

Index selection in terminal sire sheep: implications for genetic improvement in a crossbreeding system

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ABSTRACT

Using terminal sires for crossbreeding is standard practice in the UK sheep industry, where over 70% of market lambs have terminal sire breeding. Thus, selection focusing on terminal sires will translate to changes in the entire industry. Consumers perceive lamb meat as fatty and demand for it has decreased. A lean growth index was developed for terminal sire breeds to increase carcass lean content while keeping fat constant at a constant age end point. The purposes of this study were: to evaluate the effects of index selection of terminal sires on their crossbred offspring up to harvest; to evaluate the effectiveness of the index within the terminal sire breeds; to evaluate the presence and consequences of heterogeneous environmental variances and genetics by environment interactions (GxE) on genetic evaluation. The most widely used breeds of terminal sires in the UK are Charollais, Suffolk, and Texel. These breeds participated in sire referencing schemes from the early 1990s by sharing rams selected on the lean growth index. From 1999 to 2002 approximately 15 high and 15 low lean growth index score rams per breed were selected from their sire referencing schemes and mated to Welsh and Scottish Mule ewes. Their crossbred offspring were reared on 3 farms in the UK under commercial conditions. In total, 6,515 lambs were born between 2000 and 2003. Lambs were weighed at birth (BWT), 5 weeks (5WT), and 10 weeks (10WT). The average daily gain (ADG) from birth to 10 weeks was calculated. Lambs were finished to an estimated 11% subcutaneous fat by visual examination. At harvest, they were weighed (HWT), ultrasonically scanned for muscle (UMD) and fat (UFD) depth, and assessed for condition score and conformation. Lambs sired by high index rams were on average, across breeds, heavier at all ages ($P < 0.01$) with 0.07 ± 0.03 , 0.3 ± 0.1 , 0.4 ± 0.1 ,

and 1.2 ± 0.2 kg greater BWT, 5WT, 10WT, and HWT respectively. Their ADG was 5.1 ± 1.9 g/d greater than low index sired lambs. They had thicker UMD (0.7 ± 0.2 mm) and thinner UFD (0.08 ± 0.01 mm). High vs. low index sired lambs took the same amount of days to reach harvest fatness. Suffolk-sired lambs were on average heavier, with greater ADG, whereas Charollais-sired lambs were lightest with smallest ADG. Texel-sired lambs had thicker UMD than Charollais (0.7 ± 0.2 mm; $P < 0.001$) but were not different than Suffolk. Charollais-sired lambs had greater UFD than both Texel- (0.098 ± 0.016 mm) and Suffolk- (0.061 ± 0.017 mm) sired lambs ($P < 0.001$). Texel-sired lambs reached harvest condition faster than the other breeds ($P < 0.01$). Index selection produced heavier and leaner lambs at finishing. Producers have flexibility in choosing the terminal sire that best fits their production system. Heteroscedascity and GxE were found to be more important for ultrasonic traits than weight traits. Fitting a farm by sire random interaction component improved model fit, but only accounted for less than 2% of the variation in weight traits. For ultrasonic traits, it accounted for at least 10% of the variation. When fitting traits as separate but correlated by farm, genetic correlations among traits were mostly above 0.8, indicating no GxE. Reaction norms for sires were fitted. For weight traits and UMD, sires had positive slopes (were environmentally sensitive) that were similar in value, thus performance improved with improving environments. For UFD, reaction norm slopes varied from negative to positive, indicating GxE. Consequences of heteroscedasticity are not large for these data, and any consequence of GxE on breeding goals should be evaluated before explicitly modeling it in genetic evaluation. There was evidence of genetic variation in sensitivity of sires; therefore, they could be selected to be more or less sensitive depending on economic considerations.

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LIST OF ABBREVIATIONS

5WT	five-week weight	HWT	harvest weight
10WT	ten-week weight	logUFD	logarithmic ultrasonic fat depth
ADG	average daily gain	LW	live weight
AOD	age of dam	RS	reference sire
BLUP	best linear unbiased prediction	SAC	Scottish Agricultural College
BWT	birth weight	SRS	Sire referencing schemes
DHT	days to harvest	TS	terminal sires
EBV	estimated breeding value	UFD	ultrasonic fat depth
GxE	genetics by environment interaction	UMD	Ultrasonic muscle depth
IBERS	Institute of Biological Environmental and Rural Sciences	WW	weaning weigh

Chapter 1: General Introduction and Review of Literature

INTRODUCTION

Consumer preferences towards meats have changed over time, with a trend toward preferring leaner meats (Kempster et al., 1986; Harrington and Kempster, 1989; Woodward and Wheelock, 1990; Grunert, 2006). Historically, selection and management practices for sheep in the UK and other countries have produced animals that are too fat for these changing consumer preferences. Carcasses that are too fat can be trimmed to an acceptable level for consumers, but this entails extra costs and inefficiencies in production and processing (Cameron and Bracken, 1992; Jeremiah et al., 1993). Lamb, being perceived as a fatty meat, has seen a decrease in demand and consumption losing competitiveness to other, leaner, meats (Simm et al., 2002).

Most of the lamb crop in the UK has terminal sire breeding, with the most widely used breeds being Charollais, Suffolk, and Texel (Pollott and Stone, 2004). Improvement in these breeds should therefore have an impact on market animals. One cost effective and permanent way to change fat composition in the carcass is through genetic selection (Simm, 1992). A way to do this is through the lean growth index developed in the UK to increase carcass lean growth while constraining fat growth (Simm and Dingwall, 1989). This index has been adopted by terminal sire breeds, and benefits have been observed in experimental populations (Lewis et al., 1996; Simm et al., 2002).

A majority of lambs marketed in the UK are crossbreds, reared under commercial conditions on pasture. In contrast, terminal sire flocks are often managed intensively. Given that selection pressure is placed on these sires, it is important to know whether improvement in those breeds lead to improvements in their commercial crossbred offspring.

An animal's phenotype is a combination of its genetics and the environment it is reared in. When selection occurs among animals reared in different environments, they may not perform uniformly across them. Two reasons for discrepancies in performance can be heterogeneous environmental variance and genetics by environment interactions. Not taking these into account in genetic evaluation can lead to biases, and lambs may not perform as predicted in every environment.

The first part of this dissertation will focus on the consequences of index selection on commercial crossbred populations in the UK. Using this same population, the second part of this dissertation will focus on the effects of heterogeneous environmental variances and genetics by environment interactions.

Structure of the British sheep industry

Britain is the largest European sheep producer, with 15.2 million ewes mated in 2003 (Pollott and Stone, 2004), and 14.8 million ewes mated in 2007 (2008). Production of lamb meat in Britain totaled 325,000 tons in 2007, with Spain, France and Greece, the next largest producers, totaling 225,000, 125,000 and 115,000 tons, respectively (Yates and Lewis, 2009).

The British sheep industry has a unique stratified crossbreeding system (Figure 1.1) designed to take full advantage of heterosis, and to match production environments to sheep genotypes. There are three main environments in which sheep are raised in Britain: hill, upland, and lowland. These are interconnected but are characterized by distinct features of their sheep breeding enterprises. The hill sector is numerically the largest with 3.83 million ewes (Pollott and Stone, 2004), and accounts for almost half of the national flock (NSA, 2007b). This sector typically has large ewe flocks with low stocking density (about 1-2 ewes/ha). The terrain is rugged and harsh, and ewes are hardy, but with low prolificacy.

After typically 2 to 3 mating seasons in the hill environment, hill ewes are drafted for mating in the upland sector, where they are mated to Longwool crossing rams. The main crossing sire breeds are Bluefaced Leicester and Border Leicester. The crossbred F1 daughters of these matings, “mules”, are very prolific. There were 3.63 million F1 ewes produced from these matings in 2003 (Pollott and Stone, 2004).

The F1 ewes are moved to better farmland in the lowlands where they are crossed with terminal sires, mainly Texel, Suffolk and Charollais. The terminal sire breeds produce lambs with high quality carcasses and fast growth rates, and their crossbred offspring are harvested. Terminal sire crosses accounted for 71% of the lambs slaughtered.

The preferred carcass weight by abattoirs in the UK is 16-21 kg (Jones et al., 2003). The retail sector generally purchases lambs in this range, but the catering sector tends to have higher carcass weight preferences, of 22-25 kg. In the US, carcass weights of lamb are generally heavier than in the UK, and have increased over time. Carcass weights of slaughtered lambs went from an average of 23 kg in 1965 to 30 kg in 1998. The main reason for this was packer demand because slaughtering and processing heavier lambs was not much more costly than lighter lambs (Bradford, 2002).

Sire referencing schemes

Sire referencing schemes (**SRS**) are cooperative breeding schemes where members select an elite group of sires to use as reference sires (**RS**). In the participating flocks, performance and pedigree records are kept, upon which the RS are selected. One of the purposes of these schemes is to combine data across-flocks to facilitate genetic evaluation. Scheme members choose RS to mate to ewes in their own flock, usually through AI (Lewis and Simm, 2004). Within this system there is no central nucleus flock; animals are instead maintained and evaluated by individual

flock owners. In Britain in 2001, about half of performance recorded flocks, and two thirds of performance recorded sheep, participated in SRS (Simm et al., 2001).

Pedigreed sheep flocks in Britain are usually small in size, and therefore intensive selection is difficult to practice (Lewis and Simm, 2000). Combining information from many flocks in SRS, and sharing sires, can overcome this limitation by creating genetic links, or connectedness, among flocks. This ensures that the genetic merit of animals in the different flocks can be fairly evaluated. The size of flocks is effectively enlarged in SRS allowing for more intense selection of males.

The goal of SRS is to create genetic connectedness among flocks so that across-flocks genetic evaluation can be conducted, and genetic improvement can be achieved (Simm et al., 2001). Simm et al. (2001) found that with use a selection index designed to improve lean growth, response to selection in sheep from SRS was comparable to that achieved in experimental flocks. In simulation, Lewis and Simm (2000) found that genetic gains could be higher than with within-flock selection when selection intensity of the RS was highest and when it was based on estimated breeding values (**EBV**) rather than phenotypic observations. This was due to more offspring from the genetically superior RS being born in each flock with stronger genetic links being established among flocks. In this simulation study, genetic gain with intensive selection (highest ranking rams) was 1.51 to 1.73 times that of less intensive (top sixth or third of rams) selection schemes.

Although not attractive to all producers, SRS became popular in the UK in the 1990s, especially for terminal sire breeds (Lewis and Simm, 2004). Reasons for this were the widespread availability of performance recording services; improvements in laparoscopic AI techniques; the introduction of BLUP evaluation; and interactions with other breeders and

researchers (Simm et al., 2001). The SRS were advantageous in consolidating the sheep industry and thereby achieving gains that individual flocks would not have been able to achieve on their own.

Lean Growth index

Changing the sheep population through genetic selection is a permanent, cumulative, and cost effective way to change lamb carcass composition so that it meets consumer demands for leaner meats (Simm and Dingwall, 1989; Griffin et al., 1992). In the UK, genetic improvement can be targeted on TS breeds, which make a large genetic contribution to the market lamb crop. This way, selection can be focused on a relatively small number of animals that have a large effect on the market (Kvame and Vangen, 2007). The most economically relevant traits in UK sheep are growth and carcass traits, and selection can be targeted on those traits, rather than on a greater combination of production and reproduction traits (Cameron and Bracken, 1992).

To improve lamb in the UK, a “lean growth index” was developed by Simm and Dingwall (1989) that increases carcass lean weight, while keeping carcass fat constant at a constant age end point. The breeding goal of the index is lean and fat weight, with relative economic values of +3 and -1, respectively. The selection criteria used for this index were live weight at harvest (**HWT**), ultrasound fat depth (**UFD**) and ultrasound muscle depth (**UMD**). These were adjusted to 150 d. The economic values were chosen to achieve the desired gains in the traits of the breeding goal rather than being based on market returns and costs of production. Thus this index is equivalent to a restricted selection index, with changes in fat restricted to zero, or alternatively a desired gains index (Simm and Dingwall, 1989). It was derived in this manner because of the weak relationship between carcass price and fatness in Britain at the time of its

development (Simm et al., 2002). This index serves as a tool for producers to use when selecting sheep to better meet consumer demand for leaner lamb.

