the ANOVA and Kruskal-Wallis analyses, respectively.

### 4.3.4 Genetic Analysis

Performance records for the Charollais flocks that responded to the questionnaire were further analysed to determine if GxE was evident between the different clusters. The traits studied were 21 week weight (21WT), ultrasound muscle-depth (UMD) and log transformed ultrasound fat-depth (LogUFD), all of which are measured once in the lifetime of the lamb, according to Signet Sheepbreeder protocol (www.signetfbc.co.uk). Ultrasound fat-depth was transformed to approximate normality. The average age of the lambs at 21 week weight (21WT) was 149 days (range 85-215 days). UFD and UMD measurements were taken at the third lumbar on the same day as the 21WT. The pedigree file used in the analyses contained sire and dam information for a total of 161,431 animals. Heritability estimates for each trait were estimated using univariate analyses in ASReml (Gilmour et al., 2002)
across all, as well as within, each cluster identified. Random effects in the models included a direct genetic effect (animal), maternal genetic effect (dam) and the permanent environment effect (pe), i.e. variation caused by the environment which the rearing ewe (either genetic dam, embryo transfer recipient dam or foster dam) provided for the lamb.

All biologically sensible effects and interactions were tested in order to find an appropriate fixed effects model, resulting in the following model being fitted for each trait:

\[
\text{Trait} = \text{mean} + \text{sex} + \text{age} + \text{litter size} + \text{lamb birth year} + \text{birth flock} + \text{rearing dam age} + (\text{sex} \times \text{age}) + (\text{sex} \times \text{litter size}) + \text{animal} + \text{dam} + \text{pe} + \text{error}
\]

Age was the age of the lamb (in days) at measurement, treated as a covariate. Rearing dam age, however, was treated as a fixed effect and measured in years (14 levels: 1 to 14 years old). Other factors in the model included lamb birth year (21 levels: 1990-2010) and sex (2 levels: male and female) and litter size (4 levels: 1 to 4 and above).

To investigate the presence of GxE, genetic correlations for the same traits across clusters were estimated by a series of bivariate analyses in ASReml, similar to the method proposed by Falconer (1952). The models used were similar to those used for the univariate analyses, although due to convergence problems only the direct genetic effect (animal) and the permanent environment effect (pe) were fitted for all traits. As in Chapter 2 and Chapter 3, the estimated correlations were then tested using a log-likelihood ratio test (LR). The test statistic, \( LR = 2(\text{logL0} - \text{logL1}), \)
therefore had a $X^2$ distribution with one degree of freedom. Spearman’s rank and Pearson’s correlation analyses were also calculated using the EBVs estimated using the bivariate analyses, for sires with 10 or more offspring in at least two of the different cluster groups.

4.4 Results

4.4.1 Typology Analysis

The data gathered from the questionnaires, as well as the weather and lambing season information, illustrated a wide range of different farming systems and locations. Farm size ranged from 3 ha to 10930 ha (average 272 ha), representing small lowland farms to large hill farming estates. Total recorded flock size ranged from 12 to over 400 ewes. When asked to classify their farm, 3 respondents selected hill-type system, 21 selected upland and 55 selected lowland. Some farms performance recorded all of their ewes, while others only recorded a proportion. The most commonly used grazing type throughout the year was the in-by/ Improved grazing, closely followed by the hay/silage field type grazing. In terms of labour, 49% of respondents spent less than a quarter of their time working with the recorded ewe flock.

4.4.2 Principal Coordinate Analysis

Overall, the PCO analysis used 146 variables (117 discrete and 29 quantitative), including questionnaire answers, weather data and lambing dates. Although 10 dimensions explained 100% of the variation, only the initial six (PCOs 1 to 6;
explaining 73% of the variation) were subsequently retained since each additional
dimension did little to distinguish the clusters and the associated variables proved
statistically non-significant. The variables with correlation coefficients above 0.5, or
below -0.5, with any of the 6 dimensions were investigated further for interpretation
purposes (Table 4.1).

**PCO Dimension 1: Seasonal Grazing**

Dimension 1, which explained 20% of the variation, was predominantly related to
the use of in-bye/improved and hay/silage types of grazing. The in-bye/improved
grazing variables identified in this dimension were related to the ewes grazing
between pregnancy scanning and lambing, as well as the single- and multiple-rearing
ewes between the 8-week lamb weight and weaning. The hay/silage field variables
were also related to the period between the 8-week lamb weight and weaning for
single- and multiple-rearing ewes, as well as for the single-rearing ewes between
pregnancy scanning and the 8-week lamb weight. The use of lamb vitamin
supplements was also included in this dimension.

**PCO Dimension 2: Weather and Vitamin/Mineral Supplementation**

Dimension 2 was influenced by sunshine hours and rainfall and explained 14% of the
variation. The supplementation of cobalt and selenium (both ewes and lambs) and
vitamins (ewes) were also associated with this dimension.

**PCO Dimension 3: The Use of Hay/Silage Field Grazing**

Dimension 3, which explained 12% of the variation, was solely related to the grazing
of hay/silage fields: between weaning and mating; during mating; for multiple-
rearing ewes between pregnancy scanning and the 8-week lamb weight; and for single-rearing ewes between pregnancy scanning and lambing.

**PCO Dimension 4: Ram Management**

Dimension 4 was influenced by ram management (predominantly ‘bought-in’ animals) during the month prior to mating, including where rams / ram lambs were kept (housed or outside) and whether or not concentrate feeding was provided. Overall, 10% of the variation was explained by this dimension.

**PCO Dimensions 5 & 6: Use of Hill/Rough Type Grazing and Ecto-parasite Treatments**

Dimension 5 (9% of variation) was associated with just one variable, the use of hill/rough grazing by the ewes between weaning and mating, whereas dimension 6 (8% of variation) was influenced by the control of ecto-parasites, such as sheep scab and lice.
Table 4.1 Variables and correlation coefficients ($r$) used to characterise PCO dimensions 1-6. Overall differences between clusters assessed by analysis of variance (ANOVA and Kruskal-Wallis) for quantitative and discrete variables respectively

<table>
<thead>
<tr>
<th>PCO</th>
<th>$r$</th>
<th>Variable</th>
<th>Sig.</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.6</td>
<td>Do the ewes have access to improved grazing between mating and scanning?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do the barren ewes have access to improved grazing between pregnancy scanning and lambing?</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do the single bearing ewes have access to improved grazing between pregnancy scanning and lambing?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do the twin bearing ewes have access to improved grazing between pregnancy scanning and lambing?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do the single bearing ewes have access to hay/silage field-type grazing between pregnancy scanning and lambing?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do the single bearing ewes have access to hay/silage field-type grazing between lambing and lamb 8-week weight?</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>0.5</td>
<td>Do the single bearing ewes have access to improved grazing between lamb 8-week weight and weaning?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do the twin bearing ewes have access to improved grazing between lamb 8-week weight and weaning?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>-0.6</td>
<td>Do the single bearing ewes have access to hay/silage field-type grazing between lamb 8-week weight and weaning?</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>-0.6</td>
<td>Do the twin bearing ewes have access to hay/silage field-type grazing between lamb 8-week weight and weaning?</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do you give your lambs a vitamin supplement?</td>
<td>***</td>
</tr>
<tr>
<td>2</td>
<td>0.6</td>
<td>Average winter rainfall (mm)</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Average number of sun hours during the winter (hours)</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>0.7</td>
<td>Do you give your ewes a cobalt supplement?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do you give your ewes a selenium supplement?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do you give your ewes a vitamin supplement?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do you give your lambs a cobalt supplement?</td>
<td>***</td>
</tr>
<tr>
<td></td>
<td>0.6</td>
<td>Do you give your lambs a selenium supplement?</td>
<td>***</td>
</tr>
<tr>
<td>3</td>
<td>-0.5</td>
<td>Do you keep your ewes on hay/silage field-type grazing between weaning and mating?</td>
<td>*</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do you mate your ewes on hay/silage field-type grazing?</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do the twin bearing ewes have access to hay/silage field-type grazing between pregnancy scanning and lambing?</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do the single bearing ewes have access to hay/silage field-type grazing between lambing and lamb 8-week weight?</td>
<td>**</td>
</tr>
<tr>
<td></td>
<td>-0.6</td>
<td>Do the twin bearing ewes have access to hay/silage field-type grazing between lambing and lamb 8-week weight?</td>
<td>*</td>
</tr>
<tr>
<td>4</td>
<td>-0.6</td>
<td>Do you keep bought-in ram lambs outside during the month before mating?</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>-0.7</td>
<td>Do you keep bought-in shearling rams (or older) outside during the month before mating?</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do you feed bought-in shearling rams (or older) concentrates during the month before mating?</td>
<td>NS</td>
</tr>
<tr>
<td>5</td>
<td>-0.5</td>
<td>Do you keep your ewes on hill/rough grazing between weaning and mating?</td>
<td>NS</td>
</tr>
<tr>
<td>6</td>
<td>-0.5</td>
<td>Do you routinely treat your flock for/against sheep scab?</td>
<td>NS</td>
</tr>
<tr>
<td></td>
<td>-0.5</td>
<td>Do you routinely treat your flock for/against lice?</td>
<td>NS</td>
</tr>
</tbody>
</table>
4.4.3 Non-Hierarchical Cluster Analysis

Overall, it was possible to identify 3 homogenous clusters of farm environments (Figure 4.1). Of the 79 farms, 32 were in the first cluster, 25 in the second and 22 in the third. All three terminal sire breeds were represented in each of the groups (Table 4.2). Comparison of PCO dimension 1 with PCO dimension 2 clearly showed that the farm clusters were distinct (Figure 4.1), but appeared less so when other pairs of dimensions were compared (Figure 4.2). The analysis of variances (ANOVA and Kruskal-Wallis) on the descriptive variables, highlighted by each dimension, supported this distinction since the statistical significance dropped in line with the percentage variance.

<table>
<thead>
<tr>
<th>Cluster</th>
<th>Charollais</th>
<th>Suffolk</th>
<th>Texel</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>11</td>
<td>8</td>
<td>13</td>
</tr>
<tr>
<td>2</td>
<td>7</td>
<td>7</td>
<td>11</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>3</td>
<td>16</td>
</tr>
</tbody>
</table>
Figure 4.1. Positioning of farms according to the scores obtained for Principal Dimensions 1 and 2
Figure 4.2. Positioning of farms according to the scores obtained for (i) Principal Dimensions 2 and 3 and (ii) Principal Dimensions 1 and 3
**Cluster 1**

Cluster 1 flocks predominantly used in-bye/improved grazing throughout the year, significantly more so ($P<0.05$) than flocks in Cluster 2 (Appendix 3 Table A1). Few gave vitamin or mineral supplements to ewes or lambs, indeed significantly fewer ($P<0.05$) when compared to Cluster 3 and Cluster 2 for all, with the exceptions of Copper (Cluster 2 and Cluster 3) and Cobalt and Selenium (Cluster 2), (Appendix 3 Table A2). Other characteristics of Cluster 1 flocks (Appendix 3 Table A3) included an average farm size of 128 ha, an average flock size of 88.3 recorded ewes and an average of 249.4 ewes in total. Rainfall averages, throughout the year, were significantly lower ($P<0.001$) than those of Cluster 2 and Cluster 3. The average hours of sunshine, during the summer, autumn and winter months, were significantly higher ($P<0.05$) than in Cluster 3. Average temperatures for Cluster 1 flocks were significantly higher ($P<0.05$) than Cluster 3 during the spring, summer and autumn months. The average number of days that the rams were with the ewes during mating was 48.1, significantly higher ($P<0.05$) than those in Cluster 2 (33.4 days). On average, 59.8% of lambs born into these flocks were born during the winter months (Dec-Feb). Supplementary feed blocks were, on average, used for 1.2 months a year, which was significantly lower ($P<0.05$) than in Cluster 2 (3.7 months). The average number of weeks that the lambs had access to concentrate feed before weaning was 6.5. Only 44% of flocks regularly treated for liver fluke, which was significantly lower ($P<0.001$) when compared with 91% in Cluster 3.
Cluster 2

In Cluster 2, an increased proportion used hay/silage field grazing between pregnancy scanning and weaning, significantly different \((P<0.05)\) when compared to Cluster 1 (Appendix 3 Table A1). There was also a significant difference between pregnancy scanning and lambing \((P<0.05)\) when compared to Cluster 3 (Appendix 3 Table A1). The data presented in Appendix 3 Table A3 shows that farms in this cluster had significantly less \((P<0.05)\) in-by/improved grazing (26.1% as a proportion of their farm) compared to those in Cluster 3 (54.5%). The average farm size in Cluster 2 was 543.8 ha, but this was not significantly different \((P>0.05)\) to either Cluster 1 or Cluster 3, due to a high standard deviation. The average number of recorded ewes on each farm was 75.4, with an average total ewe flock of 587.7 ewes. Flocks in this cluster, on average, mated 36.6 ewes via AI, a significantly higher number \((P<0.05)\) when compared to an average of just 7 in Cluster 3. The average number of days that the ewes were with a ram was 33.4, which was significantly lower \((P<0.05)\) than Cluster 1. The average percentage of lamb births in winter was 67% and lambs had access to concentrate feed, on average, 8 weeks prior to weaning. (Appendix 3 Table A3).

Cluster 3

The third cluster, similar to Cluster 1, also relied heavily on improved/in-by grazing and less so on hay/silage field grazing. Indeed, on average, the farms within this cluster had over 50% of their farm made up of improved grazing, a significantly higher proportion \((P<0.05)\) than Cluster 2. The average farm size in Cluster 3 was 173.6 ha, the average number of recorded ewes on each farm was 87, with an
average total ewe flock of 578.3 ewes. The flocks in this cluster were associated with significantly higher ($P<0.001$) rainfall averages, throughout the year, when compared to both Cluster 1 and Cluster 2. This may be related to the fact that a significantly high proportion ($P<0.05$) of flocks within this cluster (91%), compared with those in Cluster 1 (44%), routinely treated their animals for liver fluke, a problem commonly associated with areas of higher rainfall. Flocks in Cluster 3 also experienced significantly fewer hours of sunshine ($P<0.05$) during the summer, autumn and winter months when compared to flocks in Cluster 1. Average temperatures were significantly lower ($P<0.05$) than those for Cluster 1 during the spring, summer and autumn months (Appendix 3 Table A3). A high proportion also provided their ewes and lambs with both Cobalt, Selenium and vitamin supplements (Appendix 3 Table A2), which was significantly higher ($P<0.05$) than flocks in Cluster 1. Flocks in this cluster had a high average number mated naturally (75.8) and a significantly lower ($P<0.05$) average number of ewes mated via AI (7), when compared to Cluster 2. The average percentage of lamb births registered during the spring months was 52.1% and was higher than both Cluster 1 and Cluster 2 flocks (33.9% and 28.8% respectively). Finally, the lambs, on average, had access to creep feeding 5.4 weeks before weaning, less than both Cluster 1 and 2 (6.5 and 8.1 weeks respectively), (Appendix 3 Table A3).

### 4.4.4 Genetic Analyses

Performance data were available for 18 of the 21 responding Charollais flocks and included animals sired by a total of 515 different sires, between 1990 and 2010. Data were unavailable for 3 newly-recorded flocks (2 allocated to Cluster 1 and 1
allocated to Cluster 2), whilst an additional flock from Cluster 2 had no ultrasound data. Of the 515 sires used, only 1 had offspring across all three clusters, whereas 55 had offspring across two of the cluster groups. The majority of sires used across two clusters were used between Cluster 1 and Cluster 2 (n=53). The average number of offspring that each of the 53 sires had in Cluster 1 and Cluster 2 were 41 and 13 respectively. Three sires were used between Cluster 1 and Cluster 3 whereas one was used between Cluster 2 and Cluster 3. A summary of the traits included in the genetic analysis are shown in Table 4.3.

Table 4.3. Summary of traits included in genetic analysis data set

<table>
<thead>
<tr>
<th>Trait</th>
<th>Cluster</th>
<th>Count</th>
<th>Mean</th>
<th>s.d.</th>
<th>Min.</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>21 Week Weight - 21WT (kg)</td>
<td>Overall</td>
<td>12181</td>
<td>51.25</td>
<td>10.05</td>
<td>15</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>8640</td>
<td>50.86</td>
<td>9.63</td>
<td>15</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2949</td>
<td>53.09</td>
<td>10.71</td>
<td>22</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>592</td>
<td>47.75</td>
<td>11.15</td>
<td>23</td>
<td>80</td>
</tr>
<tr>
<td>Ultrasound Muscle Depth – UMD (mm)</td>
<td>Overall</td>
<td>11534</td>
<td>29.28</td>
<td>3.51</td>
<td>15.8</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>8257</td>
<td>29.15</td>
<td>3.41</td>
<td>17</td>
<td>42</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2691</td>
<td>29.75</td>
<td>3.47</td>
<td>16</td>
<td>40.9</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>586</td>
<td>29.02</td>
<td>4.7</td>
<td>15.8</td>
<td>40.2</td>
</tr>
<tr>
<td>Ultrasound Fat Depth – UFD (mm)</td>
<td>Overall</td>
<td>11534</td>
<td>3.96</td>
<td>1.86</td>
<td>0.1</td>
<td>15.5</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>8257</td>
<td>3.88</td>
<td>1.79</td>
<td>0.3</td>
<td>15.5</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>2691</td>
<td>4.31</td>
<td>2.05</td>
<td>0.1</td>
<td>12.5</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>586</td>
<td>3.45</td>
<td>1.6</td>
<td>0.4</td>
<td>9.9</td>
</tr>
</tbody>
</table>

The heritabilities estimated for each trait across all clusters ranged from 0.39 - 0.43 and from 0.32 – 0.45 for each trait within a cluster (Table 4.4). Cluster 1 had the highest estimates for both UMD and LogUFD, whereas Cluster 2 had the highest estimate for 21WT. Those estimated for Cluster 3 were consistently lower and associated with the highest standard errors, due to the lower number of data records.
Maternal heritabilities were low and ranged from 0.01 to 0.10. The lowest values were estimated for Cluster 2 whereas the highest values were associated with Cluster 3 for 21WT and UMD, although these were also associated with high standard errors. Common environmental effects were also low and in most cases were not significantly different from zero.