Applications of the lean growth index

A Suffolk flock was established in the 1980s at the Scottish Agricultural College (SAC), and a selection and control line were created. Selection was then based on the lean growth index. Divergent performance between the selection and control line was observed: after 9 years, the selection line weighed 4.9 kg more, and had 1.1 mm thinner UFD and 2.8 mm thicker UMD at 150 days of age in both sexes than the control line (Simm et al., 2002). The expected responses in selection were associated with changes of + 233 g carcass lean and + 96 g carcass fat per year. Growth rate was 1.17 times higher in the selection line than the control line at 40 kg live weight. The lean growth index was also applied to other TS SRS in Britain, and annual response ranged from approximately 6 to 14 index points (Simm et al., 2001), consistent with results from the SAC Suffolk flock. The long-term response to index selection has served to promote the value of using lean index scores in selection. The results have clearly shown that the use of the index has moved lean into the carcass and fat away from it (Lewis and Emmans, 2007).

Effects on crossbreds reared at grass

Many TS flocks have intensive production and management systems. However, most of the lamb crop of the UK are crossbred lambs that are reared in extensive grazing systems. For this reason, several studies have been carried out to determine the effect of using high lean growth index sires on their crossbred progeny reared at grass. Lewis et al. (1996) reported that lambs from high index Suffolk sires mated to Scottish Mules (Bluefaced Leicester rams x Scottish Blackface ewes) had, at a fixed carcass weight, on average 7 g/kg more lean and 12 g/kg less fat than lambs from control line sires. Selecting sires one standard deviation above the mean

index score corresponded to a correlated response to selection of more than 50 g of fat being replaced by lean weight in a 20 kg carcass. Simm and Murphy (1996), in the same flock, found that the progeny of high index sires were 11 days younger when reaching target harvest weight, and their carcasses were worth 1.50 sterling pounds more than the progeny of control sires. They also found that the selection line progeny had lower subcutaneous fat proportion of 13 g/kg, a 0.1 kg higher weight of saleable meat yield, and a higher proportion of saleable meat yield of 4g/kg, as compared to the control line progeny. The response for lean growth persisted over a range of live weights and maturity levels in these experiments. Using high index score sires in crossbreeding systems where progeny were reared at grass thus produced lambs with leaner and more valuable carcasses. This may be due to a combination of directly changing the carcass composition of the animal and indirectly changing animal mature size (Lewis et al., 1996).

Other selection indices

Corroborating results obtained with the lean growth index in TS, van Heelsum et al. (2003) found when evaluating Mule offspring of Bluefaced Leicester sires with Scottish Blackface and Hardy Speckled Face ewes that high index sires produced offspring with more lean and less fat content in all carcass joints. The index used for these sires was also designed to increase muscle weight, and reduce fat weight, while keeping the carcass weight constant. The economic values of changing lean weight in the carcass ranged from 1.04 to 1.91 and from 1.16 to 1.93 pound sterling per kg in female and castrate crossbred offspring, respectively. Those values for changing fat weight ranged from -0.04 to -1.81 and 0.69 to -2.60 pound sterling per kg in females and castrates, respectively. Crossbred offspring of high index sires produced better and more profitable carcasses.

Simm (1992) report results from other indices used in sheep where annual rates of change in index score or in weight-adjusted backfat depth usually vary from 2.1-2.4% per year. In experiments where carcass composition was measured, selection for reduced UFD resulted in reduced carcass fat depth. One such experiment was reported by Cameron and Bracken (1992) where a selection index was developed for use in Texel-Oxford sheep that would change the proportions of lean and fat composition without affecting live weight at 20 weeks of age. After 3 years of selection for high and low index sires, the differences reported in carcass lean and fat weight were 0.72 kg and -0.04 kg, respectively, corresponding to 13.5 g/kg and -13.8 g/kg of carcass lean and fat proportion. The heritability of this index was 0.46 (0.14). Therefore selection indices have been successfully used in sheep breeding and favorable economic response has been observed.

Growth in sheep

Understanding growth is important in order to evaluate an animal's development at different points up to slaughter. The growth of sheep, and other mammals, has been widely studied and has been described as following a sigmoidal shaped curve towards a final mature weight, under non-limiting conditions (Brody, 1945; Parks, 1982). Butterfield (1988) describes the growth of a single sheep, using as an example a 100 kg Merino ram fed *ad libitum*. This ram will eat approximately 13 kg of pelleted feed per week when about 70% mature at one year old, which then declines to 10 kg per week at maturity. The growth curve of this ram can be subdivided into two descriptive stages: the "survival phase" and the "maturing phase". During the survival phase there is rapid weight gain as the lamb adapts to the environment outside of the womb. At this point there is differential growth of internal structures. The maturing phase is the growth that occurs past the inflection point of the growth curve up until maturity.

Weight increase has been found to be a function of feed intake, not time: as an animal matures, increases in its live weight decrease relative to the amounts of feed it consumes. Similarly, research has shown that if an animal's nutritional plane is constrained it will likely not reach its full growth potential (Lewis et al., 2004; Hegarty et al., 2006; Lewis et al., 2006). Further, most lean growth is independent of temporary changes in feeding levels, but excess energy is stored as fat used for maintenance and growth (Kempster et al., 1982). The different tissues of an animal grow at different rates, with bone growing slowest, followed by muscle. Fat has a higher rate of growth and thus increases as a proportion of live weight as the animal matures (Butterfield, 1988).

As an animal progresses to its mature weight the use of nutrients shifts from bone and muscle growth to fat deposition. Animals with lower mature weights are earlier maturing. Sex differences are also clear in growth patterns, with females maturing at lighter weights and fattening earlier than castrates and males; therefore, females are usually fatter at a given age (Kempster et al., 1982). In carcasses of similar weights, the percentage composition of each tissue type will vary depending on breed type and growth rate (Kempster et al., 1982; Lewis et al., 2004).

Growth rate

The rate of muscle growth in a sheep differs at distinctive periods in its development: from birth (approximately 4 kg) to about 20 kg live weight muscles grow quickly, but at different rates for different muscle groups (Butterfield, 1988). After the lamb reaches 20 kg, muscle growth becomes more uniform but not entirely so, and the growth rate slows. Butterfield (1988) reports a steady relationship between muscle weight and live weight towards maturity, and that the relative proportion of muscle to live weight declines with the fattening of the animal. Hegarty

et al. (1999) report relatively stable proportions of carcass protein to body weight in lambs fed at different nutritional planes. They also found that lambs fed at lower nutritional levels had higher rates of gain in live weight and carcass weight. This relationship is of economic importance, as the costs of producing muscle, in terms of feed, increases as the animal matures. Thus this is an important consideration in deciding when to slaughter an animal.

The muscle to bone ratio becomes important when animals are slaughtered at around 50-60% of their mature weight; at heavier weights, the proportions of muscle to bone do not change much (Butterfield, 1988). This ratio also appears to have steady values over ranges of fatness in different breeds, but is again influenced by the sex of the animal: at equal fatness levels, males will have higher muscle to bone ratios as they are less mature (Kempster et al., 1982).

The relationship between growth rate and carcass fat is more complicated than that of muscle. Fat percentages in a carcass differs between breeds and sexes, but is most affected by the degree of maturity of the animal at slaughter (Bradford, 2002). Fat has historically been considered a major factor in the determination of dressing percentage, but it has been shown that increasing fat will not necessarily increase this in the carcass (Butterfield, 1988). In fact, fat has an unfavorable influence on the dressing percentage, as animals tend to deposit fat at higher rates as they mature. The relationship between increased fat and increased dressing percentage becomes even less clear in sheep that are very fat (Butterfield, 1988).

More recent work on Suffolk sheep has shown that carcass fatness increased, and leanness decreased, with diets of decreased protein levels; however, with decreased levels of feeding, the results were opposite. Therefore, the authors suggest that “there can be no general relationship between growth rate and fatness” (Lewis et al., 2006). Similarly, Hegarty et al. (2006) under pastoral conditions, did not find differences in fat percentages in cold carcass

weight from pastures with differing nutritional availability. Lewis et al. (2002) further described that the lipid to protein ratio increased in animals as they grew and that the relationship between the two were curvilinear. Hegarty et al. (1999) reported that lambs that grew at slower rates had reduced fat at standardized slaughter weights. The authors argue that fat accumulation in the carcass is less tightly controlled than protein accumulation, and that it may reflect excess energy that is available relative to that used. Lewis et al. (2004) also found that feeding an unrestricted versus restricted diet caused an increase in the rate of fat gain as measured by computerized tomography, and that non-limited lambs were fatter across all stages of development than those fed a limiting diet. Thus the relationship between growth rate and fat is highly influenced by an animal's environment and diet.

A problem with describing growth is that animals are usually not raised in idyllic and unrestricted conditions. The environment can be limiting in terms of feed, maternal environment, etc., and thus the animal may not reach its potential growth. It becomes more complicated to describe an animal's growth when the environment is limiting, and more so when the limitations change with time, as is the case is pastoral animals (Lewis et al., 2006). Further, growth rate can be selected for, and there are interactions between genotypes and environment (Lewis et al., 2002). Lewis and Emmans (2007) found that fatness increased when lambs were fed low protein feeds, that it was greater in females than males, and higher in the control line of SAC Suffolk sheep than in the selection line (the same SAC Suffolk lines described above). Hegarty et al (2006) describe that offspring of sires selected for eye muscle depth and post weaning live weight had differential growth rates, but that these were moderated by the level of nutrition (high or low) offered to them. They found that the effects of the plane of nutrition were greater (lambs differed by 9.1 kg) than that of the sire type (lambs of sires selected for muscle depth and live

weight weighed 4.8 kg more than control lambs). Moreover, Lewis et al. (2004) found that across breeds (Suffolk or Scottish blackface), sexes and maturity stages, lambs fed a nutritionally limiting feed had 0.81 as much fat and 1.06 as much lean tissue as compared to lambs fed at a non-limiting nutritional plane. The relationship of growth to carcass and live weights is complex, and many factors go into the final product.

Conformation in sheep

Conformation and shape are the traditional methods of evaluating sheep and other livestock prior to harvest. Historically, evaluation has been based on size and shape with visual assessments being the primary way of identifying differences between animals (Kempster et al., 1982). This is subjective and its accuracy and consistency are affected by factors such as: the experience of the evaluator; the scoring scale and differences between the steps; the range of carcasses being assessed; and, the physical environment in which the evaluation is made (Kempster et al., 1982). Even though the measures are subjective, they have been responsible for the establishment of many diverse breeds and breed types, and for economic valuation of animals.

Carcass evaluation is necessary when establishing breeding programs to identify the most valuable parents, and to find which crosses are best suited for different environments and marketing schemes. Carcass fat is evaluated along with the assessment of carcass shape, and thus fatness needs to be accounted for when evaluating conformation. Conformation is generally more useful for identifying different breed types rather than predicting individual animal carcass composition (Kempster et al., 1982). Differences between breeds in carcass composition at the same fat thickness measurement is caused by differences in tissue growth and development within breeds (Kempster et al., 1982).

The value of conformation as an indicator of carcass composition has been questioned, but it still remains as one of the measures of commercial value at slaughter, and is included in the national classification systems of most sheep producing countries. Several studies have found a positive but very low correlation between conformation and carcass lean content, making estimates subject to large errors (Kempster et al., 1982). Further, breeds with better conformation do not necessarily have higher lean to bone ratios (Kempster et al., 1981). Butterfield (1988) also points out that conformation is a difficult subject to deal with because different evaluators have different ideas of what each conformation score corresponds to, and have difficulty in transmitting this knowledge. Therefore conformation, even though an economically relevant trait, is highly subjective in its measure.

Several traits serve as indicators of carcass composition in sheep. The live weight of the animal is used as an approximate guide to when an animal achieves the desired fatness level in the carcass. Still, different breeds have different live weight end points that are optimal for slaughter (Kempster et al., 1982). Visual assessment and handling of the live animal can also add accuracy to the prediction of carcass conformation, if the assessor is experienced. A problem with many of these measures is that it is difficult to distinguish between muscle and fat and thus make an accurate prediction of carcass composition. Nevertheless, the meat industry has traditionally paid more for animals with better conformation and breeders therefore ascribe economic importance to it (Kempster et al., 1982).

Genetic control of conformation

The heritabilities of visual carcass composition reported in most studies were below 0.1, and therefore response to selection for this trait will be low (Conington et al., 1998; Nsoso et al., 2000). Similarly, van Heelsum et al. (2003) found that the live conformation of sires was

uncorrelated to the lean and fat content of their crossbred offspring's carcasses. They suggest that selecting for conformation will not improve carcass muscling, but the effect on fatness was not clear. Conformation score has also been found to be positively correlated with fatness (Kempster et al., 1981; Lewis et al., 1996; Jones et al., 1999).

Carcass composition at a given age or weight is affected by the animal's level of nutrition. At a given live weight, fat percentage is strongly negatively correlated to lean percentage, but lean and fat growth are influenced quite differently by nutrition. Since muscle to bone ratio is fairly impermeable to changes in feeding, it has been suggested as an indicator of carcass composition in groups of animals under different feeding systems (Kempster et al., 1982). Lewis et al. (1996) reported a positive but low correlation between carcass fat and conformation, and Jones et al. (1999) report genetic correlations between conformation scores and tissue composition as insignificant, therefore adding little to the prediction of carcass composition.

Alternative measures of conformation

Objective measures of conformation have been sought in order to facilitate comparisons of results from different studies. Carcass composition in live sheep can be predicted through ultrasonic evaluation. Two common ultrasonic measurements are of fat thickness, an indicator of fatness, and of the depth of the cross-section of the *M. longissimus* muscle, an indicator of muscling. The major muscle in this part of the animal is the *M. longissimus dorsi*, which is rectangular and well defined, thus easier to measure and easier to reproduce the measurement position on each animal (Kempster et al., 1982). Ultrasonic measures in the UK are typically taken at the third lumbar vertebra. Ultrasound serves as a way to predict carcass characteristics of the animal before slaughter. It provides a record on live animals that can describe the body

composition and allows for the prediction of genetic differences between animals for carcass merit (Wilson, 1992). It has been successfully used in sheep, and has moderate heritability at relatively low cost (Jones et al., 2004; Kvame and Vangen, 2007; Emenheiser et al., 2010).

Grading system for sheep in the UK

The emphasis of sheep production in Britain has typically been on meat production. The grading systems for carcass conformation and fatness follows European Union guidelines. Conformation is assessed on a 5 point scale, the EUROP score, where E = excellent, U = ultra good, R = regular, O = ordinary, and P = poor. Subcutaneous fat is scored on a 1 to 5 scale, where 1 = very lean, 2 = slight fat, 3 = average, 4 = high, and 5 = very fat. The fat scores are further broken down into high and low subcategories at the 3 and 4 levels. The 1, 2, 3L, 3H, 4L, 4H, and 5 fat scores correspond to estimated subcutaneous fat percentages of 4, 8, 11, 13, 15, 17, and 20%, respectively (Kempster et al., 1986). Crossbred lambs in Britain are marketed at a target 40 kg live weight, and the ideal carcass for the domestic market was perceived to be 18 kg, with conformation score of R/U and fat class 3L (Jones et al., 2003). Fatness differences were more important than conformation differences on the premiums received for lambs at the abattoir. Carcasses that were classified as fat class 2 or 3L, and conformation E or U, received premiums consistently.

One of the criticisms of the classification system used in the UK is that it does not always give clear market signals to producers. Carcasses considered too fat were not adequately penalized partly because of the abattoir's need to maintain throughput. This discrepancy likely hinders adaption of technologies such as selection indices as producers are not getting monetary premiums for using rams of higher genetic merit (Jones et al., 2003). There is a premium paid in the UK for better conformed carcasses, but there is little evidence that carcasses with good

conformation are more profitable to the retailer than ones with poor conformation (Nsoso et al., 2000). In fact, figures from the Meat and Livestock Commission indicate a tendency for carcasses of good conformation to have lower saleable meat yield than poorly conformed carcasses (EBLEX, 2013). The premiums paid by the abattoirs therefore seem to indicate that carcass shape in of itself is important, although not as an indicator of saleable meat in the carcass. Shorter, blockier carcasses, which may not have the best carcass lean content, are given higher conformation scores (Jones et al., 2002).

Previous breed comparisons

Terminal sire breeds are widely used for finishing sheep in the UK. These animals grow at a fast rate, are large and have good carcass characteristics. The most widely used breeds are Charollais, Suffolk and Texel. Information on breed comparisons is important for producers to select rams that best suit their production system and market requirements. In the UK, producer's objectives are to obtain carcasses with a desired fatness levels at an optimum slaughter weight and age (Kempster et al., 1987). Terminal sire breeds can serve to help producers reach their breeding goals.

Growth traits

There are conflicting results regarding the effects of sire breed on growth traits. Some studies have found no influence on birth weight (More O'Ferrall and Timon, 1977; Leymaster and Jenkins, 1993; Fogarty et al., 2000), while other studies, using more sire breeds have found differences (Cameron and Drury, 1985; Fogarty et al., 2000; Freking et al., 2000). Yaqoob et al. (2005b) found that weaning weights did not differ between Suffolk and Charollais or Texel sired lambs, but differed between Charollais and Texel sired lambs. Conflicting results between experiments may be due to different strains of the sire breeds used. In the US, Kuehn et al.

(2009) report that Suffolk sheep were being divergently selected for two biological types: one for traditional TS characteristics and another with emphasis on moderate mature size and muscling. Two main strains of Texel sheep are used in the UK, Dutch Texel and French Texel. Dutch Texels are more muscular than French Texel and may have more growth potential.

Several studies have reported greater potential of growth of Suffolk- over Texel-sired lambs (More O’Ferrall and Timon, 1977; Leymaster and Jenkins, 1993; Scales et al., 2000; Yaqoob et al., 2005a). More O’Ferrall and Timon (1977) and Leymaster and Jenkins (1993) found no differences in birth weight (**BWT**) between Suffolk and Texel sired lambs, but found differences in weights measured later in life. Cameron and Drury (1985) found that Texel sired lambs had intermediate mature weights, which did not differ from those of Charollais-sired lambs; likewise, their ADG was not different. Conversely, Yaqoob et al. (2005a) found that the growth rate of Texel-, Suffolk- and Charollais-sired lambs did not differ from birth to 30 d, but growth rates of Suffolk-sired lambs were higher than Texel-sired lambs from birth to weaning and from birth to slaughter. Kempster et al. (1987) suggest that the lower growth rate of Texel- compared to Suffolk-sired lambs may be due to a lower appetite of Texel-sired lambs and difficulties in maintaining a high nutrient intake towards the end of the growing period when nutrient concentration in the grass is lower.

Carcass traits

Several studies have compared terminal sire breeds in terms of their carcass characteristics. Cameron and Drury (1985) found that when slaughtered at a fixed weight, or fixed fat cover, Texel- and Charollais-sired lambs did not differ in age or weight to reach harvest condition, or in carcass weight. However, Kempster et al. (1987) found differences in lean tissue among Texel- and Suffolk-sired lambs, with Texel lambs being leaner than Suffolk lambs.

Hopkins et al. (2007) also reported differences in Australian sheep between sire breeds for lambs slaughtered at a constant age endpoint. Differences between breeds exist, which can be taken advantage of in fitting to particular production systems.

It has been suggested that breeds with heavier mature weights tend to take longer to reach a given level of subcutaneous fat, which could result in heavier carcasses (Cameron and Drury, 1985). They suggest that mature size can be used as an indicator of crossbred offspring performance. The idea is that larger sire breeds would be expected to produce heavier and older lambs to a fixed fat level, which is how most UK lambs are marketed. Kempster et al. (1987) also found that age at slaughter was generally greater for lambs originating from sires of greater body size. They also found that among the larger breeds, Suffolk and Texel crosses grew relatively faster. Likewise, Sakul et al. (1993) report that carcasses from lambs sired by the smallest sire breeds had higher fat contents when lambs were slaughtered at a constant weight end point. The market specifications for lambs pay premiums for specific lamb carcass weight and fatness, and a more uniform product would be advantageous.

Composition of Texel animals seems to be different than that of other breeds. Studies have reported that they are leaner with a higher lean to bone ratio than other breeds when compared at a fixed level of weight or fatness (Cameron and Drury, 1985; Jones et al., 2002). A larger *m. longissimus* area has also been reported (More O'Ferrall and Timon, 1977; Wolf et al., 1980), and they have been identified as producing progeny with leaner carcasses, and larger eye muscle area, than other terminal sire breeds (Wolf et al., 1980; Kempster et al., 1987; Scales et al., 2000). Cameron and Drury (1985) suggest that Texel sired lambs produced leaner carcasses relative to their intermediate growth rate and mature size. These results were corroborated by Leymaster and Jenkins (1993), where they reported that Texel sired lambs weighted less at 189 d

of age and produced lighter, leaner carcasses of shorter length. In the same study they did not find differences in carcass composition at 25 kg carcass weight, but Texel-sired lambs had greater fat depth at the 12th rib, and more kidney-pelvic fat. This suggests that Texel-sired lambs deposit proportionally more subcutaneous and less intermuscular fat than other breeds. Texel sheep seem to be an exception to the general relationship between growth rate, mature size, and carcass composition observed in other breeds. This could be partly explained by a mutation in the myostatin gene, which is nearly fixed in UK Texels, has a gene frequency of 0.3 in Charollais, and is not present in Suffolk sheep (Hadjipavlou et al., 2008).

The eating quality of lambs is a driving factor in consumption of lamb meat. Safari et al. (2001), in Australia, found that there were no differences in lamb meat acceptability and rating from sensory panels from lambs of different genotypes. These results are in accordance to Mendenhall and Ercanbrack (1979) in a survey of US lambs, which also agrees with Notter et al. (1991), who indicate that lamb nutrition may be more important in determining eating quality than genetics. Therefore, palatability of lamb meat is likely more influenced by the nutrition of lambs than their genotype.

Most studies on lamb growth, finishing and slaughter have found no evidence of interaction between the breed of sire and breed of the dam. This suggest that the breed of the ewe is not important when comparing progeny of different sire breeds (Cameron and Drury, 1985). These results have been corroborated by several researchers (Wolf et al., 1980; Cameron and Drury, 1985; Freking and Leymaster, 2004; Hopkins et al., 2007). The lack of an interaction may be due to waning maternal effects as lambs grow. Maternal heritabilities for UMD and UFD have been generally found to be low and in some cases, not different from zero (Larsgard and Olesen,

1998; Husain et al., 2007). The terminal sire breed is more important in improving lamb performance at finishing than selection of the dam breed.

Genetic parameter estimates for growth and harvest traits

Accurate estimates of genetic parameters are necessary for genetic evaluation and to predict correlated responses to selection. These estimates require large data across generations in each population, which are not always available. When well-structured data are not available, or an overall estimate is needed, an alternative is to pool published estimates from different populations as in Safari et al. (2005). Several other studies have published estimates of genetic parameters in sheep for growth and harvest traits, and are summarized in Table 1.1 (heritabilities), Table 1.2, and Table 1.3 (genetic and phenotypic correlations).

In general, heritabilities are high enough so that genetic change is expected through selection. For growth traits, heritabilities were generally moderate and most estimates were in the teens. Heritabilities at birth and weaning were similar, but increased at HWT. Safari et al. (2005) found that heritabilities were higher for wool breeds than for dual purpose or meat breeds at all ages. On average, maternal heritabilities for growth traits were greater than direct heritabilities, and mostly decreased as lambs aged, owing to decreased maternal influence on lambs. Other studies have found that direct additive genetic effects become larger as lambs' body weights are measured at older ages (Riggio et al., 2008). Several studies have reported that genetic and environmental correlations for weights at adjacent ages increase with increasing age (Safari et al., 2005). In most estimates, phenotypic correlations were lower than genetic correlations. Safari et al. (2005) also report that growth rate was moderately genetically correlated with BWT (0.27) and highly correlated with weaning weight (**WW**) (0.79).

Reported heritabilities for HWT and ultrasonic measurements are moderate to high. In general, maternal heritabilities for these traits are lower, which is in accordance to maternal heritabilities for growth traits decreasing as lambs' age. Correlations between UMD and UFD are mostly positive, but literature estimates vary widely by breed (Conington et al., 1995). Some studies have reported relationships between fat and weights. However, Larsgard and Kolstad (2003) found, in a line selected for UFD, no correlated increases in lamb or ewe weights. This indicates that animals can be selected on lean growth without having undesired effects on live weights. Similar results were found by Conington et al. (1995), where progeny from a line of sires selected for lean weight did not differ in weights at several ages. Further, Safari et al. (2005) report that heritabilities for eye muscle measurements in live animals were lower than in the carcass. They also point out that adjusting for fat depth in live weight of finishing animals reduced genetic and phenotypic correlations to near zero, as was expected.

Heterogeneous variance in genetic evaluation

Selection often takes place among groups of animals that originate from different environments. However, the means and variances of phenotypes can differ across those environments. This type of variance heterogeneity has been found in several livestock species for different traits (i.e. See, 1998; SanCristobal-Gaudy et al., 2001; Rowe et al., 2006; Nakaoka et al., 2007; Lidauer et al., 2008) and has an impact on genetic evaluation. Not taking into account heteroscedasticity can affect the accuracy of selection. Hill (1984) found that when selection takes place among groups with the same number of animals and the same mean, the proportion of animals selected from each group varied substantially when variances were heterogeneous. In this case, under the same selection intensity, more animals were selected from the more variable

groups, which leads to bias in genetic evaluation and a reduction in selection response (Hill, 1984; Garrick and Van Vleck, 1987).