Table 4.4. Univariate direct ($h^2_d$) and maternal ($h^2_m$) heritabilities, common environmental effects ($c^2$) and phenotypic variances ($\sigma^2_p$) between clusters for each trait (s.e. in parenthesis)

<table>
<thead>
<tr>
<th>Trait</th>
<th>Cluster</th>
<th>$h^2_d$</th>
<th>$h^2_m$</th>
<th>$c^2$</th>
<th>$\sigma^2_p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>21WT</td>
<td>Overall</td>
<td>0.39 (0.02)</td>
<td>0.08 (0.01)</td>
<td>0.04 (0.01)</td>
<td>47.21 (0.80)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.42 (0.03)</td>
<td>0.08 (0.02)</td>
<td>0.05 (0.01)</td>
<td>46.48 (0.94)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.45 (0.05)</td>
<td>0.04 (0.03)</td>
<td>0.03 (0.02)</td>
<td>41.29 (1.40)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.41 (0.14)</td>
<td>0.10 (0.10)</td>
<td>0.02 (0.07)</td>
<td>45.11 (3.71)</td>
</tr>
<tr>
<td>UMD</td>
<td>Overall</td>
<td>0.41 (0.02)</td>
<td>0.03 (0.01)</td>
<td>0.02 (0.01)</td>
<td>9.09 (0.15)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.41 (0.03)</td>
<td>0.02 (0.01)</td>
<td>0.02 (0.01)</td>
<td>8.63 (0.17)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.39 (0.05)</td>
<td>0.01 (0.02)</td>
<td>0.02 (0.02)</td>
<td>7.77 (0.26)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.32 (0.14)</td>
<td>0.07 (0.08)</td>
<td>0.01 (0.06)</td>
<td>10.10 (0.78)</td>
</tr>
<tr>
<td>LogUFD</td>
<td>Overall</td>
<td>0.43 (0.02)</td>
<td>0.06 (0.01)</td>
<td>0.03 (0.01)</td>
<td>0.19 (0.003)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.45 (0.03)</td>
<td>0.06 (0.02)</td>
<td>0.03 (0.01)</td>
<td>0.18 (0.004)</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.38 (0.05)</td>
<td>0.03 (0.03)</td>
<td>0.03 (0.02)</td>
<td>0.18 (0.006)</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.40 (0.14)</td>
<td>0.03 (0.09)</td>
<td>0.09 (0.07)</td>
<td>0.14 (0.011)</td>
</tr>
</tbody>
</table>

The genetic correlations estimated between Cluster 1 and Cluster 2, for each trait, were all significantly less than 1 ($P<0.001$) and are shown in Table 4.5. The highest correlation was estimated for UMD (0.68) and the lowest for LogUFD (0.14), with the latter not significantly different from zero. The genetic correlations estimated for 21WT and LogUFD between Cluster 1 and Cluster 3 (0.25 and -0.08 respectively) were also both significantly different to 1 ($P<0.05$). All correlations estimated between Cluster 2 and Cluster 3 were high and not significantly different to 1 ($P>0.05$).
Table 4.5. Genetic correlations above diagonals (s.e. in parenthesis) and likelihood ratio \( P \)-values (in bold) below diagonals between the three different cluster groups for 21 week old weight (21WT), ultrasound muscle (UMD) and fat (LogUFD) depth.

<table>
<thead>
<tr>
<th></th>
<th>21WT</th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Cluster</td>
<td>1</td>
<td></td>
<td></td>
<td>0.29</td>
<td>0.25</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>&lt;0.001</td>
<td>1.00</td>
<td>0.70</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>0.016</td>
<td>0.322</td>
<td>0.549</td>
<td>0.454</td>
</tr>
</tbody>
</table>

The EBVs of the 53 common sires, used across Cluster 1 and Cluster 2, were further investigated. By using the EBVs for each common sire who had a minimum of 10 offspring in both cluster groups (n=9), the analysis found that a number of the sires re-ranked across the two cluster groups. The results of which, using Spearman’s Rank and Pearson correlations, are shown in Table 4.6. Negative correlations were estimated for 21WT whereas low and positive correlations were estimated for UMD. The Spearman’s Rank correlation estimated for LogUFD was low and positive, whereas the Pearson correlation estimated was low and negative.

Table 4.6. Pearson (PR) and Spearman’s Rank (SpR) Correlations between Cluster 1 and Cluster 2 for 21 week old weight (21WT), ultrasound muscle (UMD) and fat (LogUFD) depths.

<table>
<thead>
<tr>
<th></th>
<th>Cluster 2 21WT</th>
<th>Cluster 2 UMD</th>
<th>Cluster 2 LogUFD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cluster 1 21WT</td>
<td>PR</td>
<td>-0.73</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SpR</td>
<td>-0.30</td>
<td></td>
</tr>
<tr>
<td>Cluster 1 UMD</td>
<td>PR</td>
<td>0.14</td>
<td></td>
</tr>
<tr>
<td></td>
<td>SpR</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Cluster 1 LogUFD</td>
<td>PR</td>
<td></td>
<td>-0.15</td>
</tr>
<tr>
<td></td>
<td>SpR</td>
<td></td>
<td>0.10</td>
</tr>
</tbody>
</table>
4.5 Discussion

Clustering techniques, in relation to GxE, have been used in a number of studies using dairy and beef cattle. Previously, individual countries were used as the production environments, such as in the study by Lee and Bertrand (2002). However, by employing this method, such analyses do not take into account the fact that farms within countries may differ substantially and that farms in different countries may have similar environments and management systems. The studies carried out by Weigel and Rekaya (2000) and Espasandin et al. (2013) are two examples where clusters of farm environments were identified across different countries, thus allowing genetic correlations to be estimated between cluster groups rather than between countries. Similar methods have also been used within countries (Neser et al., 2008; Huquet et al., 2012).

The variables used to cluster the farms, in the cattle studies mentioned above, often included information such as climatic conditions, performance indicators (such as milk yield or weight at weaning) and herd size. However, in the present study, the extensive nature of sheep farming systems means that many more environmental variables could be involved in influencing the performance of the animals. For this reason, the present analysis investigated whether it was possible to construct clusters of farms with similar environments and management systems using typology techniques. With the exception of the study by Morgan-Davies et al. (2012), the present study differed slightly to other typology studies, due to the fact that principal coordinate analysis (PCO) was used rather than principal component analysis (PCA) (Köbrich et al., 2003; Gelasakis et al., 2012). Gower (1966), comments that the use
of PCA is not suitable when the dataset includes qualitative, or discrete, data, therefore when considering the mix of quantitative and discrete data used in the current study, PCO was selected.

The increased level of detail gained in the present study was predominantly related to grazing management throughout the season, as well as the provision of supplementary feeding, vitamins and minerals. Studies by both Macfarlane et al. (2004a, 2004b) and Speijers et al. (2009) demonstrated significant results when breed by feed type interactions were examined. Although the breeds and crossbreeds used in the study by Speijers et al. (2009) were perhaps more associated with hill farming environments, the results demonstrated clear differences between three different diets and between the different breeds used. Macfarlane et al. (2004b) observed significant differences in the growth responses of lambs grazing different sward types, which, along with the results of Speijers et al. (2009), demonstrate that differences in the magnitude of genetic superiority can exist between animals on different grazing types. This may somehow explain the differences in performance of common sire offspring across the different cluster groups in the present study.

In the present study, the farmers were asked to identify where the flock had access to graze throughout the year. They were provided with four different grassland-type options and it was up to the individual farmer in terms of how they classified the different grassland areas of their farm. It may have perhaps been preferable to have more specific grazing options, based on aspects such as sward structure, thus improving the reliability of the data. Nonetheless, the results highlight that
differences in grazing-use, throughout the year, are something that should be considered if farm environments are clustered in the future.

Significant weather differences between cluster groups are very likely to have influenced flock management, particularly lambing dates and grazing management, due to effects on length of the grass growth season, quality of grass and animal behaviour. Flocks in Cluster 1, on average, were exposed to the lowest rainfall levels, the highest number of sunshine hours and the highest temperatures throughout the year. In contrast, flocks in Cluster 3 experienced, on average, the highest rainfall, lowest sunshine hours and temperatures throughout the year. Indeed Steinheim et al. (2004) found that weather conditions often had a significant effect on the autumn weight (similar to the 21WT in the present study) of lambs in Norway.

The participation in performance and pedigree recording in the UK sheep industry has been aided through the use of AI and embryo transfer, as well as farmers progressively sourcing both male and female stock with EBVs for traits that they wish to improve. Connectedness between flocks (or clusters in this case) is necessary to ensure reliable across-flock/cluster genetic comparisons (Lewis et al., 1999). As mentioned previously in Chapter 2, the level of connectedness can be quantified through the use of prediction error correlations, also known as connectedness correlations (Lewis et al., 1999 and 2005). Kuehn et al. (2008) suggests suitable benchmarks for assessing the level of connectedness are 0.05 for “good” and 0.10 for “superior” connectedness. The flocks, and therefore clusters, in the present study were reasonably well linked genetically. The average pairwise levels of connectedness between the clusters, in 2011, were 0.11, 0.05 and 0.07 between
Cluster 1 and Cluster 2; Cluster 2 and Cluster 3; and Cluster 1 and Cluster 3 respectively (K. Moore, pers. communication). Kuehn et al. (2008) also comment that correlations above 0.10 correspond with an approximate 90% reduction in bias, therefore although correlations were calculated between all combinations of cluster groups, those calculated between Cluster 1 and Cluster 2 were deemed the most informative and reliable. The lower connectedness correlations associated with Cluster 3 and the other two cluster groups will be related to the low number of common sires used between them (only 3 flocks in Cluster 3 and low use of technologies such as AI).

The genetic correlations estimated between Cluster 1 and Cluster 2, for 21WT, UMD and LogUFD, as well as between Cluster 1 and Cluster 3 for 21WT, were significantly below unity ($P<0.05$), suggesting the presence of GxE. This was further highlighted by the values obtained from both the Pearson and Spearman’s rank correlations, indicating the presence of re-ranking between environments.

As mentioned previously, the presence of GxE can reduce genetic gain by lowering the accuracy of selection (Mulder and Bijma, 2005). This, in turn, can therefore affect the efficiency of index selection, due to unfavourable variability in terms of both predicted financial and genetic gains, as demonstrated by Dominik and Kinghorn (2008).

If the clusters identified in the present study are representative of the UK terminal sire sheep industry overall, the results, particularly between Cluster 1 and Cluster 2, suggest the reliability of genetic evaluations could be improved by taking into account the GxE observed. Providing there are suitable genetic links across clusters,
the use of a cluster model would allow an EBV for each animal to be predicted for each environment, thus allowing the identification of animals best suited to specific environments, or animals that will perform consistently across a number of environments, as suggested by Neser et al. (2008). This would potentially reduce any unwanted effects of GxE and allow farmers to select animals best suited to their farm environment.

Alternatively, as discussed by Mulder et al. (2006), different breeding strategies may be an option, depending on the level of genetic correlations estimated between the different environments. Mulder et al. (2006) observed, while investigating GxE in the dairy industry, that when genetic correlations, estimated between environments, were below 0.61, genetic gain was optimised when there was environment specific breeding programs progeny testing sires in their specific environment only. If correlations above 0.61 were estimated, a single breeding programme, progeny testing all sires in each environment and applying index selection would be optimal in order to improve performance in all environments simultaneously. Further investigation would be required in order to assess what level of correlation would affect the choice of strategy in relation to sheep breeding as well as the practicalities of progeny testing. For example, financially, from the farmer’s point of view, would the implementation of such a sire progeny testing scheme be cost effective when compared to the potential financial losses that may be incurred through the presence of GxE?

However, if clustering methods were to be further developed, for commercial use, a suitable level of information would be required to ensure the clusters identified were
a reliable and true reflection of the different farms systems within the overall industry. It may be an option for future investigation to use only variables readily available for all farms in the UK, such as those obtained through government census statistics for example. This would remove the need for farmers to actively respond to an additional survey and increase the number of farms, and therefore data, available for analysis. The additional data would also allow the investigation of breed specific clusters rather than the across breed clusters used in the present study. The clusters would also have to have the ability to incorporate any future changes to the variables involved, as well as accounting for any possible heterogeneity of variances present. The results of the present study also highlight that it is vital all environments are genetically well linked. For example, it may be that if the Texel data were used, the reliability of estimates associated, particularly between Cluster 2 and Cluster 3 would be improved due to the increased number of flocks allocated to these clusters. An alternative option available to breeders would be the potential use of reaction norms, which rely less on the connectedness between individual farms because the environments are measured on a continuous scale (Huquet et al., 2012b). Further investigation, using this method, would also be beneficial.

4.6 Conclusions

In conclusion, although the analysis presented only provides a “snap-shot” view of the UK terminal sire flock, the subsequent genetic analyses gives some indication of the problems and opportunities that could arise. The increased level of information gathered, particularly in terms of grazing and the use of vitamin and mineral supplements, enabled three distinct clusters to be identified. It remains to be seen, in
future studies, if these are representative of the overall terminal sire flock in the UK, but it does demonstrate the different variables that could be involved in grouping flocks into similar environment and management types. The genetic correlations estimated for all traits investigated, between Cluster 1 and Cluster 2, were all significantly below unity, suggesting the presence of GxE, with those for 21WT and LogUFD particularly low. The evidence of Charollais sires re-ranking between Cluster 1 and Cluster 2 suggest that the performance of their offspring was being controlled by different genes in different environments. Providing a suitable strategy can be identified, there is potential for improving the efficiency of future sheep breeding programmes, by taking into account the GxE observed. This would enable farmers to identify and select animals with an increased knowledge as to how they will perform in their specific farm environment thus reducing any unexpected differences in performance. The study has also highlighted a number of areas worthy of future investigation in order to strengthen the implications and conclusions reached.
Chapter 5: Reaction norm analysis of Texel sheep performance in different farm environments
5.1 Summary

The subject of genotype by environment interactions (GxE), and their effect in livestock breeding, can be complex and dependent on a number of different factors. In order to assess the extent of environmental sensitivity and any associated GxE, in sheep farm systems, environmental factors must be identified and quantified, after which the relationship with the traits(s) of interest can be investigated.

The objectives of this study were to develop a farm environment scale, using a canonical correlation analysis, which could then be used in linear reaction norm models to investigate the level of GxE present. Fine-scale, farm survey data, collected from a sample of 40 Texel flocks, was combined with information available at the national level, for Texel flocks across the UK. The farm survey data included information on flock size and concentrate feed use. National data included flock performance averages for 21 week old weight (21WT), ultrasound back-fat (UFD) and muscle (UMD) depths as well as regional climatic data. The canonical correlation estimated between the two sets of variables was 0.73.

The farm environment scale developed was then combined with 181,555 (21WT), 175,399 (UMD) and 175,279 (UFD) records from lambs born between 1990-2011, on 494 different Texel flocks, to predict reaction norms for Texel sires in the population. Correlations estimated between the level and slope of each reaction norm, for each trait, indicated the re-ranking of sires in different environments. A range of sire sensitivities estimated across the farm environment scale confirmed the presence of genetic variability, as both “plastic” and “robust” genotypes were observed in the population. Variation in heritability estimates were also observed indicating that the rate genetic progress will vary depending on the environment.

The ability to identify differences in sensitivity therefore potentially allows farmers to select animals best suited to specific environments as well those that will perform consistently across a range of environments. The results from this study therefore indicate that in order to improve genetic gain and flock efficiency, future genetic evaluations would benefit by accounting for the GxE observed.
5.2 Introduction

Genotype by environment interactions (GxE) can occur when genotypes respond differently to changes in the environment. Throughout the previous chapters, in order to investigate GxE, environments have been classed as individual farms (Chapter 2 and Chapter 3) or clustered into groups (Chapter 4). By considering the performance of different genotypes in the different environments as separate traits, both of these methods have allowed the estimation of genetic correlations between the environments and therefore establish if GxE exists.

As discussed in Chapter 1, as well as identifying the presence of GxE, the degree by which genotypes vary across environments is also of interest. This is often referred to as *phenotypic plasticity* (Bradshaw, 1965; de Jong and Bijma, 2002) or *environmental sensitivity* (Falconer, 1990; Kolmodin et al., 2002). Genotypes are considered “plastic” if they demonstrate highly variable phenotypes across environments or “robust” if they remain relatively constant (de Jong and Bijma, 2002; Bryant et al., 2005). Plasticity, or sensitivity, can be calculated by reaction norms, which are obtained by random regression on environmental descriptors (Strandberg et al., 2000; Kolmodin et al., 2002; Fikse et al., 2003). In other words, the model describes the phenotype expressed by a certain genotype over a number of different environments. This can be particularly useful when environments are described along a continuous scale or gradient (de Jong and Bijma, 2002).

The regression of sire breeding values on a continuous measure of environment in which records from their offspring exist, allows reaction norms to be predicted for
individual sires (Kolmodin et al., 2002). In terms of animal breeding, early studies for lactation in dairy cattle used random regression test day models to predict the lactation curves of individual dairy cows (Schaeffer and Dekkers, 1994). However more recently, interest has grown with regards to their use to describe the variation of traits across environmental gradients such as those in the dairy cattle (Calus et al., 2002; Kolmodin et al., 2002; Strandberg et al., 2009), beef cattle (Mattar et al., 2011; Santana et al., 2013a), pigs (Knap and Su, 2008) and sheep (Pollot and Greeff, 2004; Santana et al., 2013b).

In order to assess the extent of environmental sensitivity, and any associated GxE, environmental factors need to be identified and quantified, after which the relationship with the trait(s) of interest can be investigated. In experimental situations, environments can often be clearly defined, allowing relatively straightforward analyses. However, in commercial animal breeding circumstances, analyses can become more complicated, with a range of different factors determining each farm environment (FE). This is particularly true for sheep systems, which can differ in a number of aspects such as climatic conditions, flock size, health status and the level of inputs. There are a number of different methods to determine FE, including the use of specific environmental descriptors such as rainfall and temperature (Fikse et al. 2003; Ravagnolo et al. 2000), the use of phenotypic means or deviations (Calus et al. 2002; Kolmodin et al. 2002) as well as the identification of contemporary groups (Pollott and Greeff, 2004; Matter et al. 2011; Santana et al. 2013a, 2013b).
Alternatively, a method similar to the one used by Haskell et al. (2007), while assessing the effect of different environments on the lifespan of dairy cattle, may prove useful in defining FE. This method involves establishing a relationship between fine-scale information provided by a sample of farms with information available nationally for all farms. The scale developed by Haskell et al. (2007) has also been used by Strandberg et al. (2009) while investigating fertility traits in dairy cattle. The development of a similar scale, applicable to sheep systems, would potentially allow future genetic evaluations to take GxE into account, through the inclusion of reaction norm models. Farmers could identify where their system would lie along an environmental scale, from which they could select animals that would best suit their system. Any negative effects from GxE that may be evident would potentially be reduced, thus enabling farmers to improve their production level through the increased knowledge of predicted animal performance.

The aims of this study were therefore to a) relate fine-scale, farm-level data, collected from a sample of UK flocks, with information available at the national level, in order to provide a definition of FE and b) to assess the effect of FE on Texel sires for lamb performance traits across the UK.
5.3 Materials and Methods

5.3.1 Farm Environment Definition

Farm Survey

In order to obtain greater insight into the different management systems used on each farm, and therefore overall farm environments, a survey was carried out involving members of the Signet Sheepbreeder programme. A questionnaire was developed and sent to all 515 members, across the UK, in 2009. Questions posed covered aspects such as farm location and land cover; sheep numbers and breed; management of the flock throughout the year; health treatments and the use of labour. The questionnaire and results have been discussed in detail in Chapter 4. Data collected from the 40 Texel flocks that responded, were used in the current study, as this breed provided the most respondents. The data collected regarding the use of concentrate feed was selected to provide information on the level of feed inputs for each flock, from which an environmental scale could be developed.

National Data

Traits chosen to describe all farm environments across the UK were selected on the basis that they were readily available for all flocks. They included flock averages for 21 week old weight (21WT), ultrasound back-fat (UFD) and muscle (UMD) depths, as well as average annual rainfall, number of sun hours and temperature values.

The flock averages for 21WT, UFD and UMD were calculated using performance records available from Signet. After editing the data to remove outliers and all
records from lambs ± 3 SD units from the average age at the point of measurement, a total of 183,153 pure Texel lamb performance records, from 536 different flocks, between 1990 and 2011 were analysed. For each flock, adjusted averages for 21WT, UMD and UFD were obtained by applying the following fixed effects model, using ASReml (Gilmour et al., 2002):

\[
\text{Trait} = \text{mean} + \text{sex} + \text{age} + \text{litter size at birth} + \text{birth year} + \text{rearing dam age} + (\text{sex} \times \text{age}) + \text{flock} + \text{error}
\]

Age was the age of the lamb (in days) at measurement, treated as a covariate. Rearing dam age was included as a fixed effect measured in years (7 levels: 1 to ≥7). Other factors included lamb birth year (22 levels: 1990 to 2011); sex (2 levels: male and female); litter size at birth (4 levels: 1 to ≥4) and flock (536 levels).