Homogeneous environmental variances are usually assumed in genetic evaluation. These assumptions may not hold when data come from different environments or span several years. It is therefore important to account for heteroscedasticity when performing genetic evaluation. It is possible to generate accurate EBV given heterogeneous variances, if estimates of heterogeneous (co)variance are available, as the observations are automatically scaled (Gianola, 1986). The risk of ignoring heterogeneous variance in genetic evaluation is that animals will be incorrectly ranked with respect to their EBV, leading to lower selection response. Therefore, heteroscedasticity is accounted for by several breeds of livestock in their genetic evaluation systems (Winkelman and Schaeffer, 1988; Robert-Granière et al., 1999; Nakaoka et al., 2007).

An effective way to mediate bias in genetic evaluation is to test progeny in different environments. For example, in dairy cattle, it has been found that the ranking of bulls was not greatly affected by heterogeneity of variance but cow evaluations were (Winkelman and Schaeffer, 1988). This holds if daughters of bulls are randomly distributed among herds with high and low variance. The problem with cows is that high producing cows in high variance herds are over evaluated for their production (Robert-Granière et al., 1999). Sires that are proven in one environment (or country), and are imported into another, may also have a biased evaluation if they are used in more variable herds (Visscher et al., 1991). It has been shown that when heritabilities are higher in the more variable populations, assumptions of homogeneity of variances may not lead to substantial decreases in selection response (Garrick and Van Vleck, 1987). The effects of heterogeneous variance have been shown to be greater when selection is intense and when selection is on individual phenotype or within-family deviation instead of on

family mean performance (Hill and Zhang, 2004). It is therefore prudent to test the effects of heteroscedasticity, and account for it when necessary in genetic evaluation.

Management levels, genotype by environment interactions (**GxE**), segregating major genes and preferential treatment of some animals are some of the causes of variance heterogeneity (Visscher et al., 1991). It has been proposed that the production levels of herds affects heteroscedasticity due to differences in management and scale effects (Nakaoka et al., 2007), although this is not the result in all studies. Different correlations between mean and variance have been reported: some studies have found a non-zero correlation and some have not (Visscher et al., 1991). These correlations indicate that scaling may not be an important cause of variance heterogeneity. Another cause of heterogeneity is that traits can genetically change over time, making the correlation between a trait measured at one point and the same trait measured later not equal to 1 (Visscher et al., 1991). On a genetic level, heteroscedasticity may be caused by polygenes controlling residual variance (sensitivity to the environment). It may also be due to a major gene that controls the mean of the trait: the progeny of homozygote sires would be less variable than the progeny of heterozygous sires depending on the mode of inheritance (SanCristobal-Gaudy et al., 2001). Heteroscedasticity is a complex phenomenon that seems to have many causes, perhaps unique to each population.

Detecting and accounting for heteroscedasticity

The detection of heterogeneous residual variance in a population is problematic. Often, records are divided into (arbitrary) production levels, and variance components are estimated within these groups. In this case, estimates of residual variances may be biased by selection (i.e., splitting the data into these groups) (Famula, 1989). Estimates obtained from small samples may also be biased. A solution to small samples is to group data into strata, and assume homogeneity

of variance within them. However, this may not account for heterogeneity within the strata (Gianola et al., 1992). Modified Bartlett's test have been proposed for detecting the sources of heterogeneous variances (Foulley et al., 1990). Detecting and accounting for variance heterogeneity is complex and dependent on the type of data used for genetic evaluation.

Several different approaches have been developed to account for heterogeneity of variance in genetic evaluation. Simply transforming the data is a reasonable choice when the variances are strictly a function of the mean production, but this is not often the case (Kachman and Everett, 1993). The issue with these types of transformations (i.e., logarithmic, arcsine) is that a linear model in the transformed scale is not a linear model in the original scale. A logarithmic adjustment has been suggested for correcting heterogeneity of variance, which could be justified if it is due to a scale effect. This transformation would make the SD linearly related to the mean. Additionally, if the mean and variance are not genetically correlated, this transformation will increase the heritability of the trait (Visscher et al., 1991). It will also overcompensate for bias in herds with low variance and thus over evaluate some animals (Mirande and Van Vleck, 1985). This method has not been widely used due to its statistical complications, and other methods have been developed.

Hill (1984) proposed scaling observations by the estimated SD as a way to correct for heterogeneous variances. Genetic evaluation would then be done on the scaled observations. This attempts to reduce within herd phenotypic variability. Other adjustments such as a weighted average of the phenotypic SD (Brothstone and Hill, 1986), and a weighted average of phenotypic variances (Wiggans and VanRaden, 1991), have been proposed. These types of scalings are appropriate when there are no interactions with the environment, which further complicates the issue of heterogeneous variance. Several genetic evaluations are done by pre-

adjusting phenotypes to a constant variance (i.e. Urioste et al., 2001; Urioste et al., 2003; Nakaoka et al., 2007). This is a simple and useful way to account for variance heterogeneity in genetic evaluation.

A multiplicative mixed model has also been proposed to account for heterogeneity of variances (Kachman and Everett, 1993; Meuwissen et al., 1996; Robert-Granière et al., 1999). A multiplicative mixed model is different from a standard mixed model in that it adds a scaling factor to each term of the mixed model (Kachman and Everett, 1993). This model serves a similar purpose to scaling by the phenotypic SD, but it accounts for differences in variability of the different effects in the model. This method is accurate when heritabilities are relatively constant across environments, and accounts for differences in selection intensity in the different environments.

Meuwissen et al. (1996) proposed a model that simultaneously estimates breeding values and heterogeneity factors. Their method corrects for heterogeneous phenotypic variances and assumes heritabilities to be homogeneous. They use information from other groups to improve the accuracy of estimating variances within a group by applying an autoregressive model to the variances. They consider breed effects in their method because estimates of variances within groups are otherwise inflated, and subsequent correction for heterogeneous variances reduces differences between breeds or genetic groups. In effect, there is an over correction and animals merit may be under estimated, which reduces differences between breeds or genetic groups. Crossbred offspring may also be underestimated if breed effects are not taken into account. This method scales each individual parameter, and can serve when evaluating different breeds or genetic groups, which is often the case.

Bayesian methods can account for heteroscedasticity as well. Gianola et al. (1992) proposed a Bayesian method to estimate variances, where they were treated as random variables with an inverted chi-square prior distribution with known or unknown parameters. Foulley and Quaas (1995) used REML and Bayes, using an inverted gamma prior distribution. Both use an Expectation Maximization algorithm to solve the equations. The advantage of using these prior distributions is that they are conjugate to a posterior normal distribution, making estimability of the posterior distribution more straight forward. Using Bayesian methods is advantageous because they take account for all other variances when estimating a variance, and can be used when group sizes are small.

The existence of heterogeneous variances may be advantageous in some circumstances. Selection for both the mean and the variance of traits with an intermediate optimum (such as litter size in sheep) may be economically relevant (Mulder et al., 2008). Changing the variance of traits with an intermediate optimum value is possible because of the heteroscedasticity usually present. Generally, the heritability of the environmental variance is moderate, while the heritability of the mean of the trait is high. Therefore such a breeding program amounts to selection for a trait with moderate heritability and one with high heritability. Stabilizing selection may also benefit traits other than those concerning reproductive fitness. In livestock, a uniform final product is often economically beneficial because producers are paid on a grid with an optimum value.

Examples in sheep

Evidence for heterogeneity of variance is abundant for several traits in sheep. SanCristobal-Gaudy et al. (2001) found heterogeneous variances for litter size. The heterogeneity was not due to herd, year, season or age effects, but originated from the sires.

Their population had been selected for increasing mean litter size, and they therefore theorized that the heteroscedasticity was due to the presence of polygenes controlling the residual variance, or a major gene segregating in the population that controlled the mean. Therefore, progeny of homozygote sires would be expected to be less heterogeneous than those of heterozygote sires. In contrast, Nikolaou et al. (2004) found heteroscedasticity by herd-year-lactation class in dairy sheep. The best adjustment for their data was to regress the SD of the herd-year-lactation class on the population mean SD. Different breeds and types of sheep (meat or dairy) seem to be experiencing heteroscedasticity but the sources may be different.

Studying subjective conformation and condition scores, Janssens and Vandepitte (2004) report heteroscedasticity between assessors in several breeds of sheep. Their approach to accounting for this heteroscedasticity was to standardize the variances to the overall SD over the trait in a breed. They also reported sex to be a source of heterogeneous variances, so that traits in ewes and wether lambs could not be considered identical. In another study comparing different breeds, Tosh and Kemp (1994) found variable estimates of heritability for weights up to 100 d in 3 breeds (Hampshire, Polled Dorset, and Romanov). They also report heterogeneous variances in the different breeds. Taking into account breed specific variances estimates may be necessary when comparing different breeds, and for performing across-breeds genetic evaluation.

Genetics by environment interaction

The environment an animal is reared in influences its phenotype, and the expression of phenotypes may differ depending on the environment. Interactions between an animal's genetics and its environment is a common occurrence in livestock. For example, tropically adapted breeds usually perform better than breeds adapted to temperate environments in the tropics, and vice versa. A specific environment may have a greater effect on some genotypes than other. This

introduces GxE, which is particularly important if offspring of animals are reared under different conditions (Falconer and Mackay, 1992). Without this interaction, the best genotype in one environment will be superior in all other environments. In the presence of GxE this will not hold, and animals may be ranked differently in terms of their genetic merit in different environments (VanRaden, 2006).

It has been argued that the genetic basis of a trait measured in favorable and unfavorable environments is different. It is often the case that the heritability (and thus genetic variance) of a trait is higher in more unfavorable environments, and decreases in the more favorable environments (Pollott and Greeff, 2004). This suggests that the action of different genes depends on the environment. In a classical paper, Falconer (1952) suggests that with only two environments, GxE can be expressed as a genetic correlation; measurements in each environment can then be treated as different but correlated traits. This way, selection for one trait will bring about a correlated response to selection in the other. The problem with this approach is that the genetic correlation is often less than 1, and therefore selection in one environment may not lead to optimal response in another (Wei and van der Werf, 1995; Mulder and Bijma, 2005). A genetic correlation different than 1 of a trait measured in more than one environment indicates the presence of GxE.

Effects on selection

In selection regimes, where animals are often reared in different environments or farms, GxE can decrease genetic gain. Increased heritability of the traits can accelerate this loss of genetic gain: the increased heritability is due to increased genetic variation of the trait, which also lead to decreased selection accuracy (Mulder and Bijma, 2005). Ignoring GxE when estimating variance components leads to further reductions in response (Garrick and Van Vleck,

1987). Mulder and Bijma (2005) found that progeny testing schemes were more robust to GxE than sib-testing schemes: when including information on progeny, in the presence of GxE, the rate of genetic change was greater. They also found that the genetic gain increased as the genetic correlation approached 1 or -1, which implied the traits were the same between environments and thus no GxE.

Depending on the genetic correlations and heritabilities, a way to optimize selection programs in the presence of GxE and two environments is to have one overall breeding goal and to test progeny in both environments (Mulder and Bijma, 2006; Mulder et al., 2006). With a genetic correlation of 0.6 or higher, this led to greater genetic gain than testing individuals in only one environment, or having different breeding goals for each environment. Collaboration between breeders in different environments can be advantageous when genetic correlations between environments are moderate to high. Mulder and Bijma (2006) found that when the genetic correlation was higher than 0.8, a 15% increase in genetic gain could be achieved with collaboration between breeding programs. Further, in the first generations of selection, cooperation could bring about more genetic progress when the correlation was as low as 0.4. Of course, small breeding programs were more likely to benefit from cooperating than larger ones.

Accounting for genetics by environment interactions in breeding programs

Mulder and Bijma (2005) propose three ways in which GxE can be alleviated: by rearing and selecting all animals in similar environments; by standardizing the measurement and definition of traits across environments; and by applying similar statistical methods (applicable when genetic evaluation is done separately in different countries, as in dairy cattle). These factors are often times outside of breeding scheme's control: in extensive livestock industries such as sheep or cattle, rearing all animals in the same environment is impossible. This may be

more feasible for vertically integrated industries such as poultry or swine. Although in their case elite animals are reared under favorable conditions, while production animals are reared under commercial conditions. Where it is impossible to alleviate GxE in these ways, it needs to be taken into account when evaluating animals.

There are several recent examples of GxE in sheep (i.e. Maniatis and Pollott, 2002; Lewis et al., 2004; Macfarlane et al., 2004b; Pollott and Greeff, 2004; Steinheim et al., 2008). It can be a challenge to estimate the effects of GxE in sheep or other species, if there is not sufficient connectedness among flocks. If GxE is not caused by heterogeneity of variance, it could statistically be caused by poor representation of sires in some flocks (Maniatis and Pollott, 2002; Pollott and Greeff, 2004). Therefore SRS and other cooperative breeding programs can help in the estimation of parameter values that characterize GxE.

In sheep, GxE often occurs due to sire x year interactions. Hagger (1998) found that not accounting for the combined effect of ram and flock led to inflated estimates of direct and maternal (co)variance for growth traits in sheep. Similarly, Maniatis and Pollott (2002) estimated GxE by fitting a sire by flock-year as a random effect in an animal model. Introducing the sire by flock interaction into their model decreased the proportion of direct and maternal heritability and accounted for 2 to 3% of phenotypic variance, at the expense of both direct and maternal additive effects. Steinheim et al. (2008) found GxE on body weight of lambs by incorporating a random sire-flock-year effect as well. Therefore it would be prudent for breeding schemes to test for these kinds of interactions when performing genetic evaluation.

Pollott and Greeff (2004), in wool traits, found changing heritabilities depending on the environment. Fleece weight was more affected by GxE, and fiber diameter traits less so. Fleece and body weight had high heritability in poor environments and the heritabilities decreased as the

environment improved. In unfavorable environments, the genetic variability of traits was high, implying that some animals have a 'better' genetic ability to cope with poor conditions than others; conversely, in a favorable environment the genetic variability was low and genotypes responded similarly to environmental conditions. Similar results were found by Lewis et al. (2004) and Macfarlane et al. (2004a). It is assumed that different genes contribute under different environmental circumstances. A GxE is thus expected for any trait that does not have constant heritability across a range of environments, and must be taken into account when evaluating animals.

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Table 1.1. Literature estimates of direct and maternal heritabilities of growth and harvest traits from several sources.

Trait	Direct heritability±S.E.	Maternal genetic heritability±S.E.	Population	Source
Birth weight (BWT)	0.15±0.05	0.24±0.03	Meta analysis	Safari et al. (2005)
	0.15±0.04	0.18±0.04	Scottish Blackface	Rigio et al. (2008)
	0.19±0.02	0.19±0.01	Texel	Maxa et al. (2007)
	0.19±0.04	0.20±0.03	Suffolk	Maxa et al. (2007)
	0.15	0.17	Australian sheep breeds	Safari et al. (2007)
	0.35±0.04	0.17±0.03	Brazilian meat sheep	Oliveira Lôbo et al. (2009)
	0.09	0.17	Terminal sire	Moussa et al. (1999)
	0.08		Scottish Blackface	Conington et al. (1995)
Weaning weight (WW)	0.18±0.04	0.10±0.01	Meta analysis	Safari et al. (2005)
	0.14±0.05	0.12±0.04	Scottish Blackface	Riggio et al. (2008)
	0.09	0.09	Terminal sire	Moussa et al. (1999)
	0.12		Scottish Blackface	Conington et al. (1995)
Finish weight (HWT)	0.29	0.11±0.02	Welsh mountain	Dewi et al. (2002)
	0.38±0.02		Charollais	Jones et al. (2004)
	0.30±0.01		Suffolk	Jones et al. (2004)
	0.38±0.01		Texel	Jones et al. (2004)
	0.23 ± 0.04	0.29 ± 0.04	Beulah Specklefaced	Husain et al. (2007)
Ultrasonic fat depth (UFD)	0.26±0.02		Meta analysis	Safari et al. (2005)
	0.24±0.072	0.11±0.02	Welsh mountain	Dewi et al. (2002)
	0.34±0.02		Charollais	Jones et al. (2004)
	0.35±0.01		Suffolk	Jones et al. (2004)
	0.38±0.01		Texel	Jones et al. (2004)
	0.20 ± 0.04	0.18 ± 0.05	Beulah Specklefaced	Husain et al. (2007)
	0.14	0.12	Scottish Blackface	Conington et al. (1995)

Table 1.2. Genetic (below diagonal) and phenotypic (above diagonal) correlations among growth traits from several sources. Standard errors are reported where available.

Trait	BWT	WW
Birth weight (BWT)	-	0.37 ^a
		0.30 ^b
		0.43 ^d
		0.36 ^e
		-
Weaning weight (WW)	0.47 ^a	-
	0.54 ± 0.08 ^b	
	0.83±0.04 ^c	
	0.45 ^d	
	0.48 ^e	

^aSafari et al. (2005)

^bRiggio et al. (2008)

^cOliveira Lôbo et al. (2009)

^dMoussa et al. (1999)

^eConington et al. (1995)

Table 1.3. Genetic (below diagonal) and phenotypic (above diagonal) correlations among harvest traits. Standard errors are reported where available.

Trait	HWT	UFD	UMD
Finish weight (HWT)	-	0.36 ^a	0.33 ^a
		0.34 ^b	0.30 ^b
		0.46 ^c	0.58 ^c
		0.59 ± 0.01 ^d	0.68 ± 0.01 ^d
Ultrasonic fat depth (UFD)	0.36 ^a	-	0.05 ^b
	0.67 ^b		0.34 ^c
	0.40±0.02 ^c		0.35 ^f
	0.09 ± 0.14 ^d		
Ultrasonic Muscle depth (UMD)	0.34 ^a	0.33 ^a	-
	0.46 ^b	0.13 ^b	
	0.50±0.02 ^c	0.25±0.03 ^c	
	0.23 ± 0.13 ^d	- 0.08 ± 0.10 ^e	
		-0.21 ^f	

^aSafari et al. (2005)

^bDewi et al. (2002)

^cJones et al. (2004)

^dHusain et al. (2007)

^eKvame and Vangen (2007)

^fConington et al. (1995)

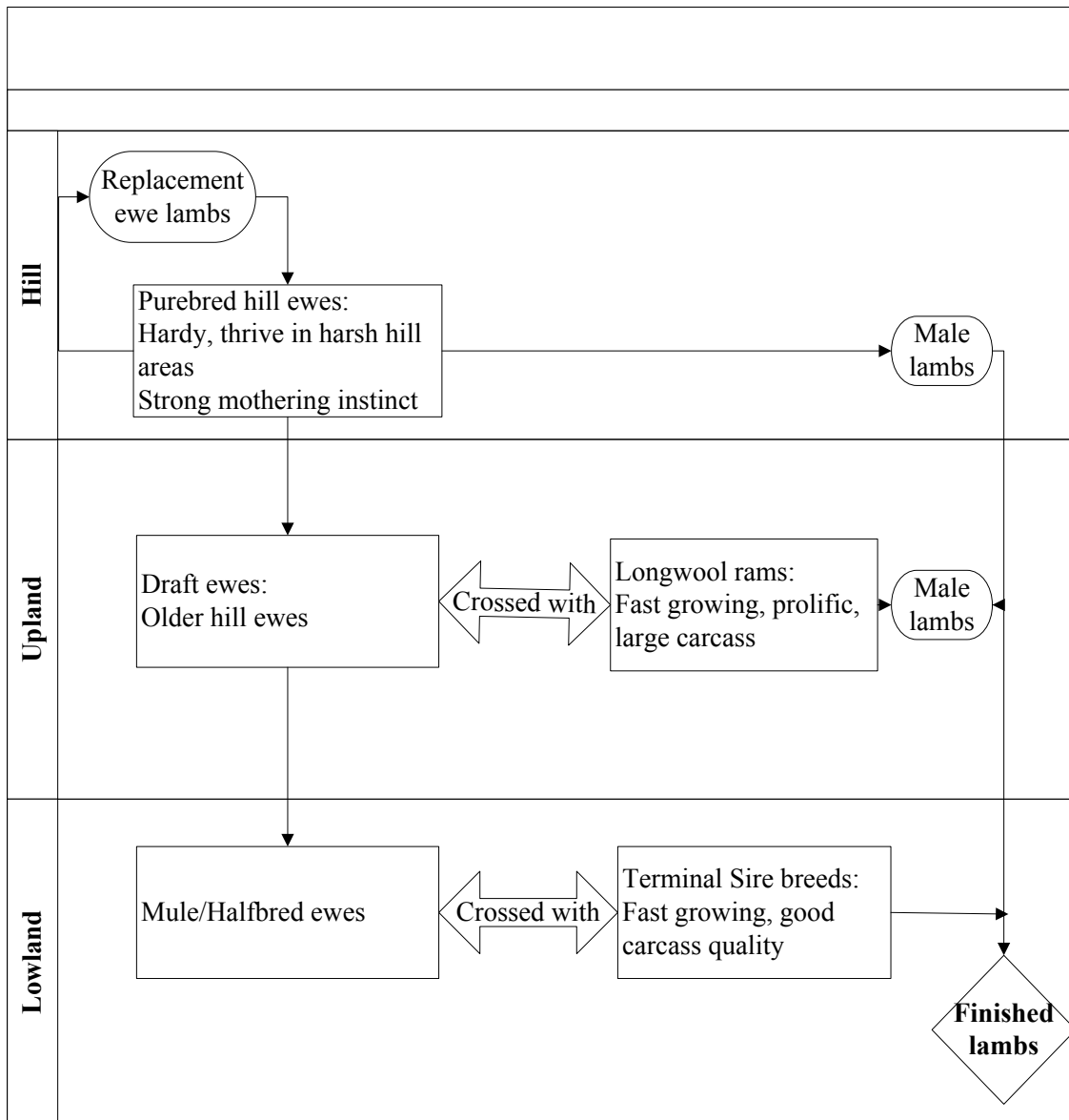


Figure 1.1. The structure of the sheep breeding industry (Adapted from NSA, 2007a)

OBJECTIVES

Weight and ultrasound data on commercial crossbred lambs were obtained in this study. Sires of lambs were selected to be of high or low lean growth index category, and had their progeny evaluated on three farms over a four-year period. In regards to index selection in terminal sire rams, the objectives of this study were 1) to test whether index selection in terminal sires has improved the quality of lambs up until the time they are harvested, and 2) to test whether benefits of index selection were consistent within breed. In regards to heterogeneous environmental variances and genetics by environment interactions, the objectives of this research were to evaluate the presence and consequences of heterogeneous variances and genetics by environment interactions on genetic evaluation, and to find ways to mitigate them if present.

HYPOTHESIS

- (i) Index selection on terminal sire rams leads to improvement in their crossbred commercial offspring.
 - a. The live weight up to harvest of lambs up to harvest sired by high index rams is greater than those sired by low index rams.
 - b. Offspring of high index sired rams will have less fat and more lean content at harvest than offspring of low index sired rams.
 - c. The number of days it takes lambs to reach harvest at a fixed fat endpoint will not differ between high and low index sired lambs.
- (ii) Given the design of this study, heterogeneous variances and genetics by environment interactions should not have large consequences on genetic evaluation for growth and harvest traits.

Chapter 2: Index selection in terminal sires improves early lamb growth

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ABSTRACT

The use of terminal sires (TS) for crossbreeding is integral to the UK sheep industry where approximately 71% of market lambs are sired by TS rams. Early growth of these crossbred lambs affects profitability. The objectives of this study were: (i) to evaluate the effectiveness of index selection among TS on the BW and ADG of their crossbred offspring; and, (ii) to compare the efficacy of that selection within TS breeds. The most widely used TS breeds in the UK are Charollais, Suffolk and Texel. These participated in sire referencing schemes (SRS) where they were evaluated on a lean growth index designed to increase carcass lean weight at a given age. From 1999 to 2002 approximately 15 high and 15 low lean growth index rams per breed (93 in total, differing in index on average by 4.6 SD) were selected from within their SRS, and mated to Welsh and Scottish Mule ewes. Their crossbred offspring were reared commercially on 3 experimental farms in England, Scotland and Wales. A total of 6,515 lambs were born between 2000 and 2003. Lambs were weighed at birth (BWT), 5 wk (5WT), and 10 wk (10WT), and their ADG from birth to 10 wk was calculated. Lambs sired by high index rams were on average, across breeds, heavier at all ages ($P < 0.01$) with 0.07 ± 0.03 , 0.3 ± 0.1 , and 0.4 ± 0.1 kg higher BWT, 5WT, and 10WT, respectively. Their ADG was 5.1 ± 1.9 g/d higher than low index sired lambs ($P < 0.01$). Suffolk sired lambs were on average heavier at all ages, with greater ADG, while Charollais sired lambs were lightest with smallest ADG. Overall, there was no significant interaction between sire index and sire breed ($P > 0.10$). Within Suffolk sired lambs, there was

little difference between high and low index sires for the traits studied ($P > 0.3$). High and low index Charollais sired lambs differed in BWT (0.09 ± 0.04 kg) and 5WT (0.3 ± 0.1 kg), and Texel sired lambs differed in 5WT (0.5 ± 0.1 kg), 10WT (0.9 ± 0.2 kg), and ADG (10.2 ± 3.3 g/d) ($P < 0.01$). Lambs from Scottish Mule dams were heavier, with greater ADG than lambs born to Welsh Mules ($P < 0.01$). Lambs reared in Scotland were heavier at all ages ($P < 0.01$). The results suggest that using index selection in TS can improve the growth of their commercial offspring reared at grass.