Farm postcodes were used to identify the farm location, using Bing Maps (http://www.bing.com/maps/), and subsequently the appropriate weather data available from the 10 regions across the UK, as provided by the Met Office (http://www.metoffice.gov.uk/climate/uk/datasets/). Average annual means were calculated for the 5-year period between 2005 and 2009 for regional temperature, rainfall and number of sun hours. This time period was the 5-year period prior to the questionnaire being distributed and was used as representative of the environmental conditions experienced by the flocks throughout the time span of the data.

### 5.3.2 Canonical Correlation Analysis

Canonical correlation analysis (CCA) is a correlation technique which measures the linear relationship between observed values of two sets of variables, the criteria
variables $P$ and the predictor variables $Q$ (Clark, 1975). Assuming there are two vectors $P = (P_1, \ldots, P_n)$ and $Q = (Q_1, \ldots, Q_n)$ of random variables, and correlations exist among them, then CCA will find linear combinations of the $P_j$ and $Q_j$ which have the highest correlation. The coefficients of the linear combinations can vary, but the method identifies the combinations of the variables which correlate most. The linear combination that provides the maximum correlation is the first canonical correlation, and the corresponding linear combinations of two different variables are the first canonical variables.

With the aim of assessing the relationship between the variables obtained from the questionnaire and the weather and production variables available for all flocks in the UK, CCA was carried out using Genstat (11th edition, VSN International Ltd, 2008), similar to the method used by Haskell et al. (2007). The $Q$-variables, in this analysis, were available for all farms and were the adjusted averages for 21WT, UMD and UFD as well as the 5-year average annual rainfall, temperature and number of sun hour values. The $P$-variables were from the flocks involved in the initial survey and were: the size of the flock (number of breeding ewes) recorded; the number of weeks lambs had access to concentrate feeding before weaning (0 to $\geq 12$ weeks); the number of months concentrate feeding was fed to the ewes (0 to 6 months) and whether or not the rams were fed concentrates during the month before mating (0 = no, 1 = yes). Overall, the analysis was based on $P$- and $Q$-variables from 39 out of the original 40 different Texel flocks, after data editing as described above.
5.3.3 Reaction Norm Analysis

The original data set was reduced to 181,555 individual lamb records after removing records that had no sire allocated as well as data from farms without data for all three traits studied (Table 5.1). The best linear combination of Q-variables, identified by the canonical correlation analysis, was then used to calculate a FE score for 494 flocks in the national data set. Table 5.2 shows the distribution of the 5,938 different sires, represented in the data, across flocks. 4,507 sires were used in only one flock, whereas 1,345 sires were used in multiple flocks, including 3 that were used in 30 or more.

<table>
<thead>
<tr>
<th>Table 5.1. Summary of traits included in the data set.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trait</td>
</tr>
<tr>
<td>-------</td>
</tr>
<tr>
<td>21WT (kg)</td>
</tr>
<tr>
<td>UMD (mm)</td>
</tr>
<tr>
<td>UFD (mm)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Table 5.2. Distribution of sires between flocks</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of flocks</td>
</tr>
<tr>
<td>No. of sires</td>
</tr>
</tbody>
</table>

Sire models, along with a sire pedigree file containing 9,775 records, were used to analyse the data. The base model (A) included sire, flock and a sire by flock interaction as random effects:

\[
\text{Trait} = \text{mean} + \text{sex} + \text{age} + \text{litter size at birth} + \text{birth year} + \text{rearing dam age} + (\text{sex} \times \text{age}) + \text{sire} + \text{flock} + (\text{sire} \times \text{flock}) + \text{error}
\]
Following on from this, phenotypic observations of lamb performance were regressed, within sire, on FE by adding an environmental variable to the random effects in the model, thus allowing the level (intercept) and slope of a linear reaction norm to be estimated for each sire. By fitting FE as a fixed covariate, the overall regression is removed. The inclusion of the \textit{sire x FE} random effect allows the deviations from the overall trend line to be represented for each sire. The second model fitted (B) was therefore:

\[
\text{Trait} = \text{mean} + \text{sex} + \text{age} + \text{litter size at birth} + \text{birth year} + \text{rearing dam age} + \text{FE} + (\text{sex x age}) + \text{sire} + (\text{sire x FE}) + \text{flock} + (\text{sire x flock}) + \text{error}
\]

The \textit{flock} and \textit{sire x flock} terms represented residual effects that were unexplained by the reaction norm for each sire. Although two flocks may have the same FE value in the regression for the reaction norm, they may have different \textit{sire x flock} terms. Haskell \textit{et al.} (2007) comment that retaining these terms is important in order to preserve the correct variance-covariance structure in the mixed model.

Preliminary analysis indicated that the environmental variance was not constant across environments. In order to estimate the heterogeneity of environmental variance, and based on the preliminary analyses, FE values were grouped into 6 environmental classes (model C). The environmental classes were based on different sections of the FE scale. For each trait, the classes were a (-1.40 to -0.5); b (-0.5 to 0); c (0 to 0.6); d (0.6 to 1.2); e (1.2 to 1.7) and f (1.7 to 2.66). Class c and d represented an average environment, centred on the middle point of the FE scale (0.6). Classes a and b represented environments at the low end of the scale, whereas classes d and f represented environments at the high end of the scale.
Models B and C were tested using the log likelihood ratio test (LR) to determine if they were significantly different. Model B assumed a constant environmental variance, whereas model C allowed for different environmental variances for each environmental class (n=6). The test statistic, $LR = 2(\log L_0 - \log L_1)$, therefore had a $X^2$ distribution with 5 degrees of freedom.

5.3.4 Sensitivity and Heritability Analysis

The use of reaction norm models allows the estimation of sire sensitivities, as well as genetic variances and heritabilities across the environment FE values, similar to the methods used by Kolmodin et al. (2002), Pollott and Greeff (2004) and Haskell et al. (2007). The sensitivity for each sire represents the extent to which the sire effect is dependent on the FE score. The values estimated for the slope of each sire reaction norm were used to represent the sensitivity. The genetic variance at each point along FE scale ($\sigma^2_{g|FE}$), was calculated using the following equation:

$$\sigma^2_{g|FE} = \sigma^2_a + FE^2 \sigma^2_b + 2FE\sigma_{ab}$$

Where $\sigma^2_a$ represents the reaction norm intercept variance, $\sigma^2_b$ represents the reaction norm slope variance and $\sigma^2_{ab}$ represents the covariance. Similarly, heritability estimates at each point along the FE scale ($h^2|FE$) were estimated using the equation:

$$h^2|FE = 4\sigma^2_{g|FE}/(\sigma^2_{g|FE} + \sigma^2_{f} + \sigma^2_{sf} + \sigma^2_e)$$

Where $\sigma^2_{g|FE}$ represents the genetic variance at each point on the FE scale, $\sigma^2_{f}$ represents the flock variance, $\sigma^2_{sf}$ represents the sire x flock variance and $\sigma^2_e$ represents the residual environmental variance. The heritability estimates for Model
C were adjusted by replacing $\sigma_e^2$ with the environmental variance for each of the 6 environmental classes (a-f).

Genetic correlations between each point along the FE scale (two levels, $FE_1$ and $FE_2$), for each trait, were also calculated using the equation:

$$r_{g_{FE1FE2}} = \frac{\sigma_a^2 + FE_1FE_2\sigma_b^2 + (FE_1+FE_2)\sigma_{ab}}{\sqrt{\sigma_{g|FE1}^2 \sigma_{g|FE2}^2}}$$

Where $\sigma_{g|FE1}^2$ and $\sigma_{g|FE2}^2$ are the genetic variances in $FE_1$ and $FE_2$ respectively,

$(\sigma_{g|FE1}^2 = \sigma_a^2 + FE_1^2 \sigma_b^2 + 2FE_1\sigma_{ab} \text{ and } \sigma_{g|FE2}^2 = \sigma_a^2 + FE_2^2 \sigma_b^2 + 2FE_2\sigma_{ab})$.

5.4 Results

5.4.1 Questionnaire Data

Figure 5.1. Concentrate feed use for (i) ewes and (ii) lambs
The overall questionnaire results are discussed in more detail in Chapter 4. The results in relation to the concentrate feed used for ewe and pre-wean lamb feeding, are shown in Figure 5.1. Rams were provided with concentrate feed during the month prior to mating in 34 out of the 39 flocks. The majority of flocks lambed during February and March. When asked to classify their overall farm, in terms of the stratified production levels, 64% classed their farms as a lowland system, 33% as an upland system and 3% as a hill system. The average flock size was 80 ewes, ranging from 12 to 220.

### 5.4.2 Canonical Correlation Analysis

The first canonical variables were scaled so that the maximum coefficient in each case was ± 1 resulting in the following equations:

\[
P \text{Value} = +1.00 \times \text{Rams fed concentrates} + 0.002 \times \text{Number of weeks concentrate feed available to lambs pre-wean} - 0.005 \times \text{Recorded ewe flock size} - 0.432 \times \text{Number of months ewes fed concentrates}.
\]

\[
Q \text{Value} = -1.00 \times \text{UFD} - 0.0001 \times \text{Rainfall} - 0.001 \times \text{Sun Hours} + 0.104 \times \text{21WT} + 0.235 \times \text{UMD} + 0.249 \times \text{Temperature}.
\]

The corresponding canonical correlation between P and Q was 0.73. The first canonical P-variate represented the level of concentrate used in each system, with large, positive, values representing farms that fed their rams and lambs prior to mating and weaning respectively. In addition, they had a lower flock size and the ewes were fed for fewer months throughout the year. Low, negative, values represented larger flocks which fed their ewes for a longer period during the year.
They did not, however, feed their rams or lambs prior to mating and weaning respectively. The corresponding Q-variate, which utilised data available for all farms, had large, positive, values for farms with high performance averages for 21WT and UMD as well as high average temperature and low average rainfall. The highest values along the scale were also associated with low UFD averages, as well as low rainfall and number of sun hours. Conversely, low values were associated with low performance averages for 21WT and UMD, as well as high average rainfall and low UFD and temperatures averages. Table 5.3 shows the correlations between all variables. Temperature and sun hours were highly correlated (r = 0.90), which may explain the change in direction for sun hours when compared to the coefficient estimated in the canonical correlation analysis. The distribution of Q-values estimated across all flocks in the population is shown in Figure 5.2. The average of the Q-values estimated across all of the flocks in the population was 0.7.

**Table 5.3. Correlations between all variables used in the Canonical Correlation analysis and the resulting P and Q variates.**

<table>
<thead>
<tr>
<th>Variable</th>
<th>P Value</th>
<th>Q Value</th>
<th>Rams Fed</th>
<th>Months Ewes Fed</th>
<th>Flock Size</th>
<th>Weeks Lambs Fed</th>
<th>Rain</th>
<th>Sun hours</th>
</tr>
</thead>
<tbody>
<tr>
<td>Q Value</td>
<td>0.73</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rams Fed</td>
<td>0.49</td>
<td>0.36</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Months Ewes Fed</td>
<td>-0.73</td>
<td>-0.53</td>
<td>0.07</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Flock Size</td>
<td>-0.32</td>
<td>-0.23</td>
<td>-0.02</td>
<td></td>
<td>-0.13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Weeks Lambs Fed</td>
<td>0.23</td>
<td>0.17</td>
<td>0.24</td>
<td>0.03</td>
<td>-0.24</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rain</td>
<td>-0.13</td>
<td>-0.20</td>
<td>-0.08</td>
<td>-0.001</td>
<td>0.23</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sun hours</td>
<td>0.08</td>
<td>0.12</td>
<td>0.15</td>
<td>0.11</td>
<td>-0.23</td>
<td>0.07</td>
<td>-0.72</td>
<td></td>
</tr>
<tr>
<td>Temperature</td>
<td>0.11</td>
<td>0.16</td>
<td>0.17</td>
<td>0.12</td>
<td>-0.28</td>
<td>0.07</td>
<td>-0.64</td>
<td>0.90</td>
</tr>
</tbody>
</table>
5.4.3 Reaction Norm Analysis

The FE scale was then calculated using the weather and production information available for all 494 nationally recorded farms. By using the Q equation developed, the values estimated along the FE scale ranged from Q-values of -1.40 to 2.66. Overall, the scale went from low performance averages and poorer weather conditions to high performance averages and improved weather conditions. To illustrate, the average FE data for the ten farms located at both extremes of the FE scale are shown in Table 5.4. The average values for 21WT, UMD and UFD were calculated using the original flock solutions (as estimated using the fixed effect model and that were used to calculate each Q-value) plus the average values across all levels of each fixed effect in the model.
Table 5.4. Farm Environment (FE) average descriptors for farms located at the 10 highest and 10 lowest points on FE scale

<table>
<thead>
<tr>
<th></th>
<th>Average Rainfall (mm)</th>
<th>Average Sun (hours)</th>
<th>Average Temperature (°C)</th>
<th>21WT Average (kg)</th>
<th>UMD Average (mm)</th>
<th>UFD Average (mm)</th>
<th>Average Q-Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>High FE score</td>
<td>1188.99</td>
<td>1392.59</td>
<td>9.42</td>
<td>52.88</td>
<td>28.78</td>
<td>0.11</td>
<td>2.25</td>
</tr>
<tr>
<td>Low FE score</td>
<td>1421.35</td>
<td>1430.73</td>
<td>9.23</td>
<td>40.07</td>
<td>25.65</td>
<td>0.29</td>
<td>-1.10</td>
</tr>
</tbody>
</table>

The variance component estimates obtained by models A, B and C are shown in Table 5.5. Based on the LR, both models B and C significantly improved the fit of the model when compared with model A (P<0.05). When models B and C were fitted, for each trait, two breeding values were produced, representing the intercept and slope of the reaction norm for each sire. The intercept value represented the average sire effect on each trait across all farm environments. The slope represented the environmental sensitivity, or in other words the amount to which the sire effect was dependent on the farm environment value.

The variances of the slope, for all of the reaction norm models were significantly different from zero. According to the LR, model C, when compared with model B, significantly improved the fit of the model for each trait (P<0.001). The correlations between the intercept and slope, using model C, were all less than one and negative, 21WT (-0.49) and UMD (-0.58) and UFD (-0.49), implying the re-ranking of sires. Similar results were also obtained using model B. The reaction norms estimated for a sample of sires (the six sires with the most offspring in the data), are shown in Figure 5.3. The graphs demonstrate both scaling and re-ranking of sire performance across the environmental scale for each trait.
Table 5.5. Estimates of fixed regression coefficients and variance components for Intercept ($\sigma^2_a$), Slope ($\sigma^2_b$), Flock ($\sigma^2_f$), Sire x Flock interaction ($\sigma^2_{sf}$), Error Variance ($\sigma^2_e$) and correlation ($r$) between Intercept and Slope from the reaction norm models for 21WT, UMD and UFD (s.e. in parenthesis).

<table>
<thead>
<tr>
<th>Trait</th>
<th>Regression Coefficient</th>
<th>$\sigma^2_a$</th>
<th>$\sigma^2_b$</th>
<th>$\sigma^2_f$</th>
<th>$\sigma^2_{sf}$</th>
<th>$\sigma^2_e$</th>
</tr>
</thead>
<tbody>
<tr>
<td>21WT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model A</td>
<td>-</td>
<td>2.26 (0.22)</td>
<td>-</td>
<td>-</td>
<td>27.12 (1.88)</td>
<td>6.89 (0.22)</td>
</tr>
<tr>
<td>Model B</td>
<td>4.58 (0.33)</td>
<td>2.80 (0.36)</td>
<td>1.33 (0.38)</td>
<td>-0.48 (0.09)</td>
<td>18.49 (1.32)</td>
<td>6.63 (0.23)</td>
</tr>
<tr>
<td>Model C</td>
<td>4.58 (0.33)</td>
<td>2.82 (0.36)</td>
<td>1.39 (0.39)</td>
<td>-0.49 (0.09)</td>
<td>18.48 (1.32)</td>
<td>6.61 (0.23)</td>
</tr>
<tr>
<td>UMD</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model A</td>
<td>-</td>
<td>0.58 (0.05)</td>
<td>-</td>
<td>-</td>
<td>3.56 (0.26)</td>
<td>1.53 (0.05)</td>
</tr>
<tr>
<td>Model B</td>
<td>1.89 (0.12)</td>
<td>0.82 (0.09)</td>
<td>0.23 (0.08)</td>
<td>-0.61 (0.08)</td>
<td>2.14 (0.17)</td>
<td>1.47 (0.05)</td>
</tr>
<tr>
<td>Model C</td>
<td>1.89 (0.12)</td>
<td>0.80 (0.09)</td>
<td>0.23 (0.08)</td>
<td>-0.58 (0.08)</td>
<td>2.14 (0.17)</td>
<td>1.47 (0.05)</td>
</tr>
<tr>
<td>UFD</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model A</td>
<td>-</td>
<td>0.08 (0.01)</td>
<td>-</td>
<td>-</td>
<td>0.52 (0.04)</td>
<td>0.28 (0.01)</td>
</tr>
<tr>
<td>Model B</td>
<td>0.01 (0.06)</td>
<td>0.10 (0.01)</td>
<td>0.06 (0.02)</td>
<td>-0.47 (0.09)</td>
<td>0.51 (0.04)</td>
<td>0.27 (0.01)</td>
</tr>
<tr>
<td>Model C</td>
<td>0.01 (0.06)</td>
<td>0.10 (0.01)</td>
<td>0.06 (0.02)</td>
<td>-0.49 (0.08)</td>
<td>0.51 (0.04)</td>
<td>0.27 (0.01)</td>
</tr>
</tbody>
</table>

6 classes = Classes a – f used for heterogeneity of variance analysis.

5.4.4 Sensitivity and Heritability Analysis

The sensitivities estimated for all sires represented in the dataset, for each trait, are shown in Figure 5.4. The histograms centred between -0.05 and 0.10 for UMD and UFD, and between -0.15 and 0.30 for 21WT. Just less than half of the 5,938 sires, with lamb 21WT records in the dataset, had positive sensitivities (49.7%). Of the 5,853 sires that had lamb records for the ultrasound scan traits, 49.6% (UMD) and 50.3% (UFD) were positive. The sensitivities estimated represent the deviation from the overall mean slope. When the fixed regression coefficient was added to each sire sensitivity estimated, the EBVs of all sires (21WT and UMD) improved as the FE improved, as demonstrated in Figure 5.3. However, when the fixed regression coefficient was added to the sensitivities estimated for UFD, there remained a mix of positive and negative slopes as the FE improved, also demonstrated in Figure 5.3. Of
the 5,853 sires with UFD information, the EBVs of 61% of sires increased and 39% of sires decreased as the FE improved. A high number of sires had sensitivities close to, or equal to zero indicating that they were relatively “robust” across all FE.