Key words: index selection, lamb growth, sheep, terminal sires

INTRODUCTION

The use of terminal sire (TS) breeds in crossbreeding programs is an integral part of sheep production in the United Kingdom. The UK enjoys a stratified crossbreeding structure, with sheep raised in 3 main environments: hills, uplands and lowlands. The hill sector is a source of ewes for the upland, where they are mated to Longwool (primarily Bluefaced Leicester) crossing rams. Crossbred ewes resulting from these matings are moved to the lowlands and bred to TS rams. The main TS breeds used in the UK are Charollais, Suffolk and Texel, and TS crosses, which together account for approximately 71% of lambs slaughtered (Pollott and Stone, 2004). These lambs typically grow quickly to yield high quality carcasses.

In the early 1990's Charollais, Suffolk and Texel breeders established sire referencing schemes (SRS), which are cooperative breeding programs with genetic links created among flocks by the mutual use of reference sires (Simm et al., 2001). Their goal was to improve carcass quality, basing selection on an index to improve lean growth rate (Simm and Dingwall, 1989). The enormous influence of TS breeds on slaughter lamb production in the UK allowed

selection to be targeted to these breeds with great effect on the market (Cameron and Bracken, 1992).

Several studies have compared sire breeds for growth characteristics (e.g., Cameron and Drury, 1985; Yaqoob et al., 2005b). However, evaluation of the effects of index selection on TS breeds has not been thoroughly undertaken. The TS are often reared under pedigree conditions with supplementary concentrates, while their crossbred offspring are reared commercially at grass. This environmental difference means that it is important to directly evaluate the performance of their lambs in a commercial system. The research had two purposes: (i) to evaluate the effectiveness of TS index selection on growth and ADG of crossbred lambs reared commercially; and, (ii) to compare the efficacy of that selection within three TS breeds.

MATERIAL AND METHODS

Animal care

The Animal Experiment Committees at the Institute of Biological Environmental and Rural Sciences (IBERS), the Scottish Agricultural College (SAC), and ADAS UK Ltd (ADAS) approved all procedures and protocols used in the experiment.

Animal resources

The Charollais, Suffolk and Texel TS rams used came from SRS within their breeds and were selected based on their values for the lean growth index of Simm and Dingwall (1989). The index was designed to increase carcass lean weight, while keeping carcass fat weight constant at a fixed age end point. The selection criteria were live weight at finishing, ultrasound fat depth, and ultrasound muscle depth, adjusted to 150 days. Relative economic values of +3 and -1 were used for lean and fat weight, respectively. These relative economic values were chosen to

achieve the desired gains in the traits of the breeding goal rather than being based on market returns and costs of production. Thus this index is equivalent to a restricted selection index, with changes in fat restricted to zero, or alternatively a desired gains index (Simm and Dingwall, 1989). It was derived in this manner because of the weak relationship between carcass price and fatness in Britain at the time of its development (Simm et al., 2002). Annual response to the index has ranged from approximately 6 to 14 index points (Simm et al., 2001).

A resource of “Mule” (crossbred) ewes was developed by mating Scottish Blackface and (Welsh) Hardy Speckled Face hill ewes to Bluefaced Leicester rams. These matings produced flocks of Scottish and Welsh Mules, respectively, described previously (van Heelsum et al., 2003, 2006; Mekkawy et al., 2009). A description of genetic evaluation system, and genetic progress in UK sheep, can be found in Amer et al. (2007).

In the first year of the experiment (2000) all ewes were primiparous 2-yr olds. In 2001 and 2002, new 2-yr old ewes were added to the ewe flock, and the older ewes remained. In 2003 no new ewes were added. Thus the average age of the flock increased over time. These Mule ewes were distributed among 3 experimental farms in the UK: Rosemaund, England (ADAS; 52°04'N, 02°43'W); Edinburgh, Scotland (SAC; 55° 57'N, 3°12'W); and, Aberystwyth, Wales (IBERS; 52°25 N, 4°4'W).

Terminal sire ram selection.

From 1999 to 2002 the Mule ewes were mated to TS rams from the Charollais, Suffolk and Texel breeds. The rams were selected to fall into either high or low lean growth index category. They were purchased from each of their respective breed’s SRS. In the first two years of the study, breeders brought rams to the Ram Selection days for each SRS. In 2001 there was an outbreak of Foot and Mouth Disease in the UK, which resulted in a ban on animal movement.

In 2001 and 2002, rams were no longer selected at Ram Selection days, but instead purchased directly off farms. Selected rams were extreme in index score within their breed. They were inspected and confirmed as physically sound by a veterinarian, and approved to be of suitable breed type by scheme judges. Between 15 and 17 high and low index rams were used from each breed over the length of the study.

In the first year of selection (1999), all rams chosen as high index had index scores above 250 points (top 5% of available rams) while those chosen as low index all had index scores below 100 points. Given the Foot and Mouth Disease outbreak in 2001, and difficulties in obtaining low index rams, the eligible index scores increased over time. In the final year of selection (2002), a score of 300 points was considered high and 150 low, thus the differential between high and low index rams was maintained within a year.

Mating design.

Matings between TS and Mule ewes were designed to balance number of rams between high and low index, and between the 3 TS breeds in each mating year (Table 2.1). They were also designed so that genetic links were achieved among farms and years. No AI was used because assessment of the natural reproductive capacity of the Mule ewes was a priority for a previous study (van Heelsum et al., 2003, 2006). To create genetic links between farms without AI, sires were used in successive breeding seasons, being moved between farms. Sires were typically used as ram lambs (8 mo of age) at the first mating, and as shearlings (20 mo of age) at the second mating. After the first mating, approximately 1/3 of sires stayed at the same farm, and the remaining 2/3 were moved to others. Thus rams had progeny in 2 locations and genetic connections existed between all farms. The design allowed for performance information on the

crossbred offspring to be combined and analyzed across the 3 locations where the Mule ewes were distributed.

On all 3 farms, similar numbers of ewes (from 26 to 39) were mated on pasture to a single sire. Rams remained with ewes for 4 to 6 weeks. In some cases ram fertility was deemed low (based on raddle marks). In those instances, approximately 1 week after the ram was removed another ram was placed in their pasture. Thus all ewes were mated and parentage identification was possible based on lamb birth dates. The number of ewes from each breed used each year is shown in Table 2.1. Approximately 35 ewes, half from each Mule genotype were mated to a ram each year.

Farms

The number and percentage of lambs born, and the number of sires used in each farm and year, are in Table 2.2. Management was standardized among farms. However, the mating period in England and Wales began in mid-October while, due to the later onset of spring weather, it began 2 weeks later in Scotland.

Lambs were reared in 3 lowland farms which differed in climate and topography. The Rosemaund farm in England is at an altitude range of 75 to 105 m above sea level, with mean annual rainfall of 660 mm and average temperatures ranging from 3 to 22°C. In Scotland, the SAC farm ranges in altitude from 150 to 200 m above sea level, with 1000 mm of rainfall per yr and average temperature ranging from 7 to 26°C. The Welsh farm has annual rainfall of 1170 mm, and average temperatures ranging from 3 to 20°C. It ranges from 10 to 70 m above sea level.

Production and finishing of crossbred lambs

Lamb pedigree, sex and weight were recorded at birth. Male lambs were castrated, and all lambs' tails docked. The ewes were condition scored, weighed, and any lambing difficulties noted. Within 48 hours of lambing, Mule ewes were turned out to pasture with no more than 2 lambs. Ewes with twin lambs were grazed separately from those with singletons and offered supplementary feed where needed. The lambs were re-weighed at approximately 5 and 10 weeks of age.

Statistical analysis

All lambs evaluated had sire and dam identification available. Birth dates were checked against mating period to confirm parentage, and lambs with uncertain parentage were removed. Lambs with poor weight gain indicative of illness were excluded from the data. Data were further edited so that lambs were at least 14 d old and at most 56 d old at their 5 week weights. A total of 6,515 lambs had birth weight (**BWT**) and 5 week weight (**5WT**) records, and 6,508 lambs had 10 week weight (**10WT**) records. Further, the ADG of each lamb from birth to its 10WT was calculated in g/d. A 2-generation pedigree was assembled on the paternal side, and a 1-generation pedigree on the maternal side, using all available ancestors.

The live weight and ADG data were analyzed with SAS software (Cary, NC) fitting a linear mixed model. Fixed effects were sire index (high or low) and breed (Charollais, Suffolk or Texel), and their interaction, sex (wether or ewe lamb), dam breed (Scottish or Welsh Mule), age of dam (**AOD**) (2-yr, 3-yr or 4- and 5-yr), and farm and birth yr, and their interaction. For BWT, birth rank (single, twin, triplet) was fitted as an additional fixed effect. For 5WT, 10WT and ADG, a combined birth-rearing rank fixed effect instead was fitted. The four categories were: single born/single reared, twin or more born/single reared, single or twin born/twin reared, and

triplet or quadruplet born/twin reared. The lamb's sire, nested within index and breed, and the rearing dam were included as random effects in addition to the residual.

For BWT the lamb's birth date within each breeding season in each farm was fitted as a covariate. Day 1 was considered the first day a lamb was born on a farm in a particular year. Day of birth therefore was adjusted for each year-farm combination, and centered to its mean birth date. For 5WT and 10WT, the lamb's age at recording was fitted as a covariate. These were centered to their expected age (e.g., 35 d for 5WT) to adjust weights to their target age. No covariate was fitted for ADG.

Adjusted means were obtained and differences among means were tested for significance using a Tukey-Kramer adjustment for multiple comparisons (Westfall et al., 1999). Analysis of variance was carried out to investigate the statistical significance of fixed effects. For interactions of sire index and breed, simple effects were tested, which assess the effects of sire index on each of the sire breeds separately. Additionally, orthogonal contrasts were performed to test the nature of any present interaction.

To disentangle the confounding of ewe age and birth yr, the data were divided into 3 subsets based on AOD, which were analyzed separately. The three age categories used were 2-yr old, 3-yr old, and 4 to 5-yr old dams. The weight and ADG of lambs from these subsets were analyzed with the linear mixed model described earlier, except the AOD fixed effect was omitted. The same analysis was conducted for 3 subsets of data but instead separated by birth year (2001, 2002, and 2003).

Some evidence of non-normality and heteroscedasticity of the variables analyzed was observed with Anderson-Darling (Anderson and Darling, 1952) and Levene's (Levene, 1960) test. The residuals from the BW and ADG models were then tested for skewness, kurtosis and

normality. The SE of skewness and kurtosis were calculated as $\sqrt{6/n}$ and $\sqrt{24/n}$, respectively, where n was the number of records (Kutner et al., 2005). Given the large n (6515 or 6508), the SE were inherently small and most residuals exhibited skewness and kurtosis to an extent judged to be formally significant at $P < 0.05$. However, in all cases the mean and median were similar, and further inspection of the distributions indicated that skewness and kurtosis were not severe. The distributions of the residuals were inspected through plots of predicted values vs. residuals, and quantile-quantile plots, and appeared normal.

There was concern that any heterogeneity in variance among sire breed and index categories could bias evaluation of these effects, including their interaction. To deal with this possibility, the weight data were tested for heteroscedasticity. Standard normal scores were calculated for each animal's weight by subtracting the mean weight of a sire breed-index category and then dividing it by its SD. Weights were then standardized as

$$WTz_i = \hat{\mu}_{BI_j} + z_i * \hat{\sigma}_{SuffH}$$

where, WTz_i is the i^{th} animal's transformed weight, $\hat{\mu}_{BI_j}$, is the mean of each combined sire breed-index category, z_i is the standard normal deviate, and $\hat{\sigma}_{SuffH}$ is the SD of the weights of high index Suffolk sired lambs. The WTz_i scores were fitted to the linear mixed model described above. The transformation ensured that WTz_i scores and the sire index category-breed variances were homoscedastic. Differences among means of index-breed categories were tested to determine whether any heteroscedasticity in the data was substantial enough to impact those comparisons.

RESULTS

Animal resources

The number of sires used and lambs born in each location are in Table 2.2. Lambs were relatively evenly distributed across locations, although the number of lambs born each year increased as more Mule ewes were mated. There was also, as shown in Table 2.1, a relative balance between ewes of each breed mated each yr.

A 2-generation pedigree was assembled to summarize paternal ancestry, and a 1-generation pedigree for maternal ancestry. No sires in the project were full sibs, although some were half sibs. Almost all paternal grand sires (67 of 75) had only 1 ram offspring included in the study, but 2 paternal grand sires had 2 half-sib offspring, and 6 paternal grand sires had 3 half-sib offspring. No high and low index sires in the project were related at the level of the pedigree assembled.

Table 2.3 shows the differences between high and low index rams of each breed for index score and EBV for scanning and live weight at 150 d in each birth year of the lambs. The EBV were obtained from the across-flock animal model BLUP evaluation conducted within breed in each year. High index rams were on average 198 ± 8 points higher in index score than low index rams. In all breeds, high index rams had more positive EBV for live weight (**LW**) (6.6 ± 0.5 kg) and ultrasonic muscle depth (**UMD**) (2.3 ± 0.2 mm) than low index rams. Overall, high index rams had more negative EBV for ultrasonic fat depth (**UFD**) (-0.49 ± 0.12 mm), although the differences were small and significant ($P < 0.01$) only for the Charollais.

Effects of sire index, and sire and dam breed

The mean ages at weighing for 5WT and 10WT were 37 d (SD 6) and 71 d (SD 7), respectively. For all traits studied, the effects of the index and breed of the sire were significant ($P < 0.01$), although their overall interaction was not ($P > 0.10$). Least squares means for sire index and breed are presented in Table 2.4. Lambs sired by high index rams were 0.07 ± 0.03 , 0.3 ± 0.1 , and 0.4 ± 0.1 kg heavier at BWT, 5WT, and 10WT, respectively, with 4.9 ± 1.9 g/d higher ADG ($P < 0.01$).

On average, Suffolk sired lambs were heavier for all weight traits and had highest ADG ($P < 0.01$). This is shown for 10WT in Figure 2.2. Charollais sired lambs were the lightest and had the lowest ADG, although they did not differ in weight from Texel sired lambs at birth, 10 week or for ADG ($P > 0.10$). Suffolk sired lambs were not different from Texel sired lambs in BWT and 5WT ($P > 0.10$).

Analysis of the simple effect of index category within a breed revealed that high index Charollais sired lambs were heavier than low index sired lambs for BWT (0.09 ± 0.04 kg) and 5WT (0.3 ± 0.1 kg) ($P < 0.01$), but not for 10WT ($P = 0.2$) or ADG ($P = 0.4$). Within Suffolk sired lambs, there were no differences between high and low index sires in the weights of their offspring for BWT ($P = 0.3$), 5WT ($P = 0.6$), 10WT ($P = 0.2$), or ADG ($P = 0.7$). For Texel sired lambs, there was no difference between high and low index categories for BWT ($P = 0.06$). However, the high index Texel sired lambs had higher values for 5WT (0.5 ± 0.1 kg), 10WT (0.9 ± 0.2 kg) and ADG (10.7 ± 3.3 g/d) ($P < 0.01$). In all instances, high index sired lambs were numerically heavier than low index sired lambs within a breed, as shown for BWT in Figure 2.1.

Although no overall interaction between index and sire breed was detected, the difference between index categories varied among breeds. Weights and ADG were most distinct between

index categories in the Texel sired lambs. Orthogonal contrasts were therefore constructed to test the interaction between Texel vs. combined Suffolk and Charollais sire breeds with index category. For 10WT and ADG a mild interaction was detected ($P < 0.05$), substantiating the larger difference between index categories in Texel sired lambs for these two traits.

Dam breed was a significant source of variation for all traits studied ($P < 0.01$). Adjusted means are shown in Table 2.4. Lambs born to Scottish Mule dams were heavier ($P < 0.01$) than lambs born to Welsh Mules for BWT (0.29 ± 0.03 kg), 5WT (0.8 ± 0.1 kg), 10WT (1.2 ± 0.1 kg), and had higher ADG (12.5 ± 1.2 g/d; $P < 0.01$).

Analysis of normalized weight scores (WTz) revealed no interaction between sire index and sire breed (BWT, $P = 0.8$; 5WT, $P = 0.2$; 10WT, $P = 0.1$; ADG, $P = 0.1$), while the individual effects of sire index and sire breed did affect performance ($P < 0.01$). This indicated that the lack of significant interaction between sire index and sire breed in the non-normalized data was not due to heterogeneity of variance within sire index and breed categories.

Effects of location and year

The main effects of farm, year, and their interaction, were significant ($P < 0.01$). Even though the interaction was present, in all cases the ranking of farms did not change over the years; lambs in Scotland were always heavier, followed by those in England and Wales. Weights fluctuated with year, but not in a systematic way.

Adjusted means for the three farm locations are in Table 2.5. On average, lambs born in Scotland were heavier at all ages and had higher ADG than lambs born in other farms ($P < 0.01$). These lambs were born later in the year since mating was two weeks later. Lambs differed in BWT between farms across all years ($P < 0.01$). Lambs in Wales and England did not differ in 5WT or 10WT ($P > 0.1$).

The analysis of the 3 subsets of data formed by AOD (i.e., 2-yr old, 3-yr old, and 4- and 5-yr old), showed that 5WT, 10WT, and ADG of lambs increased with dam age. This pattern was less consistent for BWT. When the data were split into birth year rather than AOD subsets, similar results were obtained. In 2001 and 2002, lambs born to older ewes were heavier and grew more quickly than lambs born to younger ewes ($P < 0.001$). In 2003, 4- and 5-yr-old ewes did not differ amongst themselves, but lambs from 3-yr-old ewes weighed less and grew more slowly ($P < 0.001$).

DISCUSSION

Comparison of index categories

Mule ewes were mated to TS rams to test the efficacy of the index selection that had been used in the 3 sire breeds since the early 1990's. Using sires of different lean growth index categories allowed quantification of the progress achieved by the different SRS in improving lamb performance. The design of this experiment allowed valid comparisons among lambs reared in different environments and sired by rams of different breeds.

Differences between index categories of rams for live weight and scanning traits (Table 2.3) were expected given the selection on index scores. Because of the way the index was devised, high index sheep typically had positive EBV for LW and UMD and, in general, slightly negative EBV for UFD (Simm et al., 2002). The differences between UFD EBV of Texel and Suffolk rams were for the most part not different from 0. This may be due to breeders' preference for rams that are fatter at the same index score; they may see this as a way to achieve sufficient fatness at the target finish weight in commercial lambs. The difference in index points between high and low index sires in each breed was substantial. Therefore we anticipated differences in lean growth rate between sire categories would be expressed in the performance of

their crossbred progeny. Such an effect has been observed previously (Lewis et al., 1996, 2004; Simm and Murphy, 1996; Jones et al., 1999), and here.

Sire index and breed influences

Index selection has been found to be an efficient way to improve economically relevant traits in sheep. In TS SRS where the lean growth index used in this study was applied, annual response to selection ranged from approximately 6 to 14 index points (Simm et al., 2001). The results from other experiments have also shown that the use of the lean growth index has increased lean weight in the carcass while reducing fat weight (Lewis and Emmans, 2007). Lewis et al. (1996) found that commercial lambs sired by high lean growth index sires produced leaner and more valuable carcasses. Corroborating these results, van Heelsum et al. (2003), studying the Scottish and Welsh Mules used as dams in the current study, found that their Bluefaced Leicester sires with higher index scores produced wethers with more lean and less fat content in all carcass joints (e.g., shoulder, leg and loin).

In the current study, sire breed impacted 5WT, 10WT and ADG ($P < 0.01$), indicating that breed differences can be exploited for the economic benefit of producers. The lack of difference in BWT was favorable given possible problems of dystocia associated with higher BWT. Some studies on the effects of sire breed have found no influence on BWT (More O'Ferrall and Timon, 1977; Leymaster and Jenkins, 1993; Fogarty et al., 2000), while other studies, using more diverse sire breeds, have found differences (Cameron and Drury, 1985; Fogarty et al., 2000; Freking et al., 2000). Yaqoob et al. (2005b) found that weaning weights of Texel sired lambs were higher than those of Charollais sired lambs, but Suffolk sired lambs did not differ from either of these breeds. Cameron and Drury (1985) did not detect such a difference between Texel and Charollais sired lambs; their ADG did not differ either. Conversely, Yaqoob

et al. (2005a) found that the ADG of Texel, Suffolk and Charollais sired lambs did not differ from birth to 30 d, but that ADG of Suffolk was higher than that for Texel sired lambs from birth to weaning and from birth to slaughter. Charollais sired lambs did not differ from the other breeds at these ages.

Possibly conflicting results between experiments may be due to different strains of the sire breeds used. For example, in the US, Kuehn et al. (2009) reported that Suffolks were being selected for two biological types: one for traditional TS characteristics like large mature size, and another with emphasis on moderate mature size and muscling. Two main strains of Texel are used in the UK, Dutch Texel and French Texel, which may differ in several respects. French Texel was the strain primarily used in the present study.

Suffolk sired lambs were heavier at all ages than those sired by the other two breeds (shown for 10WT on Figure 2.2). The lack of difference in performance between high and low index Suffolk sired lambs was unexpected. We hypothesize that the progeny of the high index Suffolk rams performed less well than anticipated, and that this may be due to one or more factors. Firstly, this may be an environmental (nutritional) constraint, which is first seen as growth and metabolic demands become higher. It has been found that superior genotypes can express their superiority only to an extent that is set by the quality of the environment (Lewis et al., 2002; Macfarlane et al., 2004). The genetic difference in growth rate was found to decrease steadily as the environment worsened, both between selection lines (Lewis et al., 2002) and between breeds (Macfarlane et al., 2004).

Similarly, differences in husbandry between purebred and commercial farms may play a role. On commercial farms where conditions were limiting, with little or no supplementary concentrates and a reliance on grass, the genetic potential of Suffolk rams may not have been

achieved. This is in agreement with Eikje et al. (2008), who observed that genetic change was higher than phenotypic change in Norwegian sheep. In that case the environment was not sufficiently beneficial for lambs to realize their genetic potential.

Unlike the current results, index selection has been effective for Suffolk sheep in the past. A long-term selection experiment tested the efficacy of index selection in Suffolks, and differential responses in growth between the selection and control line were observed (Simm and Murphy, 1996; Simm et al., 2002; Lewis et al., 2004; Lewis and Emmans, 2007). Lewis and Emmans (2007) reported that the growth rate in the selection line of Suffolk was 1.17 times higher than the control line at 40 kg.

High index Charollais and Texel sired lambs performed better than low index sired lambs in this study. Lean growth index category affected some traits but not others in these breeds, but the lack of differences was not persistent across all traits as it was in Suffolk sired lambs. It must be noted, that even though not significant, high index sired lambs within a breed were always numerically heavier, with greater ADG, as shown for BWT in Figure 2.1. The goal of the index was to improve the carcass of animals, and several studies have shown its effectiveness in doing so (e.g., Simm et al., 2001; 2002). Selection programs designed to improve lean growth rate will improve carcass merit and their uptake should be encouraged.

Fixed effects relating to dams

The influence of ewes on lamb growth and development is substantial (e.g., Maniatis and Pollott, 2002; Safari et al., 2005; Riggio et al., 2008). Litter size and rearing type were a significant source of variation in all traits studied ($P < 0.01$). The BWT of triplet and quadruplet born lambs was not significantly different, but single born lambs were heaviest, followed by twin born lambs (results not shown). These results agree with previous estimates from the literature

(Peeters et al., 1996; Fogarty et al., 2005): ewes with single lambs have significantly more resources to dedicate to their lambs, and they were heavier at all ages.