The heritabilities estimated from model A, for 21WT, UMD and UFD were 0.13 (+0.01), 0.17 (+0.02) and 0.17 (+0.02) respectively. When using model C, the range of heritability estimates for 21WT, UMD and UFD, along the FE scale were, 0.15 - 0.50, 0.18 - 0.55 and 0.15 – 0.63 for each trait respectively (Figure 5.5). The highest heritability estimates for 21WT and UFD were observed at each end of the scale and lowest at the mid-point, approximately 0.6 on the FE scale. The heritability estimates for UMD followed a similar pattern, although the estimates at the high end were slightly lower than those estimated at the low end (Figure 5.5). It should also be noted that the largest standard errors, for all traits, were associated with heritability estimates at both extremes of the FE. The genetic variances estimated followed a similar pattern as the heritability estimates (Figure 5.5).

The genetic correlations estimated across the FE scale, are shown in Figure 5.6 and Figure 5.7. The correlations estimated ranged from -0.42 to 1 for 21WT, -0.22 to 1 for UMD and -0.51 to 1 for UFD (Figure 5.6). The correlations shown in Figure 5.7, for all three traits, are estimated for flocks with an average Q-value in the population (0.7) as well as those ±1 SD from the average.
Figure 5.3. Reaction norms, for a sample of 6 sires, for (a) 21WT, (b) UMD and (c) UFD estimated breeding values (EBVs) across different farm environments (using model B).
Figure 5.4. Sire Sensitivities, estimated using model B, for 21WT, UMD and UFD.
Figure 5.5. Heritability ($h^2$) and Genetic Variance ($\sigma^2_g$) estimates, using model C, for 21WT, UMD and UFD as functions of the farm environment.
Figure 5.6. Genetic correlations estimated between environments along the FE scale for 21WT, UMD and UFD (using model B).
Figure 5.7. Genetic correlations estimated for 21WT, UMD and UFD, across the FE scale. Graphs shown are between flocks with environment values of -1 SD from average, average and +1 SD from average, respectively, and all other environmental values along the FE scale (using model B).
5.5 Discussion

5.5.1 Defining Farm Environment

The canonical correlation analysis used in the present study provided an opportunity to relate fine scale information gathered from a sample of farms, with information available from farms at a national level. The feed related variables obtained from the farm survey were selected for further analysis in order to improve our knowledge of the effects that different feeding regimes may have.

The canonical correlation estimated in the current study was reasonably high (0.73) and therefore suggested that the first canonical Q-variable was a useful measure of system input (in terms of the use of supplementary feed), and therefore FE overall. The correlation estimated by Haskell (et al., 2007) when defining dairy farm FE, using a similar method, was 0.62. An interpretation of the first Q variable suggests, in terms of the production averages, high FE values were associated with high performance averages for 21WT and UMD, and low averages for UFD. The Terminal Sire Index, within which the majority of Texel breeders record, has weightings on each of these traits in order to improve 21WT and UMD while reducing any associated rise in UFD (Simm and Dingwall, 1989; Macfarlane and Simm, 2007). Therefore the FE scale developed is a good reflection of the overall aim of the breeding index. Similarly, the direction of the weather variables, in general, suggests that the highest FE values are associated with higher average temperatures and lower rainfall. This would agree with the general assumption that areas with better weather conditions have improved environments in terms of aspects such as pasture availability and quality. The number of sun hours is the only variable
that perhaps does not go in the expected direction, but with a correlation coefficient of 0.001, the effect is low compared to other variables included in defining the FE scale.

The first canonical P-variable, using data from the survey farms, provided an interesting result, when compared with the corresponding canonical Q-variable. Farms with a high P value were associated with a higher use of ram and pre-weaned lamb concentrate feeding, but less so with ewe feeding and the overall flock size. The majority of flocks fed their rams during the month before mating. However, there was quite a range in the number of weeks before weaning, during which lambs had access to supplementary feed. The increased use of concentrate feed, particularly for pre-weaned lambs, is likely to have helped improve the production averages. However, when considered alongside the weather variables, it would seem that these farms already had a favourable FE and therefore these farms have chosen to try and improve it further by allowing their lambs access to feed before they are weaned.

Farms with a lower P value fed their ewes for a longer period during the year than those at the other end of the scale. This could again be related to the weather variables. In areas with lower average temperatures and higher rainfall, the increased use of feeding could be used to help maintain the condition of the ewe throughout pregnancy, and possibly post-pregnancy. This could be because the ewes have been kept outside in potentially poorer conditions where grass growth can be limited for a greater number of months. Alternatively, in order to remove the effects of the poorer weather conditions, they may have been housed for a longer period of time before and during lambing. Whatever the system used, both rely on the use of substantial
amounts of supplementary feed for the ewes. The emphasis has therefore moved from just improving lamb performance further, to perhaps better maintaining the ewe throughout pregnancy.

With the variation over the past few years in the price of concentrate feed, if feed prices increase, while the price of lamb does not increase at a similar rate, farmers may decide to make adjustments to their management system. Should they cut back on the level of feed that they provide to their flocks, by using the scale described in the present study, farmers could potentially identify sires best suited to which ever system they choose to pursue.

Although the initial aim of the analysis was to identify a way of measuring the level of concentrate feed use, the resulting FE scale, as estimated using the first canonical Q-value, was not dissimilar to a production level-type scale. Similar scales have been used in studies such as those by Strandberg et al. (2009), who, in addition to using the FE scale developed by Haskell et al. (2007), also used herd averages for production and fertility-related descriptors to define environments. Kolmodin et al. (2002), defined environments as the deviation from the overall herd-year averages of protein production (production environment) and days open (fertility environment). Studies using sheep, such as Pollot and Greeff (2004), defined Merino production environments using the average value of each trait analysed, for each contemporary group identified. Similar methods have also been used by Santana et al. (2013b) when studying Santa Ines sheep in Brazil.
5.5.2 Reaction Norm Analysis

The reaction norms estimated for each trait suggest GxE was evident, in terms of both re-ranking and scaling. The results observed for 21WT and UMD found that the performance (as represented by the EBVs) of all sires increased as the FE improved. However, approximately half of the sire sensitivities estimated for 21WT and UMD were positive and half negative. The EBVs of those with negative sensitivities still increased as the FE improved, but not as much as the average (as represented by the fixed regression coefficient). The EBVs of those identified as having positive sensitivities increased at a higher rate than the average, or in other words, were more “plastic”. The results for UFD were slightly different. Although the majority (61%) of sire EBVs increased as the FE improved, 39% fell as the FE improved. This result provides some evidence that there an increased amount of variation present in the population for this trait. It also potentially allows farmers, at either end of FE scale, to identify sires with high or low EBVs for fat depth depending on what they feel suitable for their system. As mentioned earlier, the Terminal Sire Index aims to reduce fat levels, whilst increasing weight and muscle measurements (Simm and Dingwall, 1989; Macfarlane and Simm, 2007). The results observed in the current study therefore suggest that it would be possible to identify sires suitable for this, at all positions along the FE scale.

It should be noted though that a high proportion of sires, across all traits, had sensitivities close to, or equal to, zero, indicating that there was very little variation in their performance across environments. As a result, the offspring of these sires performed relatively consistently across the FE scale, used in the present study, and
were therefore not influenced as much by changes in feeding regimes. Similar examples of scaling and re-ranking were observed by both Pollot and Greeff (2004) and Santana et al. (2013b), when using random regression models to investigate a number of sheep performance traits including faecal egg counts, wool, body and growth characteristics. Overall, as suggested by Haskell et al. (2007), the presence of environmental sensitivity provides an opportunity for farmers to choose sires based on the FE of their farm. Should any FE changes occur, such as those mentioned previously with regards to feed prices, farmers would be able to identify sires that would be predicted to perform consistently regardless of feed inputs, or identify those most suited to the specific levels of feed use.

When heterogeneous residual variances were investigated, their inclusion significantly improved the fit of the overall random regression model for all traits. Similar results were also observed by Pollot and Greef (2004), Cardoso and Tempelman (2012) and Santana et al. (2013b). Strandberg (2006) comments that this is not unexpected, particularly when using sire models. The 6 environmental classes (a-f) used for the analyses were kept consistent across the traits, and were selected based on the different sections of the FE scale, representing low, average and high environments. Although these classes provided significant improvements to the fit of the model, it may be that the fit could be improved further by adjusting the classes further and using different classes for the different traits. Nonetheless, the results presented here highlight that it may be beneficial for any similar analyses in the future to account for such heterogeneous variances.
5.5.3 Heritability of Traits Across Different Environments

When using environment scales based on production levels, such as those used by Kolmodin et al. (2007) and Strandberg et al. (2000), the heritabilities estimated often rose as the environment improved. When the heritabilities of the three traits were estimated across the FE scale, in the present study, the highest values were estimated at the extremes of the scale for 21WT and UFD. However, it should be noted that these estimates were also associated with the highest standard errors. The lowest values, and lowest standard errors, for these traits were estimated at the mid-point of the scale. These results are similar to those estimated by Pollot and Greeff (2004) for faecal egg count across environments. The estimates for UMD were slightly different than those for 21WT and UFD. The highest values estimated at the low end for the scale and the lowest values slightly above the mid-point, but again the standard errors were larger at the extremes of the FE scale and smaller nearer the mid-point.

The heritability estimates for 21WT, UMD and UFD found that at the low end of the FE scale (poorer FE environment in terms of production and weather), indicate that the genetic variation for these traits is high. This suggests that some rams have the ability to produce lambs with higher than average 21WT, UMD and UFD values even when the environment is classed as poorer. Similarly, and perhaps somewhat more expected, at the higher end of the FE scale, the heritabilities increase as the environment improves. The rate of increase is highest for UFD, followed by 21WT, suggesting that that genetic control over these traits is affected more by the improvement in environment than UMD. At the mid-point of the scale, the animals are generally more similar in their genetic control of each trait. The lowest
heritability values for UMD were estimated just above the mid-point of the scale. This, along with the fact that the UMD heritability estimates were the highest overall at the poorer end of the scale, indicates that improvements in this trait can also be made when environmental conditions are not so favourable.

In terms of the different feeding levels, the results suggest that by increasing the amount of feed available to lambs, although improvements will be found with regard to all traits, the rate of genetic progress associated with UFD will be the greatest. This may prove costly if carcasses become over-fat and result in a financial penalty to the farmer. At the lower end of the FE scale, if the lambs are fed less feed, but the ewes are fed more, the rate of genetic progress of all three traits will also improve at a similar rate.

5.5.4 Genetic Correlations Between Environments

A wide range of genetic correlations were estimated within each trait, between pairs of environments across the FE scale. The results suggest that there would be less GxE evident, in terms sires ranking, if the environmental conditions of the two environments were similar. For example, flocks with below average Q-values on the FE scale were relatively highly correlated with similar flocks located at that end of the FE scale and similarly, above average flocks were more highly correlated with other flocks at the top end of the FE scale. However, as the environments become more divergent (e.g. the lowest points of the FE scale and the highest points on the FE scale) the correlations fell, with a number of correlations becoming negative. Sires suitable for flocks at the lower end of the FE scale are therefore not
necessarily as suitable for those at the higher end of the FE scale and this further emphasises that GxE is evident in the population. These results were similar to those reported by Santana et al. (2013) for the body weight of Santa Ines sheep at 180 days of age as well as Cardoso and Tempelman (2012) for postweaning weight gain of Angus cattle.

5.5.5 Accounting for GxE in Genetic Evaluations

Overall, the use of reaction norm analyses provide an opportunity for future genetic evaluations to take into account any interactions that may be present between genotypes and environments. Providing a suitable “measure of environment” can be agreed, the method can allow the prediction of unique rankings for each level of environment. This would potentially allow farmers to use an environmental value, which has been calculated for their specific farm from the overall environment scale, in order to identify sires best suited to their farm system. Additionally, sires that perform consistently across a range of different FE could also be identified.

The method presented in the current study combined fine-level detail, with particular emphasis on the use of concentrate feed, with information available nationally for all flocks that are members of Signet. By using the environment scale developed, GxE was observed for all Texel lamb traits investigated, both in terms of re-ranking and scaling. The variation in heritability estimates across different environments, as well as the range of genetic correlations estimated between environments, all need consideration in future selection programmes. It may also be useful to investigate if the FE scale developed in this study is applicable to other breeds, or if another way of quantifying FE should be investigated. Another option would be to analyse more
than one trait together as investigated by Kolmodin et al. (2007) and Strandberg et al. (2009).

5.6 Conclusions

The method developed in this study has proven to be useful in defining sheep farm environments. Evidence of GxE was observed for all of the lamb performance traits investigated. The range of sire sensitivities estimated across the environment scale confirmed the presence of genetic variability, as both “plastic” and “robust” genotypes were observed in the population. The ability to identify differences in sensitivity allows farmers to select animals best suited to specific environments as well those that will perform consistently across a range of environments. The variation in heritability estimates also suggests that the rate genetic of progress will vary depending on the environment. Overall, the results from this study indicate that in order to improve genetic gain and flock efficiency, future genetic evaluations would benefit by accounting for the GxE observed.
Chapter 6: General Discussion
Summary of findings: GxE in the UK sheep industry

6.1 Model Comparisons

Throughout this study, two main methods for investigating GxE have been used. The multi-trait method, used between farms (Chapters 2 and 3), and between clusters of farms (Chapter 4), as well as the reaction norm analyses used across an environmental scale (Chapter 5).

6.1.1 Multi-Trait Method

The use of the multi-trait method, which considers the expressions of a trait in two, or more, environments as different traits, has allowed the incorporation of a variety of different environmental variables at one time. From the point of view of the farmer, the genetic correlations estimated are a useful and interpretable measure of the level of GxE between the different environments. Any estimate that is significantly below unity suggests GxE is evident and that they should be aware of this when selecting animals for breeding.

A large scale version of this model has been used for some time by Interbull when estimating international breeding values for dairy bulls. The multiple across-country evaluation (MACE) procedure considers each country as a different environment, between which all combinations of genetic correlations are estimated (Schaeffer 1994). However, concerns have been raised as to whether environments based on geographical boundaries such as these are the most appropriate. As a result, clustering methods have been investigated in a number of studies, including those by Weigel and Rekaya (1999) and Zwald et al. (2003a). These studies have
demonstrated methods of grouping similar production environments together (often across borders) and therefore reducing the number of unique production environments required for comparison. Although on a much smaller scale than the dairy industry, the use of clustering methods, as demonstrated in Chapter 4, may prove useful in the UK sheep industry, provided that suitable environmental variables can be agreed and used to identify distinct clusters. This would potentially allow a breeding value to be estimated for each animal, for each cluster group, providing farmers with information relevant to the cluster type that their farm belongs to.

The disadvantages, however, include the fact that these different environments relate to a specific time point based on when the data, used for clustering, were collected. As a result, the relevance of the clusters estimated may reduce over a period of time due to changes in farm management, climatic conditions and such like. Another issue, as observed in Chapter 4, is that there needs to be a suitable level of genetic connectedness between the different environments. The higher the level of connection, the more reliable the correlation and breeding value estimates. Also, from a computational point of view, and ease of understanding by the farmers, ideally the number of “environments” should be relatively low. If too many are identified, the system could become over-complicated and the levels of genetic connections would become too variable. Alternatively, if too few are identified, there could still be a high level of variation in performance within each “environment”. Further complications could also arise when considering multiple traits across multiple environments. With many of the selection indices used in the UK involving a number of different traits, particularly maternal breeds that include both ewe and
lamb traits, the production of breeding values for each animal, for each trait, in each cluster could, computationally, involve a lot of work, as well as increase the potential for error in estimation or interpretation.

6.1.2 Reaction Norm Method

From a computational point of view, the use of the reaction norm model is perhaps a more attractive method when a large number of different environments are to be considered. An advantage of this model is that it does not rely so heavily on genetic connections between each individual environment because the environment is measured on a continuous scale rather than between groups (Strandberg et al. 2000). In the current study, the reaction norms estimated were assumed to be linear, but in some circumstances they can also be quadratic (with a convex or concave curve) or sigmoid (with a logistic curve) in nature. Quadratic reaction norms can occur, for example, when the progeny of sires perform well in the mid-range of the scale and poorly at the extremes. Calus and Veerkamp (2003) reported quadratic reaction norms for protein yield in relation to fat:protein ratio and milk yield in relation to peak calving date. Sigmoid reaction norms can occur when the trait of interest has upper and lower asymptotes within the environment. David et al. (1994) observed sigmoid shaped reaction norms when investigating the variation of wing/thorax ratio in Drosophila according to growth temperature.

The model also provides a measure of environmental sensitivity. The sensitivity of genotypes, represented by the slope of a linear reaction norm, gives an indication of the degree by which genotypes vary across environments. As discussed in Chapter 5, genotypes that are highly variable, across environments, are considered “plastic”
whereas those that are relatively constant, are considered “robust”. It has been shown that environmental sensitivity can be changed by genetic selection, therefore there is the possibility of including the sensitivity of a trait as a future breeding objective (Kolmodin et al. 2003). Overall, by using this method of analysis, providing farmers know where their farm lies along the environmental scale, the method allows the identification of animals best suited to specific environments.

However, one of the main issues to overcome when considering the use of reaction norm models is the definition of the environmental scale. In theory, the scales can be based on any single variable such as feed levels, rainfall, temperature, longitude or latitude. In reality, the environments associated with sheep farms are much more complex, therefore interest is not in a specific variable, but rather a combination of variables. To overcome this, some studies have identified variables, often readily available for all farms, to provide an indication of the complex nature of the environment influencing animal performance. Examples include quantifying the average performance of all genotypes, in each environment, for the trait of interest (Kolmodin et al. 2002). However, as Strandberg (2000) commented, although this method provides a good indication of the type of environment the animal is exposed to, problems can arise. As well as the fact the trait of interest is both the dependent and independent variable, the phenotypic average of a flock will also contain the genetic component of all the phenotypes within the flock. If animals are continually selected based on the trait used for the environmental scale, and not used randomly, across flocks, a level of bias could be introduced. In other words, flocks with a high average genetic merit could potentially have an environmental value that is biased upwards. The method used in Chapter 5, for defining the farm environment scale,
could therefore be a suitable alternative. Although performance variables were used as an indicator of the original feed related variables from the survey data, each had a different weighting therefore a reduced level of bias would be introduced.

6.2 Limitations of the Study

6.2.1 Hill Breed Analysis

Although the Scottish Blackface breed is well known for being a hardy and adaptable hill breed, within the UK hill sheep industry, there are sometimes concerns related to differences in management of pedigree animals compared to commercially-reared animals. The differences are often related to the levels of concentrate feed use, particularly in terms of the male animals, which are destined for pedigree sales. Currently, the majority of male animals are selected and sold based on phenotypic traits only. The management of these animals, prior to pedigree sales, is therefore often aimed at increasing body size through the use of higher quality grazing and concentrate feeding. However, when these animals move to commercial hill farms, and are expected to work in often harsher conditions to those that they have been accustomed to, it is possible that their performance may not live up to the expectations at the time of purchase.

The divergence between these systems, and the potential for variation in animal performance, suggest GxE may be an issue and would be worthy of investigation. Unfortunately, a relatively low number of pedigree and commercial hill farms performance record their flocks, thus the availability of both performance data and pedigree information is limited. In general, the uptake of performance recording has been low, primarily due to constraints in labour and resources, at critical recording
points throughout the year, as well as an unwillingness to move away from the more traditional methods of selection.

Due to the low number of flocks recording, as well as only a small number responding to the farm questionnaire, there was not enough data to identify environment cluster groups or use the reaction norm method. As a result, it was decided for Chapters 2 and 3 of this study, to undertake a two-farm comparison using data that had previously been collected as part of a larger research project designed to investigate selection indices for hill sheep production. This provided a well recorded dataset, for a number of different traits, spanning a number of generations.

However, even though the two farm environments were divergent in a number of different factors such as climatic conditions, topography and grazing types, the increased level of monitoring and strict experimental protocols associated with these flocks may have caused the flock management, within the environments, to be quite similar. Although GxE was observed for lamb birth weights and ewe mature weights, the problems observed with convergence, and the difficulty in estimating standard errors for the correlations, for the other traits investigated suggests that the underlying correlation was close to, or equal to, one. It may be, therefore, if other hill farms within the industry were used, a greater divergence between environments could be established and the effects of GxE further investigated. Alternatively, if an environmental scale could be developed, appropriate to hill farm systems, the use of reaction norms may prove a more useful option, particularly as it reduces the dependency on genetic links between all environments.
6.2.2 Questionnaire Design

The analyses in Chapters 4 and 5 were based, to varying degrees, on information gathered using the questionnaire sent to all members of the Signet Sheepbreeder programme. With over 30 different breeds recording as part of Signet, the questionnaire was developed to incorporate all breed types and as a result may have included some questions not relevant to all. In hindsight, it may have been a better option to target specific breed types separately (for example certain hill and terminal sire breeds) and use a different questionnaire for each. Another alternative would have been to identify specific parts of the flock management and concentrate questions on these areas only, rather than trying to get as much information as possible across the whole system. When compared with other livestock systems, such as those found in the dairy industry, the extensive nature of sheep farming means that many more environmental variables could be influencing the performance of the animals. By targeting specific variables only, the number of overall questions would have been reduced, thus potentially encouraging more farmers to respond and therefore improving the likelihood that the results obtained relate to, or are indicative of, the industry as a whole.

Additionally, the PCO analysis used in Chapter 4 identified the grazing-related variables as a highly distinguishing factor between the clusters. This section of questions was designed to try to understand the grazing management of the ewes (and lambs) throughout the production year. The farmers were asked to identify where the flock had access to graze throughout the year. The options provided to the farmers were hill/rough grazing, in-bye/improved grazing, hay/silage field type
grazing or any other crop fields, and it was up to the individual farmer in terms of how they classified the different grassland areas of their farm. These options were chosen as a basic breakdown of grazing quality. At the poorer end of the scale, due to factors such as poor drainage, rough terrain, and the lack of any improvement practices carried out, was the hill/rough grazing. Both the inbye/improved grazing and the hay/silage field type grazing are examples of improved permanent pasture. Although both can be subject to improvement through management practices such as liming or fertiliser application, fields that are used, or suitable, for hay/silage production were generally considered to be of better quality. This being because of a possible increased use of reseeding, better drainage and other management practices, as well as increased swards of species such as ryegrass and clover. However, because it was up to the individual farmer to classify the different grazing available on their farm, these results should be treated with some caution, since what may be considered as rough grazing by one farmer may be considered as permanent pasture by another. There is, therefore, the possibility that the options provided in the questionnaire were too subjective and any future questionnaires should be designed to be more specific.

6.2.3 Genetic Connections

As discussed in Chapter 4, the low number of common sires used across all identified clusters affected the genetic connections and therefore the reliability of the correlations and breeding values estimated, particularly between Cluster 2 and Cluster 3. It may be that if data from the Texels were used for this analysis, more reliable results would have been obtained. However, it does highlight the point, as
mentioned previously, that if clustering methods were to be used in the future to identify and account for GxE, it is vital that all environments are genetically well-linked.

6.3 Implications for Future Genetic Evaluations

The genetic improvement of animals is associated with the objective to improve the performance of future generations. In order to optimise this, what must also be considered is the future environments in which these animals may be expected to perform in. Should the environments, as classed throughout this study, remain relevant, the presence of GxE observed, particularly for traits associated with the terminal sire lambs, may have implications for future sheep breeding programmes. With evidence of a number of sires re-ranking between environments, as well as the presence of scaling, there is an opportunity to increase selection efficiency and genetic progress by taking GxE into account in future genetic analyses. Providing a suitable “measure of environment”, as well as method of analysis, can be agreed, the identification of sires that perform well in specific environments, as well as those who perform consistently across a number of different environments, would be beneficial for farmers. This would potentially remove any unwanted effects of GxE and allow the farmer to select animals best suited to their overall farm environment.

If a clustering method was to be further developed, a suitable level of information would be required to make sure the clusters were a reliable and true reflection of the farming systems within the industry. As discussed in Chapter 4, if genetic correlations estimated between the clusters were below a certain level, genetic gain might be improved through the use of environment specific breeding programmes. In
the dairy industry, Mulder et al. (2006) observed that this was the case when correlations were below 0.61. However, further investigation would be required in order to assess what level of correlation would affect the choice of strategy in relation to sheep breeding.

As mentioned previously, the use of reaction norms allows the identification and selection of animals that are “plastic” and “robust”, based on their environmental sensitivity. Kolmodin et al. (2003) and Kolmodin and Bijma (2004) observed that it was possible to select for both “plasticity” as well as “robustness”. However, care would need to be taken. Although, in the short term, breeding for high environmental sensitivity, or “plasticity”, could improve performance in a specific environment, should any changes in the environment arise, the performance of these animals could reduce dramatically. The selection of “robust” animals may therefore seem a more preferable option. However, as Kolmodin (2007) commented, if changes occur in the environment when breeding for “robustness” (for example changes out-with the range of the environment scale), animals may not have the ability to react or respond to these changes. It may therefore, as suggested by Bryant et al. (2006), be better to maintain a sufficient level of genetic diversity within the overall population to ensure that animals are able to adapt and evolve in response to any environment.

Overall, selection could also be optimised by increasing the cooperation between flocks, using systems such as sire-reference or ram-circle schemes as discussed earlier in Chapter 1. If environments are defined using clustering methods, the use of such schemes could help with maintaining genetic links between the clusters therefore increasing the reliability of the breeding values estimated, which was a
problem which was highlighted in Chapter 4. They would also allow the possibility of progeny testing animals across a range of different environment types. In addition to identifying animals suited to specific environments, in order to maintain genetic diversity across the population, the identification of animals with high levels of robustness could be achieved by using such schemes. By including farms at both the low and high ends of the environment scale, when using reaction norms, and identifying animals with similar breeding values in different clusters, robust animals could be identified and used across the population.

6.4 Future Research

6.4.1 Environment Definition

Throughout this study, a number of areas have been identified as worthy of additional investigation. As mentioned previously, the identification of appropriate environment definitions, in terms of both multi-trait and reaction norm methods, is vital if these methods are to be adopted by the sheep industry.

As highlighted earlier in this chapter, it may be worthwhile, to investigate the possible use of information collected from alternative sources, such as government statistics which would allow data to be collected from all farms, in order to establish more accurate environment definitions. Another interesting point perhaps worthy of future consideration is the fact that both Kolmodin et al. (2002) and Strandberg (2006) highlight that different traits can have different environmental scales. There is therefore the possibility that a scale used for lamb performance traits is not appropriate for ewe performance traits, for example. It may also be the case that
different environment scales would be appropriate for different sheep breeds, or breed types.

### 6.4.2 Further Investigation into Reaction Norm Methods

The results observed in Chapter 5 indicate the presence of GxE and varying levels of environmental sensitivity within the Texel population. Further investigation into other breeds would be valuable in order to increase our knowledge of GxE within the overall sheep industry. In addition to the other Terminal Sire breeds, the reduced need for genetic connections between all environments means that this method may also be useful when considering Hill Sheep breeds, such as the Scottish Blackface, where structured breeding schemes and performance recording are less common.

Additional investigation considering multiple-trait reaction norms, allowing more than one trait to be analysed at a time, as well as non-linear reaction norms would also be worthwhile. Kolmodin et al. (2002) observed, while investigating protein yield and fertility in dairy cattle, that genetic correlations between two different traits changed depending on the environment. Whereas Pollot and Greef (2004) observed that fitting a quadratic, when compared to a linear, reaction norm significantly improved the model for faecal egg count.

### 6.5 Conclusions

Overall, this thesis has demonstrated the presence of GxE within the UK sheep industry, for a number of different traits, using two different methods. As a result, future genetic evaluations would benefit by accounting for GxE. The use of clustering and reaction norms, for analysing GxE, both have merits for future use.
Providing suitable measures of environment can be agreed, recorded accurately, and the results can be presented, and understood, by farmers, there is scope for the optimisation of future breeding programmes. The ability to identify breeding stock that are “plastic” or “robust” will allow farmers to make selection decisions with an increased knowledge as to how the animals will be expected to perform in a given environment, thus increasing overall flock performance and genetic gain.


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Appendicies
Appendix 1. Questionnaire sent to all Signet Sheepbreeder members.

[Image of questionnaire]

1. What is your farm type? [ ] Hill [ ] Upland [ ] Lowland
2. Is your farm organic? [ ] Yes [ ] No
3. What is the height/altitude of your farm? _______ to _______ ft/m (please circle scale)
4. What is the total size of your farm? _______ acres/ha (please circle scale)
5. How many breeding ewes do you have? (Both pure and cross-breeds)
   - Breed 1: _______ No. of ewes: _______
   - Breed 2: _______ No. of ewes: _______
   - Breed 3: _______ No. of ewes: _______
   - Breed 4: _______ No. of ewes: _______

Extra space is available at the end of the questionnaire if required.

6. How many ewes from each breed do you Signet record?
   - Breed 1: _______ Breed 2: _______ Breed 3: _______ Breed 4: _______

7. If applicable, what breeds of sire and dam are used for the cross breeds?

For the remaining sections, please select the main breed that you record & answer accordingly.

Breed selected is: _______ Signet Flock Number: _______

Mating

8. In the table below please indicate the location and supplementary feeding details for your rams and ram lambs during the month before mating.
   For each row, please tick all that apply.

<table>
<thead>
<tr>
<th>Location</th>
<th>Feeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>Housed</td>
<td>Outside</td>
</tr>
</tbody>
</table>

Eg. Home-bred Ram Lambs
- Home-bred Ram Lambs
- Home-bred Shearlings or older
- Bought-in Ram Lambs
- Bought-in Shearlings or older

9. How many of your ewes are mated naturally _______ and/or by AI _______
10. For those mated naturally, on average, how many days are they with a ram? _______
11. What is the average Ram:Ewe ratio and for your recorded sheep at mating? (e.g. 1:45)
   Groups using Shearlings or older _______ Groups using Ram Lambs _______ AI Group _______
Pregnancy Scanning & Lambing

12. Do you pregnancy scan your recorded ewes?
   - Yes (all ewes scanned) □
   - Yes (some ewes scanned) □
   - No □

13. Where do you lamb each group of recorded ewes? (Tick all that apply)
   - 1st time lambers
     - Single bearing: Hill/Rough grazing □
     - Multiple bearing: Hill/Rough grazing □
   - Ewes
     - Single bearing: Hill/Rough grazing □
     - Multiple bearing: Hill/Rough grazing □
   - Any additional comments - Extra space is available at the end of the questionnaire

14. Approximately how many recorded ewes each year do you assist with lambing? ______
15. Approximately how many recorded lambs are lost each year to predation? ______
16. Approximately how many recorded male lambs do you castrate each year? ______

Grazing & Feeding

17. During what months do you provide the ewes with the following? (Tick all that apply)

18. In the boxes below, please indicate where the recorded ewes have access to graze:
   - Section A: For each row, please tick all that apply
   - Section B: B = Barren ewes, S = Single bearing ewes, M = Multiple bearing ewes
   - For each row, please tick all that apply

<table>
<thead>
<tr>
<th>Section A</th>
<th>In-bye/Improved Grazing, Rough/Hill Grazing, Hay/Silage Fields, Other Crop Fields, Shed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eg. Wean - Mating</td>
<td>✗</td>
</tr>
<tr>
<td>Weaning - Mating</td>
<td>✗</td>
</tr>
<tr>
<td>Mating - Scanning</td>
<td>✗</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Section B</th>
<th>In-bye/Improved Grazing, Rough/Hill Grazing, Hay/Silage Fields, Other Crop Fields, Shed</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eg. Scan - Lamb</td>
<td>✗</td>
</tr>
<tr>
<td>Scanning to Lambing</td>
<td>✗</td>
</tr>
<tr>
<td>Lambing - 8 week Wt</td>
<td>✗</td>
</tr>
<tr>
<td>8 week Wt - Weaning</td>
<td>✗</td>
</tr>
</tbody>
</table>
Weaning & Sales

19. For approximately how many weeks before weaning is creep feed made available to the recorded lambs? _________

20. How many recorded male & female lambs do you retain for breeding each year?
   Male _______ Female _______

21. Do you winter your recorded ewe lamb replacements off farm?  Yes ☐ No ☐

22. How many ewe replacements, and rams, do you buy in each year?
   Ewe replacements _______ Rams _______

23. Approximately how many recorded ewes are culled for the following each year?
   Bad/Broken mouths _______ Foot problems _______
   Lambing associated problems _______ Repeated barreness _______
   Age ______ Mastitis ______ Other (please specify) _______

Land Information

24. What areas of your farm are: (please circle the scale used)
   Improved grazing _______ha/acre  Hay/Silage fields _______ha/acre
   Hill/Rough grazing _______ha/acre  Crop fields _______ha/acre

25. Overall, how would you rate the quality of grazing available to the recorded ewes during the following times of year?  (Please circle the appropriate number)
   1 = Poor Quality – 5 = High Quality
   Weaning – Mating 1____2____3____4____5  Lambing 1____2____3____4____5
   Mating – Scanning 1____2____3____4____5  8 Wk WI – Weaning 1____2____3____4____5
   Scanning – Lambing 1____2____3____4____5

26. Please give details of any reseeding over the past 5 years? (year, areas, mixtures used)
   Extra space is available at the end of the questionnaire if required

<table>
<thead>
<tr>
<th>Year</th>
<th>Area Reseeded</th>
<th>Mixtures used (if known)</th>
</tr>
</thead>
</table>

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Health

27. Do you routinely treat for/against the following. (Tick all that apply)
   Fluke [ ] Worms [ ] Clostridial diseases [ ] Abortions [ ] Orf [ ] Ticks [ ] Scab [ ] Lice [ ]
   Blowfly [ ] Other (please specify) __________________________

28. Has there been any chemical resistance identified on your farm? Yes [ ] No [ ]
   If Yes, which ones:
   Triclabendazole (eg. Fasimex) [ ] Levamisole (eg. Yellow wormers) [ ]
   Benzimidazoles (eg. White wormers) [ ] Ivermectins (eg. Clear wormers) [ ]
   Other (please specify) __________________________

29. Do you supplement with any of the following: (Tick all that apply)
   **Ewes**
   Copper [ ] Cobalt [ ] Selenium [ ] Vitamins [ ]
   **Lambs**
   Copper [ ] Cobalt [ ] Selenium [ ] Vitamins [ ]
   Other (please specify) __________________________

30. Do you have problems with the following, in an average year, in the recorded lambs?
    Yes [ ] No [ ] If yes, approximately how many lambs are affected
    Orf [ ] [ ] ____________
    Foot problems [ ] [ ] ____________
    Yellowosis [ ] [ ] ____________
    Joint III [ ] [ ] ____________
    Other [ ] [ ] ____________

Labour & Management

31. How many people are involved in the day to day care of the recorded flock? ________

32. When compared with the other flocks, livestock and crops that you have on the farm, how much of your time do you spend on this group of recorded sheep over the course of a year?
   Less than a ¼ [ ] Between ¼ and ½ [ ] Between ½ and ¾ [ ]
   Between ¾ and 100% [ ] 100% [ ]

33. Have you made any changes in the management of the ewes over the past 5 years?
    If so, please give brief details of what changes have been made, the years these changes were implemented and the reasons for change.
    Extra space is available at the end of the questionnaire if required

<table>
<thead>
<tr>
<th>Year</th>
<th>Change Made</th>
<th>Reason</th>
</tr>
</thead>
</table>

Should we require any further information, would you be happy for us to contact you again? Yes [ ] No [ ]

Thank you for taking the time to complete this questionnaire
Appendix 2. Statistical analysis used for Chapter 4 analyses.

Customised Genstat Programme (as used by C. Morgan-Davies et al., 2012)

"open file <<file>>.GSH"
"open file names.GSH"

**Step 1.**

"preliminary data processing"

**Step 2.**

"define variables etc and put into pointers for programming convenience"
variate [nvalues=1] pnlevfff[1...nofff]
calc vfff[1...nofff]=fff[1...nofff]
getattribute [attribute=levels,labels,nlevels] fff[1...nofff];attfff[1...nofff][nlevels]’
"1: continuous, 2: binary, or c: categorical with c levels"

variate [nvalues=nofff] typeoffff
equate old=pnlevfff;new=typeoffff

variate [nvalues=1] whichfff

equate old=namefff;new=whichfff
"put types into pointer"

variate [nvalues=1] pnamefff[1...nofff]
equate old=namefff;new=pnamefff
"put names into pointer"

calc pvvv[1...novvv]=Latitude,Longitude,altfrm,altto,sizeha,AvWinRain,AvSprTemp, AvWinSunH,AvSprSunH,TotalEwe,%ChOfFlck,nomatnat, nomatai,ramdays,ewpersh,ewperlb,ewperiAI,WINTAV,SPRAV,NMblck,Nmhay,Nmsil,Nmconc, fprewean,imgarea%,hayarea%,hrgarea%,otharea%,people

text [nvalues=novvv;values=('Latitude','Longitude','altfrm','altto','sizeha','AvWinRain','AvSprTemp','AvWinSunH','AvSprSunH','TotalEwe','%ChOfFlck','nomatnat','nomatai','ramdays','ewpersh','ewperlb','ewperiAI','WINTAV','SPRAV','NMblck','Nmhay','Nmsil','Nmconc','fprewean','imgarea%','hayarea%','hrgarea%','otharea%','people')]

"define variables"
calc ntypefff=29

"put all variate names below"
calc vvfff[1...nofff]=Latitude,Longitude,altfrm,altto, sizeha,AvWinRain,AvSprTemp, AvWinSunH,AvSprSunH,TotalEwe,%ChOfFlck,nomatnat, nomatai,ramdays,ewpersh,ewperlb,ewperiAI,WINTAV,SPRAV,NMblck,Nmhay,Nmsil,Nmconc, fprewean,imgarea%,hayarea%,hrgarea%,otharea%,people
text [nvalues=novvv;values=('Latitude','Longitude','altfrm','altto','sizeha','AvWinRain','AvSprTemp','AvWinSunH','AvSprSunH','TotalEwe','%ChOfFlck','nomatnat','nomatai','ramdays','ewpersh','ewperlb','ewperiAI','WINTAV','SPRAV','NMblck','Nmhay','Nmsil','Nmconc','fprewean','imgarea%','hayarea%','hrgarea%','otharea%','people')]

"define xxx"
calc noxxx=novvv+nofff
calc xxx[1...noxxx]=vvv[1...novvv],vfff[1...nofff]
text [nvalues=noxxx] namexxx
append [namexxx] namevvv,namefff
variate [nvalues=noxxx] typeofxxx
append [typeofxxx] typeofvvv,typeofff

"just a variate indicating the variable no (coxxx)"

variate [nvalues=noxxx;value=(1...noxxx)] whichxxx
fspreadsheet whichxxx,namevvv,typeofxxx

"put names into pointer"
text [nvalues=1] pnamexxx[1...noxxx]
equate old=namexxx;new=pnamexxx
"put types into pointer"

variate [nvalues=1] ptypeofxxx[1...noxxx]
equate old=typeofxxx;new=ptypeofxxx

"create a dummy factor with a single level to be used in trellis plots, since trellis will not run unless you give it a factor for different frames (different graphs) and sometimes you may want graphs with only one frame (see later)"
calc lenxxx=nvalues(xxx[1])
variate [nvalues=lenxxx;values=#lenxxx(1)] dummy
groups dummy;fdummy
Step 3.