The age and parity of ewes also exerts significant influence on lamb weights. Peeters et al. (1996) found that lambs of 1 year old ewes had significantly lower birth weight and postnatal growth rate compared to lambs of multiparous ewes, in accordance with other literature (Freetly and Leymaster, 2004; Alvarez et al., 2010). Similar results were found presently, with older ewes producing heavier lambs. In the current study, increases in lamb weights over the years were related in part to ewe age and parity. In 2000 all ewes were primiparous, and had not yet reached full maturity. The mean age of the flock increased over the duration of the study, with the consequence that weights and ADG of lambs increased overall. Concurrently, the Bluefaced Leicester sires of the Mule ewes were being selected on an index that included increased weight as part of its goal (van Heelsum et al., 2003, 2006; Mekki et al., 2009). Therefore the Mule ewes were better every year. This is reflected in the current results: regardless of sire index, lambs from ewes of the same age improved every yr, in part because their dams improved.

Two different ewe genotypes were used in the current study. The Scottish Mules were heavier at birth, 10, and 16 wk than the Welsh Mules (van Heelsum et al., 2003), which is to be expected as their Scottish Blackface dams are generally larger than Welsh Speckled Faced dams. It has been reported that animals from larger mature size breeds grow more rapidly than those from smaller mature size breeds (Bradford, 2002). Other studies have also found differences in BWT of lambs from different dam breeds (Johnston et al., 1999; Fogarty et al., 2000). The profitability of using larger or smaller ewe genotypes depends on the production system and on the resources available for ewes, as larger ewes will require more inputs than smaller ewes, but may produce heavier lambs.

As part of model selection, an interaction between dam and sire breed was tested. As none was found ($P = 0.9$) it was not fitted in the final analytical model. This result is in accordance with at least some literature (Cameron and Drury, 1985; Freking et al., 2000). On the other hand, Kempster et al. (1987) found the interaction to be significant. The sire and dam breeds used were not the same as those used in the current study, which differed appreciably. Since no interaction was detected even in this case, different levels of heterosis from specific breed crosses would seem unlikely. It would appear that dam breed will not necessarily be important when comparing progeny of sires from different breeds.

Environmental influences

The influence of farm and year, and their interaction, was significant for all measures ($P < 0.01$). As shown in Table 2.5, lambs reared in Scotland were always heavier with greater ADG, followed by those in England and Wales, which only differed in BWT. The heavier weights in Scotland may be explained by environmental conditions. Because the early season climate is harsher in Scotland, the lambing season began approximately 2 weeks later than in the more southern farms. In addition, mid-summer rainfall tends to be lower in England and Wales, which, combined with different soil types, results in a temporary decline in DM yield not observed in Scotland at the time that requirements for lambs are increasing. The day length in mid-summer Scotland is longer than in England and Wales; this also has a positive effect on the DMI of lambs.

On average the 5WT and 10WT of lambs increased most years, owing to ongoing selection in the sires of both the dams and lambs. A decrease in 5WT, 10WT and ADG was observed in 2001, which may reflect 2 conditions in that year. First, many ewes were primiparous, thus producing lighter offspring than in latter year. Second, and probably of most

importance, 2001 was the year of the Foot and Mouth Disease outbreak in the UK. Although the project ewes were not directly affected by the disease, differences in weights were site specific, with 5WT decreasing in Wales and England, but not Scotland, and 10WT and ADG decreasing across all sites. The constraints in animal movement were put in place earlier in England and Wales than in Scotland, which limited those farms' ability to provide better forage, and increased the incidence of parasitism.

Conclusions

Based on our results, selection on the lean growth index in TS breeds can bring about improvements in the growth of their commercial offspring reared at grass. Since TS breeds have a large influence on the production of market lambs in the UK, index selection therefore offers an effective way of improving meat production. Its utility has been observed for growth (e.g., Lewis et al., 2002; Lewis and Emmans, 2007) and carcass (e.g., Cameron and Bracken, 1992; Simm et al., 2001; Lewis et al., 2004; Conington et al., 2006) traits. Importantly, an advantage of index selection is that genetic changes are permanent, cumulative, and cost effective (Simm and Dingwall, 1989). Our results support the wider uptake of this methodology as a means for improving the efficacy of sheep production systems.

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Table 2.1. No. of sires used for mating by index and breed category, and no. of dams used

Category	Breed	Birth yr of lambs							
		2000		2001		2002		2003	
		High ¹	Low	High	Low	High	Low	High	Low
Sire	Charollais	3	3	6	6	8	7	9	9
	Suffolk	2	3	6	6	7	7	10	7
	Texel	3	3	6	7	7	7	9	8
Dam	Scottish Mule	242		455		593		565	
	Welsh Mule	249		486		645		644	

¹Index category.

Table 2.2. No. of lambs born in each location each birth yr and no. of rams used in that location each birth yr

Location	Birth yr of lambs							
	2000		2001		2002		2003	
	Lambs (%) ¹	Rams	Lambs (%)	Rams	Lambs (%)	Rams	Lambs (%)	Rams
Wales	262 (34)	6	500 (33)	12	525 (25)	14	677 (32)	17
Scotland	264 (34)	5	603 (40)	13	804 (38)	14	703 (33)	18
England	254 (32)	6	419 (27)	12	776 (37)	15	728 (35)	17

¹No. of lambs in each farm and percentage by location within a year.

Table 2.3. Differences (high-low) in index scores and mean EBV for scanning traits by breed for rams used in the project¹

Sire breed	Birth yr of lambs	Difference in	Difference in EBV ²		
		Index \pm SED, points	LW ² \pm SED, kg	UMD \pm SED, mm	UFD \pm SED, mm
Charollais	2000	185 \pm 6	7.05 \pm 0.84	0.67 \pm 0.74	-1.51 \pm 0.55
	2001	236 \pm 15	7.42 \pm 0.96	2.56 \pm 0.38	-1.12 \pm 0.50
	2002	205 \pm 16	3.91 \pm 1.31	2.53 \pm 0.59	-1.12 \pm 0.31
	2003	232 \pm 18	6.47 \pm 1.53	2.77 \pm 0.47	-0.89 \pm 0.38
	avg ³	213 \pm 13	5.97 \pm 0.78	2.15 \pm 0.35	-1.14 \pm 0.21
Suffolk	2000	217 \pm 9	8.14 \pm 1.01	5.29 \pm 0.58	-0.45 \pm 0.46
	2001	243 \pm 27	4.72 \pm 1.28	2.48 \pm 0.91	-0.99 \pm 0.30
	2002	165 \pm 5	6.23 \pm 1.18	1.23 \pm 0.56	0.03 \pm 0.36
	2003	205 \pm 20	7.12 \pm 1.14	2.03 \pm 0.42	0.15 \pm 0.22
	avg	211 \pm 14	6.51 \pm 0.75	2.53 \pm 0.40	-0.27 \pm 0.18
Texel	2000	146 \pm 10	4.96 \pm 0.95	3.36 \pm 0.44	0.01 \pm 0.17
	2001	186 \pm 10	8.66 \pm 1.62	1.96 \pm 0.40	0.05 \pm 0.58
	2002	184 \pm 18	6.35 \pm 1.13	1.76 \pm 0.84	-0.58 \pm 0.22
	2003	174 \pm 17	9.13 \pm 0.88	1.69 \pm 0.93	0.06 \pm 0.22
	avg	172 \pm 10	7.37 \pm 0.74	2.10 \pm 0.37	-0.11 \pm 0.16
Overall across breeds	avg ⁴	198 \pm 8	6.6 \pm 0.5	2.3 \pm 0.2	-0.49 \pm 0.12

¹EBV were obtained from across-flock animal model BLUP conducted within each sire referencing scheme.

²At 150 d of age: LW = live weight; UMD = ultrasonic muscle depth; UFD = ultrasonic fat depth.

³Differences averaged over years.

⁴Differences averaged over years and breeds.

Table 2.4. Adjusted least square means of growth traits in lambs by sire breeds and index categories and dam breeds¹

	No. ²	BWT ³ ± SE, kg	5WT ± SE, kg	No. ⁴	10WT ± SE, kg	ADG ± SE, g/d ³
Sire index						
High	3265	4.62±0.05 ^a	16.6±0.1 ^a	3262	27.4±0.1 ^a	321.8±1.7 ^a
Low	3250	4.54±0.05 ^a	16.3±0.1 ^b	3246	26.9±0.1 ^b	316.8±1.7 ^b
Sire breed						
Charollais	2323	4.53±0.05 ^b	16.2±0.1 ^b	2321	26.9±0.2 ^b	315.7±2.0 ^b
Suffolk	2038	4.64±0.05 ^a	16.6±0.1 ^a	2035	27.6±0.2 ^a	324.4±2.0 ^a
Texel	2154	4.56±0.05 ^{ab}	16.5±0.1 ^a	2152	27.1±0.2 ^b	317.9±2.0 ^b
Dam breed						
Scottish Mule	3090	4.73±0.05 ^a	16.8±0.1 ^a	3086	27.8±0.13 ^a	325.5±1.6 ^a
Welsh Mule	3425	4.43±0.05 ^b	16.1±0.1 ^b	3422	26.6±0.13 ^b	313.1±1.6 ^b

¹Means within a category in a column with different subscripts are significantly different ($P < 0.05$).

²No. of lambs weighed at birth and 5 wks.

³BWT = birth weight; 5WT = 5 wk weight; 10WT = 10 wk weight; ADG = ADG from birth to 10 wk.

⁴No. of lambs weighted at 10 wk.

Table 2.5. Adjusted least square means of growth traits in lambs by location¹

Location	No. ²	BWT ³ ± SE, kg	5WT ± SE, kg	No. ⁴	10WT ± SE, kg	ADG ± SE, g/d ³
England	2177	4.37±0.05 ^c	15.8±0.1 ^b	2177	25.8±0.1 ^b	304.4±1.9 ^b
Scotland	2374	4.80±0.05 ^a	17.8±0.1 ^a	2373	29.7±0.2 ^a	349.8±2.0 ^a
Wales	1964	4.57±0.05 ^b	15.7±0.1 ^b	1958	26.1±0.1 ^b	303.8±1.9 ^b

¹Means within a column with different subscripts are significantly different ($P < 0.05$).

²No. of lambs weighed at birth and 5 wks.

³BWT = birth weight; 5WT = 5 wk weight; 10WT = 10 wk weight; ADG = weight ADG from birth to 10 wk.

⁴No. of lambs weighted at 10 wk.

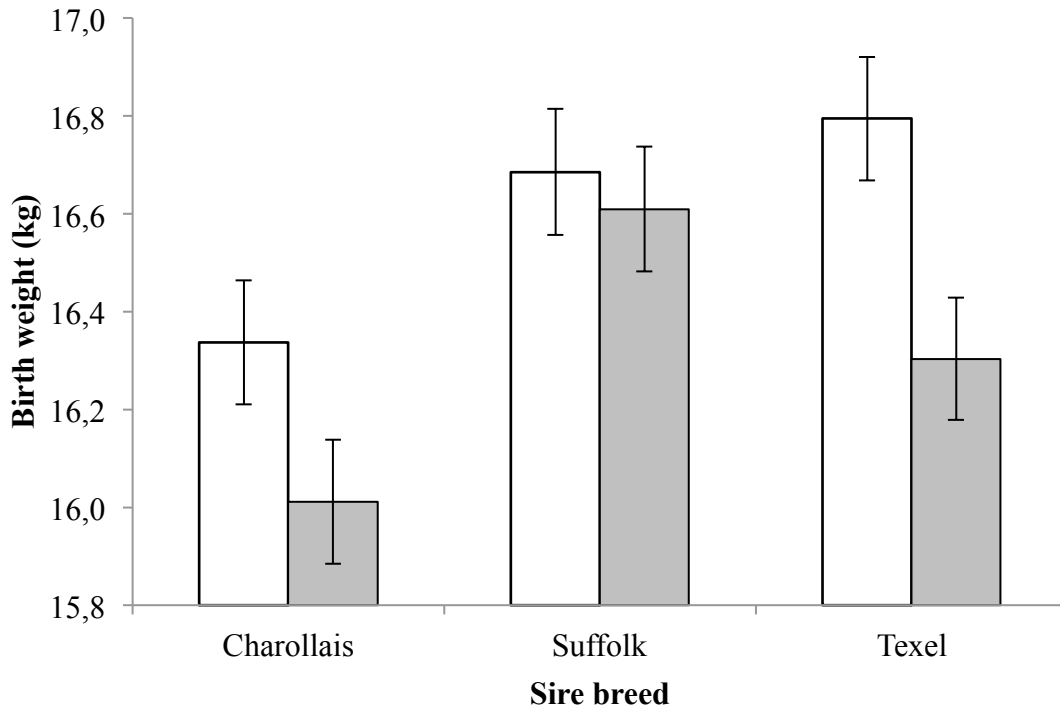


Figure 2.1. Adjusted means with standard error bars for birth weight of lambs sired by either high (white) or low (grey) index sires from the Charollais, Suffolk or Texel breeds.