"relationships between variables - correlations"

delete [redefine=yes] corr, pcorr
CORRELATE [PRINT=*, CORRELATIONS=corr] xxx[1...noxxx]
FSPREADSHEET corr
DELETE [REDEFINE=yes] _clprob, _cuprob, _probs
PRCORRELATION [NOBS=INVAL(xxx[1])] ABS(corr); CLPROB=_clprob; CUPROB=_cuprob
DELETE [REDEFINE=yes] pcorr
SYMMETRIC [ROWS=lp(xxx[1...noxxx])] pcorr; EXTRA='Probabilites'
CALC pcorr = 1 - _clprob + _cuprob
FSPREADSHEET pcorr

Step 4.

"clustering of farms"

"construct similarity matrix"

"get similarity matrices for each xxx"

for coxxx=1...noxxx
DELETE [Redefine=yes] sim[coxxx]
if ptypeofxxx[coxxx].gt.1
FSIMILARITY [SIMILARITY=sim[coxxx];UNITS=tfarm] xxx[coxxx]; TEST=simplematching
else
FSIMILARITY [SIMILARITY=sim[coxxx];UNITS=tfarm] xxx[coxxx]; TEST=Euclidean
endif
"fspreadsheet sim[coxxx]"
endfor "coxxx"

"fspreadsheet sim[5]" "say, if you want to see farm by farm matrix for one var or factor"

"get weights for contribution to overall similarity matrix of each farm covariate - assuming equal weights"
calc wgtmethod=1
variate [nvalues=noxxx] vwgt
scalar wgt[1...noxxx]
calc wgt[1...noxxx]=1/noxxx"THIS COULD BE ALTERED (BUT THEY MUST SUM TO 1) IF YOU WANT TO MAKE
SOME COVARIATE/FACTOR MORE IMPORTANT THAN OTHERS"
equate old=wgt;new=vwgt
fspreadsheet vwgt
calc sumwgts=sum(vwgt)
print sumwgts

"calc similarity matrix according to above weights"
calc simil=0*sim[1]
calc totwgt=0
for coxxx=1...noxxx
  calc simil=simil+wgt[coxxx]*sim[coxxx]
endfor
"take care of rounding errors on diagonal (1 was actually 0.9999999....):"
calc simil=simil-simil*(simil.eq.1)+1*(simil.eq.1)"#####"
fspreadsheet simil
"THIS SHOWS SIMILARITY BETWEEN PAIRS OR farms"

"examine dendogram for HCA based on original similarity matrix - ie startmethod=3"

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HCLUSTER [METHOD=nearestneighbour] simil;permutation=_perm
GETATTRIBUTE [ATTRIBUTE=rows] simil; _ps
HDISPLAY [PRINT=*] simil; TREE=_ddmst
DDENDROGRAM [ORDER=given; DSIMILARITY=yes] DATA=_ddmst; PERM=_perm; WINDOW=1; LABELS=tfarm
"THIS IS A QUICK CLUSTER TO SHOW DENDOGRAM"

Step 5.

"carry out principal coordinates analysis on similarity matrix"

"setting for PCO and nHCA"

"set number of pco roots initially investigated"
calc maxnoofroots=10

"set max accumulated % of roots for further investigation"
calc maxpcoaccpergraphe=100
"set max number of roots for further investigation"
calc maxnorootsforgraphest=6"####"

"set accumulated % of roots included for clustering"
calc maxpcoaccperclus=100
"set min number of roots included for clustering"
calc minnorootsforclus=2
"set max number of roots included for clustering"
calc maxnorootsforclus=6"####"
"set minimum and maximum number of grps for the cluster analysis"
calc minnogrps=2
"set min and max number of roots included for clustering"
calc maxnogrps=9
"set min and max start method for cluster analysis:
calc minstartmethod=1
calc maxstartmethod=1
"1: use classify"
"2: use HCA results on pcos to be included for cluster as start"
"3: use HCA results on original similarity matrix as start"

"work out how many pco roots are positive"
calc noroots=maxnoofroots
DELETE [REDEFINE=YES] pcolatrootvect,pcodistances,rootno,pcoroots
PCO [PRINT=*, NROOTS=noroots] simil; LRV=pcolatrootvect; DISTANCES=pcodistances
"FSPREADSHEET pcolatrootvect[‘Vectors’]
FSPREADSHEET pcolatrootvect[‘Roots’]
FSPREADSHEET pcolatrootvect[‘Trace’]
FSPREADSHEET pcodistances"
variate [nvalues=noroots;values=1...noroots] rootno
variate [nvalues=noroots] pcoroots
equate old=pcolatrootvect[‘Roots’];new=pcoroots
"fspreadsheet rootno,pcoroots"
calc posstoprootno=max(rootno*(pcoroots.gt.0))
print 'number of positive roots from pco: ',posstoprootno

"examine % variation for all positive roots"
calc noroots=posstoprootno
DELETE [REDEFINE=YES] pcolatrootvect,pcodistances,rootno,pcoroots,pcopercvar
PCO [PRINT=roots, NROOTS=noroots] simil; LRV=pcolatrootvect; DISTANCES=pcodistances
"FSPREADSHEET pcolatrootvect[‘Vectors’]
FSPREADSHEET pcolatrootvect[‘Roots’]
FSPREADSHEET pcolatrootvect[‘Trace’]"
FSPREADSHEET pcdistances"

```
variate [nvalues=noroots;values=1...noroots] rootno
variate [nvalues=noroots] pcoroots,pcopercent,pcoaccpercent
variate [nvalues=1] pcpopercent[1...noroots],pcoaccpercent[1...noroots]
equate old=pcolatrootvect['Roots'];new=pcoroots
calc pcpopercent=100*pcoroots/sum(pcoroots)
equate old=pcpopercent;new=ppcpopercent
for coroot=2...noroots
  calc colastroot=coroot-1
  calc pcpopercent[coroot]=pcpopercent[colastroot]+pcpopercent[coroot]
endfor
equate old=pcoaccpercent;new=pcoaccpercent
```
fspreadsheet rootno,pcoroots,pcopercent,pcoaccpercent

"plot % variation versus root number"

```
FRAME [RESET=yes] WINDOW=1; BOX=omit
XAXIS [RESET=yes] WINDOW=1; TITLE='rootno'; TPOSITION=middle; TDIRECTION=parallel;
  LPOSITION=outside; LDIRECTION=parallel; MPOSITION=outside; ARROWHEAD=omit; ACTION=display; marks=1
YAXIS [RESET=yes] WINDOW=1; TITLE='pcopercent'; TPOSITION=middle; TDIRECTION=parallel;
  LPOSITION=outside; LDIRECTION=perpendicular; MPOSITION=outside; ARROWHEAD=omit; ACTION=display;
```

"Set colours for plotting"

```
COLOUR [RESET=yes] 30,12,16,22,11,25,27,15; RED=3(128),192,255,2(128); GREEN=128,
  0,64,0(128); BLUE=2(128,0),128,2(192),128
PEN [RESET=yes] 1; METHOD=line; SYMBOL=2; SIZE=1; CSYMBOL=2
DGRAPH [WINDOW=1; TITLE='% var vs root no'] Y=pcopercent; X=rootno; PEN=1
COLOUR [RESET=yes] 30,12,16,22,11,25,27,15
PEN [RESET=yes] 1
```

"plot accumulated % variation versus root number"

```
FRAME [RESET=yes] WINDOW=1; BOX=omit
XAXIS [RESET=yes] WINDOW=1; TITLE='rootno'; TPOSITION=middle; TDIRECTION=parallel;
  LPOSITION=outside; LDIRECTION=parallel; MPOSITION=outside; ARROWHEAD=omit; ACTION=display; marks=1
YAXIS [RESET=yes] WINDOW=1; TITLE='accpopercent'; TPOSITION=middle; TDIRECTION=parallel;
  LPOSITION=outside; LDIRECTION=perpendicular; MPOSITION=outside; ARROWHEAD=omit; ACTION=display;
  lower=0; upper=105
```

"Set colours for plotting"

```
COLOUR [RESET=yes] 30,12,16,22,11,25,27,15; RED=3(128),192,255,2(128); GREEN=128,
  0,64,0(128); BLUE=2(128,0),128,2(192),128
PEN [RESET=yes] 1; METHOD=line; SYMBOL=2; SIZE=1; CSYMBOL=2
DGRAPH [WINDOW=1; TITLE='accumulated % var vs root no'] Y=pcoaccpercent; X=rootno; PEN=1
COLOUR [RESET=yes] 30,12,16,22,11,25,27,15
PEN [RESET=yes] 1
```

"further investigation of pcoscores"

"you have to run this section before doing cluster analysis"

calc invstoprootno=max(rootno*(pcoaccpercent.lt.maxpcoaccpercentforgraphsetc)-
  10000*(pcoaccpercent.gt.maxpcoaccpercentforgraphsetc))
calc invstoprootno=invstoprootno*(invstoprootno.lt.maxnorootsforgraphsetc)+
  maxnorootsforgraphsetc*(invstoprootno.ge.maxnorootsforgraphsetc)
print 'number of roots for further investigation: ',invstoprootno

```
```
"examine pcos up to stoprootno"

"you have to run this section before doing cluster analysis"

calc noroots=invstoprootno
DELETE [REDEFINE=YES] pcolatrootvect,pcodistances,pcoscores,matpcoscores,trmatpcoscores
PCO [PRINT=roots, scores, residuals, centroid; NROOTS=noroots] simil; LRV=pcolatrootvect;
DISTANCES=pcodistances
variate [nvalues=nofarms] pcoscores[1...noroots]
matrix [columns=noroots;rows=nofarms] matpcoscores
equate old=pcolatrootvect['Vectors'];new=matpcoscores
calc trmatpcoscores=transpose(matpcoscores)
equate old=trmatpcoscores;new=pcoscores
fspreadsheet pcoscores[1...noroots]

"get labelling for pcscores to be used in plots"
variate [nvalues=noroots;values=(1...noroots)] vshortnamepcoscores
ftext vshortnamepcoscores;shortnamepcoscores
variate [nvalues=noroots;values=(noroots...1)] indextosortwith
sort [index=indextosortwith] old=shortnamepcoscores;new=revshortnamepcoscores

"various plots of pcscores"

"to plot pcscores labelled by farms"

"3d plot of first 3 pcos only"
"you can change code to do other pcscores - e.g. 1,2,4; 2,3,4 etc"
"you can rotate this plot in 3d to see if there is obvious 3d clustering"

FRAME [RESET=yes] WINDOW=1; BOX=include
XAXIS [RESET=yes] WINDOW=1; TITLE='pcoscores[1]'; TPOSITION=middle; TDIRECTION=parallel;
| LPOSITION=outside; LDIRECTION=perpendicular; MPOSITION=outside; ARROWHEAD=omit; ACTION=display
YAXIS [RESET=yes] WINDOW=1; TITLE='pcoscores[2]'; TPOSITION=middle; TDIRECTION=parallel;
| LPOSITION=outside; LDIRECTION=perpendicular; MPOSITION=outside; ARROWHEAD=omit; ACTION=display
ZAXIS [RESET=yes] WINDOW=1; TITLE='pcoscores[3]'; TPOSITION=middle; TDIRECTION=parallel;
| LPOSITION=outside; LDIRECTION=perpendicular; MPOSITION=outside; ARROWHEAD=omit; ACTION=display

"Set colours for plotting"
COLOUR [RESET=yes] 30,12,16,22,11,25,27,15; RED=3(128),192,255,2(128); GREEN=128,
| 0,64,0(128,0); BLUE=2(128,0),128,2(192,128)

VARIADE _scolour; !(1,2,3,4,30,7,5,6,12,8)
VARIADE _symb; ![1,-1,-1,-1,-1,-1,-1,-1,-1]
VARIADE _symsize; ![1,1,1,1,1,1,1,1,1,1]

PEN [RESET=yes] 1...nofarms; METHOD=point; SYMBOL=#_symb; SIZE=#_symsize; CSYMBOL=#_scolour
D3GRAPH [WINDOW=1; TITLE='first 3 pcos'; AZIMUTH=225; ELEVATION=25] X=pcoscores[1]; Y=pcoscores[2];
Z=pcoscores[3]; PEN=farm
PEN [RESET=yes] 1...nofarms
COLOUR [RESET=yes] 30,12,16,22,11,25,27,15

"to examination of which xxx (covariates) are related to which pcoscores"

delete [redefine=yes] corr,pcorr
CORRELATE [PRINT=*, CORRELATIONS=corr] xxx[1...noxxx],pcoscores[1...noroots]
FSSPREADSHEET corr
DELETE [REDEFINE=yes] _clprob, _cuprob, _probs
PRCORRELATION [NOBS=NVAL(xxx[1])] ABS(corr); CLPROB=_clprob; CUPROB=_cuprob
DELETE [REDEFINE=yes] pcorr

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Step 6.

"carry out non hierarchical cluster analysis (nHCA) on pcoscores"

--------------------------------------------------
print 'maximum number of roots for clustering: ', cluststoprootno
endif

"nonHCA"
calc minnoroots=minnorootsforclusteranal
calc maxnoroots=cluststoprootno

delete [redefine=yes] startgrpning,fstartgrpning
calc caseno=0
for conoroots=minnoroots...maxnoroots
calc pnoroots=conoroots
calc pngrps=cogroups
for cstartmethod=mnstartmethod...maxstartmethod
calc caseno=caseno+1
print caseno
for caseno=0

calc pchastartfailed=0

---endcal---
if startmethod.eq.1 "start cluster by using classify"
  FACTOR _start
  CLASSIFY |p(pcoscores[1...conoroots]); NGROUPS=cogroups; GROUPS=_start
  calc startgrping[caseno]=_start
endif
if startmethod.eq.2 "start cluster by using results from HCA based on Eucl similarity from pcos"
  DELETE [Redefine=yes] similpco
  FSIMILARITY [SIMILARITY=similpco; UNITS=tspeciesid] pcoscores[1...conoroots]; TEST=euclidean
  calc foundstart=0
  for cothresh=10000...9000
    calc theshold=cothresh/100
    HCLUSTER [METHOD=nearestneighbour] similpco; groups=hcsgroups; gthreshold=theshold
    "fspreadsheet hcsgroups"
    if (nlevels(hcsgroups).eq.cogroups)
      calc startgrping[caseno]=hcsgroups
      print 'found hca start ',theshold
      calc foundstart=1
    endif
  endfor
  if foundstart.eq.0
    print 'no HCA soln found for cocase ',caseno
    calc phcastartfailed[caseno]=1
    FACTOR _start
    CLASSIFY |p(pcoscores[1...conoroots]); NGROUPS=cogroups; GROUPS=_start
    calc startgrping[caseno]=_start
  endif
endif
if startmethod.eq.3 "start cluster by using results from HCA based on original similarity matrix"
  calc foundstart=0
  for cothresh=9500...7200
    calc theshold=cothresh/100
    HCLUSTER [METHOD=nearestneighbour] simil; groups=hcsgroups; gthreshold=theshold
    "fspreadsheet hcsgroups"
    if (nlevels(hcsgroups).eq.cogroups)
      calc startgrping[caseno]=hcsgroups
      print 'found hca start ',theshold
      calc foundstart=1
    endif
  endfor
  if foundstart.eq.0
    print 'no HCA soln found for cocase ',caseno
    calc phcastartfailed[caseno]=1
    FACTOR _start
    CLASSIFY |p(pcoscores[1...conoroots]); NGROUPS=cogroups; GROUPS=_start
    calc startgrping[caseno]=_start
  endif
endif
if startmethod.eq.4 "start cluster by using classification as in grppriorbelief"
  calc startgrping[caseno]=grppriorbelief
endif
groups startgrping[caseno]; fstartgrping[caseno]
"find within group SofS for start grouping"
delete [redefine=yes] nobspscoscores,tnobspscoscores,VARPSscores,tvarpscores,sospcscores,initcritvalpergrp
variate [nvalues=cogroups] nobspscoscores[1...conoroots],varpscores[1...conoroots]
tabulate [classification=fstartgrping[caseno]]
pscores[1...conoroots]; var=varpscores[1...conoroots]; nobservations=tnobspscoscores[1...conoroots]
equate old=tnobspscoscores[1...conoroots]; new=nobspscoscores[1...conoroots]
equate old=tvarpscores[1...conoroots]; new=varpscores[1...conoroots]
calc sospscores[1...conoroots]=varpscores[1...conoroots]*(nobspscoscores[1...conoroots]-1)
"fspreadsheet sospscosores[1...conoroots]"
calc initcritvalpergrp=vsum(sospcoscores)
"fspreadsheet initcritvalpergrp"
calc pinitcritval[caseno]=sum(initcritvalpergrp)

CLUS\_TR\_C\_PR\_C\_\(\text{PRINT}=\text{criterion, optimum, units, typical, initial};\text{DATA}=!p(pcoscores[1...conoroots]);\text{CRITERION}=\text{sums};\text{\ INTERCHANGE}=\text{transfer};\text{START}=\text{fstartgrping}[\text{caseno}]\) \text{NGROUPS}=\text{cogroups}; \text{GROUPS}=\text{grpnhca}[\text{caseno}]

"find within group SofS for final grouping"
delete [\text{redefine=yes}] nosbpcoscores,tnosbpcoscores,varpcoscores,tvarpcoscores,sospcoscores,critvalpergrp

\text{variate [nvalues=\text{cogroups}] nosbpcoscores[1...conoroots],varpcoscores[1...conoroots]}\n\text{tabulate [classification=grpnhca[\text{caseno}]]}
pccoscores[1...\text{conoroots}];\text{var}=(\text{varpcoscores}[1...\text{conoroots}])\n\text{equate old=tnosbpcoscores[1...\text{conoroots}];new=nosbpcoscores[1...\text{conoroots}]}\n\text{equate old=tvarpcoscores[1...\text{conoroots}];new=varpcoscores[1...\text{conoroots}]}\n\text{calc sospcoscores[1...\text{conoroots}]=varpcoscores[1...\text{conoroots}]*(nosbpcoscores[1...\text{conoroots}] - 1)}\n"fspreadsheet sospcoscores[1...\text{conoroots}]"
calc critvalpergrp=vsum(sospcoscores)
"fspreadsheet critvalpergrp"
calc pcritval[caseno]=sum(critvalpergrp)
"find total SofS"
delete [\text{redefine=yes}] totsospcoscores

calc totsospcoscores[1...\text{conoroots}]=((\text{nofarms} - 1)\text{\text{\*}}\text{variance(pcoscores[1...\text{conoroots}])})\n\text{calc ppercinitcritoftotsos[caseno]=100*(1-(pinitcritval[caseno]/ptotsos[caseno])})\n\text{calc pperccritoftotsos[caseno]=100*(1-(pcritval[caseno]/ptotsos[caseno])})
endforall "startmethod"
endforall "cogroups"
endforall "coconoroots"

calc maxcaseno=\text{caseno}
calc pcaseno[1...maxcaseno]=1...maxcaseno
fttext pcaseno[1...maxcaseno];tpcaseno[1...maxcaseno]
fttext pwgtmethod[1...maxcaseno];tpwgtmethod[1...maxcaseno]
fttext pnoroots[1...maxcaseno];tpnoroots[1...maxcaseno]
fttext pnggrps[1...maxcaseno];tpnggrps[1...maxcaseno]
fttext pstartmethod[1...maxcaseno];tpstartmethod[1...maxcaseno]
fttext pchcastartfailed[1...maxcaseno];tpchcastartfailed[1...maxcaseno]
fttext pphotos[1...maxcaseno];tpotos[1...maxcaseno]
fttext pinicitritval[1...maxcaseno];tpinicitritval[1...maxcaseno]
fttext pcrival[1...maxcaseno];tpcrival[1...maxcaseno]
fttext pperccritoftotsos[1...maxcaseno];tpperccritoftotsos[1...maxcaseno]
fttext pperccritoftotsos[1...maxcaseno];tpperccritoftotsos[1...maxcaseno]

text [\text{nvalues=13};\text{values=('caseno','simmethod','wgtmethod','noroots','ngrps','startmethod','hcastartfail','critmetho d','d','totsos','initcritval','critval','percinitcritval','percritval')}} details

for cocaseno=1...\text{maxcaseno}
append [newvector=\text{settings}[cocaseno]]
\text{oldvector=tpcaseno[cocaseno],psimmethod[cocaseno],tpwgtmethod[cocaseno],tpnoroots[cocaseno],tpnggrps[cocaseno],tpstartmethod[cocaseno],tpchcastartfailed[cocaseno],tpcrival[cocaseno],tpotos[cocaseno],tpinicitritval[cocaseno],tpcrival[cocaseno],tpperccritoftotsos[cocaseno],tpperccritoftotsos[cocaseno]]
endfor

\text{fspreadsheet details,settings[1...maxcaseno]}
\text{fspreadsheet fstartgrping[1...maxcaseno],grpnhca[1...maxcaseno]}

"plot %sos explained versus caseno"

\text{variate [nvalues=\text{maxcaseno},values=(1...maxcaseno)] vcaseno}
\text{variate [nvalues=\text{maxcaseno}] vperccritoftotsos}
equate old=vperccritoftotsos;new=vperccritoftotsos
“Set colours for plotting”

COLOUR [RESET=yes] 30,12,16,22,11,25,27,15; RED=3(128),192,255,2(128); GREEN=128,0,64,0,4(128); BLUE=2(128,0),128,2(192),128
PEN [RESET=yes] 1; METHOD=line; JOIN=ascending; SYMBOL=0; LINESIZE=1; THICKNESS=1; 
SIZE=1; CLINE=1
DGRAPH [WINDOW=1; TITLE='% sos'] Y=vperccritoftotsos; X=vcaseno; PEN=1
PEN [RESET=yes] 1
COLOUR [RESET=yes] 30,12,16,22,11,25,27,15

“examine pcoscores with cluster groups for chosen casenumbers”

calc thiscaseno=34 “change this as required”

fspreadsheet tfarm,grpnhca[thiscaseno]

“resort by chosen clustering”

delete [redefine=yes] sortgrpnhca,sorttfarm,sortxxx[1...noxxx]
sort [index=grpnhca[thiscaseno],farm] grpnhca[thiscaseno],tfarm,xxx[1...noxxx];
sortgrpnhca,sorttfarm,sortxxx[1...noxxx]
fspreadsheet sortgrpnhca,sorttfarm,sortxxx[1...noxxx]

“to plot all pcs by cluster groups”

calc noroots=pnoroots[thiscaseno]
calc nlevgrpnhca=nlevels(grpnhca[thiscaseno])
variate [nvalues=noroots;values=(1...noroots)] tempvshortnamepcoscores
ftext tempvshortnamepcoscores;tempshortnamepcoscores
variate [nvalues=noroots;values=(noroots...1)] tempindextosortwith
sort [index=tempindextosortwith] old=tempshortnamepcoscores;new=tempprevshortnamepcoscores
PEN [RESET=yes] 1...nlevgrpnhca
PEN 1...nlevgrpnhca; LABELS=“;symbol=2; size=0.7
dscatter [pcoscores[1...noroots];tempshortnamepcoscores;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno])

“include species labelling”
PEN [RESET=yes] 1...nlevgrpnhca
PEN 1...nlevgrpnhca; LABELS=“;symbol=2; size=0.7
dscatter [pcoscores[1...noroots];tempshortnamepcoscores;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno])
delete [redefine=yes]
tempvshortnamepcoscores,tempshortnamepcoscores,tempindextosortwith,tempprevshortnamepcoscores

“to plot all pcs by cluster groups - one pair of pcscores at a time”

calc noroots=pnoroots[thiscaseno]
calc nlevgrpnhca=nlevels(grpnhca[thiscaseno])
PEN [RESET=yes] 1...nlevgrpnhca
PEN 1...nlevgrpnhca; LABELS=“;symbol=2; size=1
calc topcoroot1=noroots-1
calc topcoroot1=topcoroot1...1
calc botcoroot2=coroot1+1
for coroot2=noroots...botcoroot2
dscsatter [pcoscores[coroot1];tcoroot1;ticksandlabels=yes”;equal=yes”;pen=grpnhca[thiscaseno]]
pocoscores[coroot2];tcoroot2
endfor”coroot2
endfor”coroot1”

“3d plot of first 3 pcos only”

“you can change code to do other pcoscores - e.g. 1,2,4; 2,3,4 etc”
“you can rotate this plot in 3d to see if there is obvious 3d clustering”

calc nlevgrpnhca=nlevels(grpnhca[thiscaseno])
PEN [RESET=yes] 1...nlevgrpnhca
FRAME [RESET=yes] WINDOW=1; BOX=omit
XAXIS [RESET=yes] WINDOW=1; TITLE=’pcoscores[1]”; TPOSITION=middle; TDIRECTION=parallel;
LPOSITION=outside; LDIRECTION=parallel; MPOSITION=outside; ARROWHEAD=omit; ACTION=display
YAXIS [RESET=yes] WINDOW=1; TITLE=’pcoscores[2]”; TPOSITION=middle; TDIRECTION=parallel;
LPOSITION=outside; LDIRECTION=perpendicular; MPOSITION=outside; ARROWHEAD=omit; ACTION=display
ZAXIS [RESET=yes] WINDOW=1; TITLE=’pcoscores[3]”; TPOSITION=middle; TDIRECTION=parallel;
LPOSITION=outside; LDIRECTION=perpendicular; MPOSITION=outside; ARROWHEAD=omit; ACTION=display

“Set colours for plotting”

COLOUR [RESET=yes] 30,12,16,22,11,25,27,15; RED=3(128),192,255,2(128); GREEN=128,
0,64,0,4(128); BLUE=2(128,0),128,2(192),128
VARIATE _scolour; !(1,2,3,4,30,7,5)
VARIATE _symb; !(-1,-1,-1,-1,-1,-1)
VARIATE _symsize; !(1,1,1,1,1,1,1)

PEN [RESET=yes] 1...nlevgrpnhca;
pen 1...nlevgrpnhca;
LABELS=tfarm;symbol=2;size=0.6
text [nvalues=5] tempnamexxx
append [tempnamexxx] pnamexxx[1...5]
dscsatter [xxx[1...5];tempnamexxx;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno]]
pocoscores[noroots...1];tempprevshortnamepcoscores
append [tempnamexxx] pnamexxx[6...10]
dscsatter [xxx[6...10];tempnamexxx;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno]]
pocoscores[noroots...1];tempprevshortnamepcoscores
append [tempnamexxx] pnamexxx[11...15]
dscsatter [xxx[11...15];tempnamexxx;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno]]
pocoscores[noroots...1];tempprevshortnamepcoscores
append [tempnamexxx] pnamexxx[16...20]
dscsatter [xxx[16...20];tempnamexxx;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno]]
pocoscores[noroots...1];tempprevshortnamepcoscores
append [tempnamexxx] pnamexxx[21...25]
dcscatter [xxx[21...25];tempnamexxx;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno]]\ 
pcoscores[noroots...1];temprevshortnamepcoscores 
append [tempnamexxx] pnamexxx[26...31] 
dcscatter [xxx[26...31];tempnamexxx;ticksandlabels=no”;equal=yes”;pen=grpnhca[thiscaseno]]\ 
pcoscores[noroots...1];temprevshortnamepcoscores

“tables of xxx (covarites) by cluster groups”

delete [redefine=yes] tcogrpnhcaftrait,tcogrpnhca 
tabulate [classification=grpnhca[thiscaseno],counts=tcogrpnhca] 
fspreadsheet tcogrpnhca 
for coxxx=1...noxxx 
tabulate [classification=grpnhca[thiscaseno]] xxx[coxxx];means=tmeansxxxbygrpnhca[coxxx] 
"fspreadsheet tmeansgrpnhcaftrait[cotrait]"
endfor”coxxx" 
fspreadsheet tmeansxxxbygrpnhca

"useful to add tables here to show factors by clusters"
<table>
<thead>
<tr>
<th>Factor</th>
<th>Detail</th>
</tr>
</thead>
<tbody>
<tr>
<td>typ</td>
<td>System type (according to stratified levels: hill, upland or lowland)</td>
</tr>
<tr>
<td>org</td>
<td>Organic (yes/no)</td>
</tr>
<tr>
<td>breed1</td>
<td>Breed (Charollais, Suffolk or Texel)</td>
</tr>
<tr>
<td>hbrlout</td>
<td>Home-bred ram lambs kept outside during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbsout</td>
<td>Home-bred older rams kept outside during the month before mating (yes/no)</td>
</tr>
<tr>
<td>birlout</td>
<td>Bought-in ram lambs kept outside during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bisout</td>
<td>Bought-in rams kept outside during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbrlcon</td>
<td>Home-bred ram lambs fed concentrates during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbrlhay</td>
<td>Home-bred ram lambs fed hay during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbrlsil</td>
<td>Home-bred ram lambs fed silage during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbrlstrew</td>
<td>Home-bred ram lambs fed straw during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbrlblick</td>
<td>Home-bred ram lambs fed feed blocks during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbrlnon</td>
<td>Home-bred ram lambs fed nothing during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbscon</td>
<td>Home-bred older rams fed concentrates during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbshay</td>
<td>Home-bred older rams fed hay during the month before mating (yes/no)</td>
</tr>
<tr>
<td>hbstrew</td>
<td>Home-bred older rams fed straw during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bsbhlick</td>
<td>Home-bred older rams fed feed blocks during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bshnnon</td>
<td>Home-bred older rams fed nothing during the month before mating (yes/no)</td>
</tr>
<tr>
<td>birlhcon</td>
<td>Bought-in ram lambs fed concentrates during the month before mating (yes/no)</td>
</tr>
<tr>
<td>birlhay</td>
<td>Bought-in ram lambs fed hay during the month before mating (yes/no)</td>
</tr>
<tr>
<td>birlstrew</td>
<td>Bought-in ram lambs fed straw during the month before mating (yes/no)</td>
</tr>
<tr>
<td>birlblick</td>
<td>Bought-in ram lambs fed feed blocks during the month before mating (yes/no)</td>
</tr>
<tr>
<td>birlnon</td>
<td>Bought-in rams fed nothing during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bishhcon</td>
<td>Bought-in older rams fed concentrates during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bishhay</td>
<td>Bought-in older rams fed hay during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bishstrew</td>
<td>Bought-in older rams fed straw during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bishblick</td>
<td>Bought-in older rams fed feed blocks during the month before mating (yes/no)</td>
</tr>
<tr>
<td>bishnon</td>
<td>Bought-in older rams fed nothing during the month before mating (yes/no)</td>
</tr>
<tr>
<td>allscan</td>
<td>Are the ewes pregnancy scanned (yes/no)</td>
</tr>
<tr>
<td>esinlamb</td>
<td>Location of single bearing ewes at lambing (hill/rough grazing, improved pasture, shed, other)</td>
</tr>
<tr>
<td>emullamb</td>
<td>Location of multiple bearing ewes at lambing (hill/rough grazing, improved pasture, shed, other)</td>
</tr>
<tr>
<td>wminmgrz</td>
<td>Between weaning and mating, do the ewes have access to graze in-bye/improved grazing? (yes/no)</td>
</tr>
<tr>
<td>wmrhgrz</td>
<td>Between weaning and mating, do the ewes have access to graze hill/rough grazing? (yes/no)</td>
</tr>
<tr>
<td>wmhayf</td>
<td>Between weaning and mating, do the ewes have access to graze hay/silage fields? (yes/no)</td>
</tr>
<tr>
<td>wmoothf</td>
<td>Between weaning and mating, do the ewes have access to graze other crop fields? (yes/no)</td>
</tr>
<tr>
<td>wmshed</td>
<td>Between weaning and mating, are the ewes kept in the shed? (yes/no)</td>
</tr>
<tr>
<td>mtimgrz</td>
<td>During mating, do the ewes have access to graze in-bye/improved grazing? (yes/no)</td>
</tr>
<tr>
<td>mtrhgrz</td>
<td>During mating, do the ewes have access to graze hill/rough grazing? (yes/no)</td>
</tr>
<tr>
<td>mthayf</td>
<td>During mating, do the ewes have access to graze hay/silage fields? (yes/no)</td>
</tr>
<tr>
<td>mtshed</td>
<td>During mating, are the ewes kept in the shed? (yes/no)</td>
</tr>
<tr>
<td>Code</td>
<td>Description</td>
</tr>
<tr>
<td>----------</td>
<td>-----------------------------------------------------------------------------</td>
</tr>
<tr>
<td>msimgrz</td>
<td>Between mating and preg. scanning, do the ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>msrhgrz</td>
<td>Between mating and preg. scanning, do the ewes have access to graze hill?</td>
</tr>
<tr>
<td>mshayf</td>
<td>Between mating and preg. scanning, do the ewes have access to graze hay?</td>
</tr>
<tr>
<td>msothf</td>
<td>Between mating and preg. scanning, do the ewes have access to graze other?</td>
</tr>
<tr>
<td>msshed</td>
<td>Between mating and preg. scanning, are the ewes kept in the shed?</td>
</tr>
<tr>
<td>%0slimgr</td>
<td>Between preg. scanning and lambing, do barren ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%1slimgr</td>
<td>Between preg. scanning and lambing, do single bearing ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%2slimgr</td>
<td>Between preg. scanning and lambing, do multiple ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%0srhgr</td>
<td>Between preg. scanning and lambing, do barren ewes have access to graze hill/rough?</td>
</tr>
<tr>
<td>%1srhgr</td>
<td>Between preg. scanning and lambing, do single bearing ewes have access to graze hill/rough?</td>
</tr>
<tr>
<td>%2srhgr</td>
<td>Between preg. scanning and lambing, do multiple ewes have access to graze hill/rough?</td>
</tr>
<tr>
<td>%0shaygr</td>
<td>Between preg. scanning and lambing, do barren ewes have access to graze hay/silage?</td>
</tr>
<tr>
<td>%1shaygr</td>
<td>Between preg. scanning and lambing, do single bearing ewes have access to graze hay/silage?</td>
</tr>
<tr>
<td>%2shaygr</td>
<td>Between preg. scanning and lambing, do multiple ewes have access to graze hay/silage?</td>
</tr>
<tr>
<td>%0slotgr</td>
<td>Between preg. scanning and lambing, do barren ewes have access to graze other?</td>
</tr>
<tr>
<td>%1slotgr</td>
<td>Between preg. scanning and lambing, do single bearing ewes have access to graze other?</td>
</tr>
<tr>
<td>%2slotgr</td>
<td>Between preg. scanning and lambing, do multiple ewes have access to graze other?</td>
</tr>
<tr>
<td>%0shed</td>
<td>Between preg. scanning and lambing, are barren ewes kept in the shed?</td>
</tr>
<tr>
<td>%1shed</td>
<td>Between preg. scanning and lambing, are single bearing ewes kept in the shed?</td>
</tr>
<tr>
<td>%2shed</td>
<td>Between preg. scanning and lambing, are multiple ewes kept in the shed?</td>
</tr>
<tr>
<td>%0imgr</td>
<td>Between lambing and 8-week weight, do barren ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%1imgr</td>
<td>Between lambing and 8-week weight, do single bearing ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%2imgr</td>
<td>Between lambing and 8-week weight, do multiple ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%0rhgr</td>
<td>Between lambing and 8-week weight, do barren ewes have access to graze hill/rough?</td>
</tr>
<tr>
<td>%1rhgr</td>
<td>Between lambing and 8-week weight, do single bearing ewes have access to graze hill/rough?</td>
</tr>
<tr>
<td>%2rhgr</td>
<td>Between lambing and 8-week weight, do multiple ewes have access to graze hill/rough?</td>
</tr>
<tr>
<td>%0haygr</td>
<td>Between lambing and 8-week weight, do barren ewes have access to graze hay/silage?</td>
</tr>
<tr>
<td>%1haygr</td>
<td>Between lambing and 8-week weight, do single bearing ewes have access to graze hay/silage?</td>
</tr>
<tr>
<td>%2haygr</td>
<td>Between lambing and 8-week weight, do multiple ewes have access to graze hay/silage?</td>
</tr>
<tr>
<td>%0otgr</td>
<td>Between lambing and 8-week weight, do barren ewes have access to graze other?</td>
</tr>
<tr>
<td>%1otgr</td>
<td>Between lambing and 8-week weight, do single bearing ewes have access to graze other?</td>
</tr>
<tr>
<td>%2otgr</td>
<td>Between lambing and 8-week weight, do multiple ewes have access to graze other?</td>
</tr>
<tr>
<td>%0shed</td>
<td>Between lambing and 8-week weight, are barren ewes kept in the shed?</td>
</tr>
<tr>
<td>%1shed</td>
<td>Between lambing and 8-week weight, are single bearing ewes kept in the shed?</td>
</tr>
<tr>
<td>%2shed</td>
<td>Between lambing and 8-week weight, are multiple ewes kept in the shed?</td>
</tr>
<tr>
<td>%0imgr</td>
<td>Between 8-week weight and weaning, do barren ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%1imgr</td>
<td>Between 8-week weight and weaning, do single bearing ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>%2imgr</td>
<td>Between 8-week weight and weaning, do multiple ewes have access to graze in-by/de?</td>
</tr>
<tr>
<td>Question</td>
<td>Response Options</td>
</tr>
<tr>
<td>-------------------------------------------------------------------------</td>
<td>-------------------</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do multiple ewes have access to graze in-bye/improved grazing?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do barren ewes have access to graze hill/rough grazing?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do single bearing ewes have access to graze hill/rough grazing?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do multiple ewes have access to graze hill/rough grazing?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do barren ewes have access to graze hay/silage fields?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do single bearing ewes have access to graze hay/silage fields?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do multiple ewes have access to graze hay/silage fields?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do barren ewes have access to graze other crop fields?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, do multiple ewes have access to graze other crop fields?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, are barren ewes kept in the shed?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Between 8-week weight and weaning, are multiple ewes kept in the shed?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Quality of grazing between weaning and mating (1-5 scale)</td>
<td></td>
</tr>
<tr>
<td>Quality of grazing during mating (1-5 scale)</td>
<td></td>
</tr>
<tr>
<td>Quality of grazing between weaning and mating (1-5 scale)</td>
<td></td>
</tr>
<tr>
<td>Quality of grazing between preg. scanning and lambing (1-5 scale)</td>
<td></td>
</tr>
<tr>
<td>Quality of grazing during lambing (1-5 scale)</td>
<td></td>
</tr>
<tr>
<td>Quality of grazing between lambing and 8-week weight (1-5 scale)</td>
<td></td>
</tr>
<tr>
<td>Quality of grazing between 8-week weight and weaning (1-5 scale)</td>
<td></td>
</tr>
<tr>
<td>Do you routinely treat the flock for fluke?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for worms?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for clostridial diseases?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for abortions?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for orf?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for ticks?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for sheep scab?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for lice?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for blowfly?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you routinely treat the flock for any else?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Has Triclabendazole resistance been identified on your farm?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Has Levamisole resistance been identified on your farm?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Has Benzimidazole resistance been identified on your farm?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you supplement the ewes with copper?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you supplement the ewes with cobalt?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you supplement the ewes with selenium?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you supplement the ewes with vitamins?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you supplement the lambs with copper?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you supplement the lambs with cobalt?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Do you supplement the lambs with selenium?</td>
<td>(yes/no)</td>
</tr>
<tr>
<td>Question</td>
<td>Description</td>
</tr>
<tr>
<td>----------------------------------</td>
<td>-------------------------------------------------------</td>
</tr>
<tr>
<td>Isupvit</td>
<td>Do you supplement the lambs with vitamins? (yes/no)</td>
</tr>
<tr>
<td>othersup</td>
<td>Do you supplement with anything else? (yes/no)</td>
</tr>
<tr>
<td>time14</td>
<td>Do you spend less than a 1/4 of your time working with the recorded flock? (yes/no)</td>
</tr>
<tr>
<td>time1412</td>
<td>Do you spend between a 1/4 and 1/2 of your time working with the recorded flock? (yes/no)</td>
</tr>
<tr>
<td>time1234</td>
<td>Do you spend between a 1/2 and 3/4 of your time working with the recorded flock? (yes/no)</td>
</tr>
<tr>
<td>time34fu</td>
<td>Do you spend between a 3/4 and all of your time working with the recorded flock? (yes/no)</td>
</tr>
<tr>
<td>timefull</td>
<td>Do you spend all of your time working with the recorded flock? (yes/no)</td>
</tr>
<tr>
<td>Variate</td>
<td>Detail</td>
</tr>
<tr>
<td>-------------</td>
<td>-------------------------------------------------------------</td>
</tr>
<tr>
<td>Latitude</td>
<td>Latitude of farm (value)</td>
</tr>
<tr>
<td>Longitude</td>
<td>Longitude of farm (value)</td>
</tr>
<tr>
<td>altfrm</td>
<td>Altitude of farm - lowest level (m)</td>
</tr>
<tr>
<td>altto</td>
<td>Altitude of farm - highest level (m)</td>
</tr>
<tr>
<td>sizeha</td>
<td>Size of farm (ha)</td>
</tr>
<tr>
<td>AvWinRain</td>
<td>Average winter rainfall (mm)</td>
</tr>
<tr>
<td>AvSprTemp</td>
<td>Average Spring Temperature (°C)</td>
</tr>
<tr>
<td>AvWinSunH</td>
<td>Average Winter Sunshine Hours (hours)</td>
</tr>
<tr>
<td>AvSprSunH</td>
<td>Average Spring Sunshine Hours (hours)</td>
</tr>
<tr>
<td>TotalEwe</td>
<td>Total number of ewes on farm</td>
</tr>
<tr>
<td>%ChOFick</td>
<td>% of total ewe number that is the recorded flock</td>
</tr>
<tr>
<td>nomatnat</td>
<td>Approx. number of ewes mated naturally</td>
</tr>
<tr>
<td>nomatai</td>
<td>Approx. number of ewes mated by artificial insemination (AI)</td>
</tr>
<tr>
<td>ramdays</td>
<td>Average number of days ewes with a ram</td>
</tr>
<tr>
<td>ewpersh</td>
<td>Older ram: ewe ratio</td>
</tr>
<tr>
<td>ewperlb</td>
<td>Ram lamb: ewe ratio</td>
</tr>
<tr>
<td>ewperai</td>
<td>AI sire: ewe ratio</td>
</tr>
<tr>
<td>WINTAV</td>
<td>Proportion of lambs born during the winter months (%)</td>
</tr>
<tr>
<td>SPRAV</td>
<td>Proportion of lambs born during the spring months (%)</td>
</tr>
<tr>
<td>NMbck</td>
<td>Number of months during the year feed blocks available to ewes</td>
</tr>
<tr>
<td>Nmhay</td>
<td>Number of months during the year hay available to ewes</td>
</tr>
<tr>
<td>Nmsil</td>
<td>Number of months during the year silage available to ewes</td>
</tr>
<tr>
<td>Nmconc</td>
<td>Number of months during the year concentrate feed available to ewes</td>
</tr>
<tr>
<td>fprewean</td>
<td>Number of weeks pre-weaning concentrate feed available to lambs</td>
</tr>
<tr>
<td>imgarea%</td>
<td>Proportion of farm in-byre/improved grazing (%)</td>
</tr>
<tr>
<td>hayarea%</td>
<td>Proportion of farm hay/silage field grazing (%)</td>
</tr>
<tr>
<td>hrgarea%</td>
<td>Proportion of farm hill/rough grazing (%)</td>
</tr>
<tr>
<td>otharea%</td>
<td>Proportion of farm any other grazing (%)</td>
</tr>
<tr>
<td>people</td>
<td>Number of people involved in day to day care of flock</td>
</tr>
</tbody>
</table>
Appendix 3. Supplementary tables of results for Chapter 4

Appendix Table A1. Cluster comparisons for grazing use between pregnancy scanning and weaning

<table>
<thead>
<tr>
<th>Time Period</th>
<th>Cluster 1</th>
<th>Cluster 2</th>
<th>Cluster 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Scanning - Lambing</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Single rearing ewes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in-byre/improved</td>
<td>81%ᵃ</td>
<td>16%ᵇ</td>
<td>73%ᵃ</td>
</tr>
<tr>
<td>rough/hill</td>
<td>0%</td>
<td>8%</td>
<td>18%</td>
</tr>
<tr>
<td>hay/silage field</td>
<td>22%ᵃ</td>
<td>64%ᵇ</td>
<td>9%ᵃ</td>
</tr>
<tr>
<td>other crop field</td>
<td>0%</td>
<td>4%</td>
<td>0%</td>
</tr>
<tr>
<td>shed</td>
<td>19%</td>
<td>32%</td>
<td>14%</td>
</tr>
<tr>
<td>Multiple rearing ewes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in-byre/improved</td>
<td>78%ᵃ</td>
<td>16%ᵇ</td>
<td>77%ᵃ</td>
</tr>
<tr>
<td>rough/hill</td>
<td>0%</td>
<td>8%</td>
<td>5%</td>
</tr>
<tr>
<td>hay/silage field</td>
<td>22%ᵃ</td>
<td>60%ᵇ</td>
<td>23%ᵃ</td>
</tr>
<tr>
<td>other crop field</td>
<td>0%</td>
<td>8%</td>
<td>5%</td>
</tr>
<tr>
<td>shed</td>
<td>25%</td>
<td>32%</td>
<td>23%</td>
</tr>
<tr>
<td><strong>Lambing-8 Week Weight</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Single rearing ewes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in-byre/improved</td>
<td>56%ᵃ</td>
<td>20%ᵇ</td>
<td>68%ᵃ</td>
</tr>
<tr>
<td>rough/hill</td>
<td>0%</td>
<td>12%</td>
<td>5%</td>
</tr>
<tr>
<td>hay/silage field</td>
<td>9%ᵃ</td>
<td>44%ᵇ</td>
<td>36%ᵇ</td>
</tr>
<tr>
<td>other crop field</td>
<td>3%</td>
<td>12%</td>
<td>0%</td>
</tr>
<tr>
<td>shed</td>
<td>41%ᵃ</td>
<td>48%ᵃ</td>
<td>5%ᵇ</td>
</tr>
<tr>
<td>Multiple rearing ewes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in-byre/improved</td>
<td>60%</td>
<td>24%</td>
<td>64%</td>
</tr>
<tr>
<td>rough/hill</td>
<td>0%</td>
<td>12%</td>
<td>5%</td>
</tr>
<tr>
<td>hay/silage field</td>
<td>9%ᵃ</td>
<td>40%ᵇ</td>
<td>41%ᵇ</td>
</tr>
<tr>
<td>other crop field</td>
<td>3%</td>
<td>12%</td>
<td>0%</td>
</tr>
<tr>
<td>shed</td>
<td>44%ᵃ</td>
<td>52%ᵃ</td>
<td>9%ᵇ</td>
</tr>
<tr>
<td><strong>8-Week Weight - Weaning</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Single rearing ewes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in-byre/improved</td>
<td>78%ᵃ</td>
<td>24%ᵇ</td>
<td>73%ᵃ</td>
</tr>
<tr>
<td>rough/hill</td>
<td>3%</td>
<td>8%</td>
<td>0%</td>
</tr>
<tr>
<td>hay/silage field</td>
<td>9%ᵃ</td>
<td>48%ᵇ</td>
<td>32%ᵇ</td>
</tr>
<tr>
<td>other crop field</td>
<td>6%</td>
<td>12%</td>
<td>5%</td>
</tr>
<tr>
<td>shed</td>
<td>13%</td>
<td>12%</td>
<td>0%</td>
</tr>
<tr>
<td>Multiple rearing ewes</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>in-byre/improved</td>
<td>78%ᵃ</td>
<td>24%ᵇ</td>
<td>73%ᵃ</td>
</tr>
<tr>
<td>rough/hill</td>
<td>0%</td>
<td>8%</td>
<td>0%</td>
</tr>
<tr>
<td>hay/silage field</td>
<td>13%ᵃ</td>
<td>56%ᵇ</td>
<td>32%ᵇ</td>
</tr>
<tr>
<td>other crop field</td>
<td>6%</td>
<td>12%</td>
<td>5%</td>
</tr>
<tr>
<td>shed</td>
<td>16%</td>
<td>12%</td>
<td>0%</td>
</tr>
</tbody>
</table>

ᵃᵇValues within a row with different superscripts differ significantly at *P*<0.05
### Appendix Table A2. Cluster comparisons for vitamin and mineral supplementation

<table>
<thead>
<tr>
<th></th>
<th>Cluster 1</th>
<th>Cluster 2</th>
<th>Cluster 3</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ewes - Copper</strong></td>
<td>13%</td>
<td>12%</td>
<td>41%</td>
</tr>
<tr>
<td><strong>Ewes - Cobalt</strong></td>
<td>6%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>28%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>77%&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Ewes - Selenium</strong></td>
<td>16%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>48%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>86%&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Ewes - Vitamins</strong></td>
<td>16%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>68%&lt;sup&gt;b&lt;/sup&gt;</td>
<td>82%&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Lambs - Copper</strong></td>
<td>6%</td>
<td>12%</td>
<td>27%</td>
</tr>
<tr>
<td><strong>Lambs - Cobalt</strong></td>
<td>0%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>36%&lt;sup&gt;b&lt;/sup&gt;</td>
<td>64%&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Lambs - Selenium</strong></td>
<td>3%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>52%&lt;sup&gt;b&lt;/sup&gt;</td>
<td>86%&lt;sup&gt;b&lt;/sup&gt;</td>
</tr>
<tr>
<td><strong>Lambs - Vitamins</strong></td>
<td>6%&lt;sup&gt;a&lt;/sup&gt;</td>
<td>72%&lt;sup&gt;b&lt;/sup&gt;</td>
<td>64%&lt;sup&gt;b&lt;/sup&gt;</td>
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<sup>a,b</sup> Values within a row with different superscripts differ significantly at \( P<0.05 \)
## Appendix Table A3. Cluster comparisons for quantitative variables

<table>
<thead>
<tr>
<th>Variable</th>
<th>Cluster 1</th>
<th>Cluster 2</th>
<th>Cluster 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Altitude from (m)</td>
<td>102.8</td>
<td>98.7</td>
<td>142.1</td>
</tr>
<tr>
<td>Altitude to (m)</td>
<td>136.1</td>
<td>169.7</td>
<td>216.8</td>
</tr>
<tr>
<td>Size of farm (ha)</td>
<td>128.0</td>
<td>543.8</td>
<td>173.6</td>
</tr>
<tr>
<td>Average winter rainfall 2005-2009 (mm)</td>
<td>224.6\a</td>
<td>289.2\b</td>
<td>364.5\c</td>
</tr>
<tr>
<td>Average spring rainfall 2005-2009 (mm)</td>
<td>189.4\a</td>
<td>230.0\b</td>
<td>268.7\c</td>
</tr>
<tr>
<td>Average summer rainfall 2005-2009 (mm)</td>
<td>240.0\a</td>
<td>282.4\b</td>
<td>309.0\c</td>
</tr>
<tr>
<td>Average autumn rainfall 2005-2009 (mm)</td>
<td>254.6\a</td>
<td>318.3\b</td>
<td>390.9\c</td>
</tr>
<tr>
<td>Average winter temp. 2005-2009 (°C)</td>
<td>4.6</td>
<td>4.6</td>
<td>4.3</td>
</tr>
<tr>
<td>Average spring temp. 2005-2009 (°C)</td>
<td>8.7\a</td>
<td>8.5\b</td>
<td>7.9\b</td>
</tr>
<tr>
<td>Average summer temp. 2005-2009 (°C)</td>
<td>15.5\a</td>
<td>15.0</td>
<td>14.3\b</td>
</tr>
<tr>
<td>Average autumn temp. 2005-2009 (°C)</td>
<td>10.7\a</td>
<td>10.4\b</td>
<td>9.9\b</td>
</tr>
<tr>
<td>Average winter sun 2005-2009 (hours)</td>
<td>182.3\a</td>
<td>171.9\ab</td>
<td>216.1\b</td>
</tr>
<tr>
<td>Average spring sun 2005-2009 (hours)</td>
<td>481.6</td>
<td>473.9</td>
<td>473.3</td>
</tr>
<tr>
<td>Average summer sun 2005-2009 (hours)</td>
<td>549.4\a</td>
<td>518.9\ab</td>
<td>492.4\b</td>
</tr>
<tr>
<td>Average autumn sun 2005-2009 (hours)</td>
<td>312.8\a</td>
<td>290.5\ab</td>
<td>272.8\b</td>
</tr>
<tr>
<td>Total number of ewes on farm</td>
<td>249.4</td>
<td>587.7</td>
<td>578.3</td>
</tr>
<tr>
<td>Average no. of performance recorded ewes on farm</td>
<td>88.3</td>
<td>75.4</td>
<td>87.0</td>
</tr>
<tr>
<td>Average no. of recorded ewes mated naturally</td>
<td>59.1</td>
<td>54.6</td>
<td>75.8</td>
</tr>
<tr>
<td>Average no. of recorded ewes mated via artificial insemination (AI)</td>
<td>20.2\ab</td>
<td>36.6\a</td>
<td>7.1\b</td>
</tr>
<tr>
<td>Average number of days recorded ewes with ram</td>
<td>48.1\a</td>
<td>33.4\b</td>
<td>44.1\ab</td>
</tr>
<tr>
<td>Average recorded ewe:ram ratio</td>
<td>32.0</td>
<td>26.6</td>
<td>31.4</td>
</tr>
<tr>
<td>Average recorded ewe:ram lamb ratio</td>
<td>16.3</td>
<td>13.6</td>
<td>17.5</td>
</tr>
<tr>
<td>Average recorded ewe:AI ram ratio</td>
<td>14.2\ab</td>
<td>24.7</td>
<td>5.8\b</td>
</tr>
<tr>
<td>Lambs born in winter 2005-2009 (%)</td>
<td>59.8</td>
<td>67.2</td>
<td>43.4</td>
</tr>
<tr>
<td>Lambs born in spring 2005-2009 (%)</td>
<td>33.9</td>
<td>28.8</td>
<td>52.1</td>
</tr>
<tr>
<td>No. of months feed blocks provided to ewes</td>
<td>1.2\a</td>
<td>3.7\b</td>
<td>2.6\ab</td>
</tr>
<tr>
<td>No. of months hay provided to ewes</td>
<td>2.3</td>
<td>2.3</td>
<td>2.1</td>
</tr>
<tr>
<td>No. of months silage provided to ewes</td>
<td>1.1</td>
<td>2.1</td>
<td>1.4</td>
</tr>
<tr>
<td>No. of months concentrates provided to ewes</td>
<td>3.8</td>
<td>4.0</td>
<td>3.3</td>
</tr>
<tr>
<td>No. of weeks pre-weaning lambs have access to conc. feed</td>
<td>6.5</td>
<td>8.1</td>
<td>5.4</td>
</tr>
<tr>
<td>Percentage of farm in-by/e improved grazing (%)</td>
<td>40.5\ab</td>
<td>26.1\a</td>
<td>54.5\b</td>
</tr>
<tr>
<td>Percentage of farm hay/silage field grazing (%)</td>
<td>22.5</td>
<td>32.9</td>
<td>22.3</td>
</tr>
<tr>
<td>Percentage of farm hill/rough grazing (%)</td>
<td>5.9</td>
<td>13.6</td>
<td>14.7</td>
</tr>
<tr>
<td>Percentage of any other type of grazing/crop fields (%)</td>
<td>14.2</td>
<td>16.5</td>
<td>6.6</td>
</tr>
</tbody>
</table>

\a,b \text{Values within a row with different superscripts differ significantly at } P<0.05
Appendix 4. Glossary of grazing and productions terms

Creep Feed –
Supplementary concentrate feed offered to young animals while they are still with their mothers. A creep feeder allows lambs to have access to the concentrate feed but not the ewes.

Dyke –
Dry stone wall

Feed Blocks –
Concentrate feed (often a mix of molasses, protein, vitamins and minerals for example) supplied in a solidified block.

Hay –
Grass that has been cut, dried and then stored to be used as animal feed at a later date.

Hay/Silage Fields –
Arable grassland (often found in-by) suitable for conserving as winter feeding (eg. hay or silage).

Hill Grazing –
‘Rough grazings’ means land containing semi natural vegetation including heathland, heather moorland, bog and rough grassland used or suitable for use as grazing.

In-by–
‘In-by’ is the part of the farm which is used mainly for arable and grassland production and which is not hill and rough grazings.
Although ‘in-by land’ has traditionally meant the enclosed grass and arable fields close to the house and steading and below the ‘hill or moorland dyke, it is quite possible to have an area of ‘in-by’ land above the ‘hill dyke’ (e.g. a hill park) - an enclosed area of improved or unimproved grassland once reclaimed from the hill, moorland or heath.

Improved Grassland –
‘Improved grassland’ means either land used for grazing (other than arable land) where over one third of the sward comprises, singly or in mixture, ryegrass, cocksfoot or timothy, or land that has been improved by management practices such as liming and top dressing, where there is not a significant presence of sensitive plant species indicative of native unimproved grassland.

Current management will affect its condition; the sward may be retained as ‘improved grassland’ or it may revert to ‘unimproved grassland’ where, for example, the grazing regime is more extensive and no fertiliser or lime is applied.
Rough / Unimproved –

‘Unimproved grassland’ means land used for grazing or mowing which is not normally treated with mineral fertiliser or lime and does not constitute either improved grassland or rough grazings. Unimproved grassland contains a significant presence of sensitive plant species indicative of native unimproved grassland.

Shearlings –

Any sheep that has been shorn once. Often used to describe rams over one year old, but can also be used to describe ewes of the same age as well.

Silage –

Grass that has been cut and stored to allow fermentation (either in plastic wrapped bales, in a silo or in a large covered pit).

Sward –

Land covered in grass

Taken from:
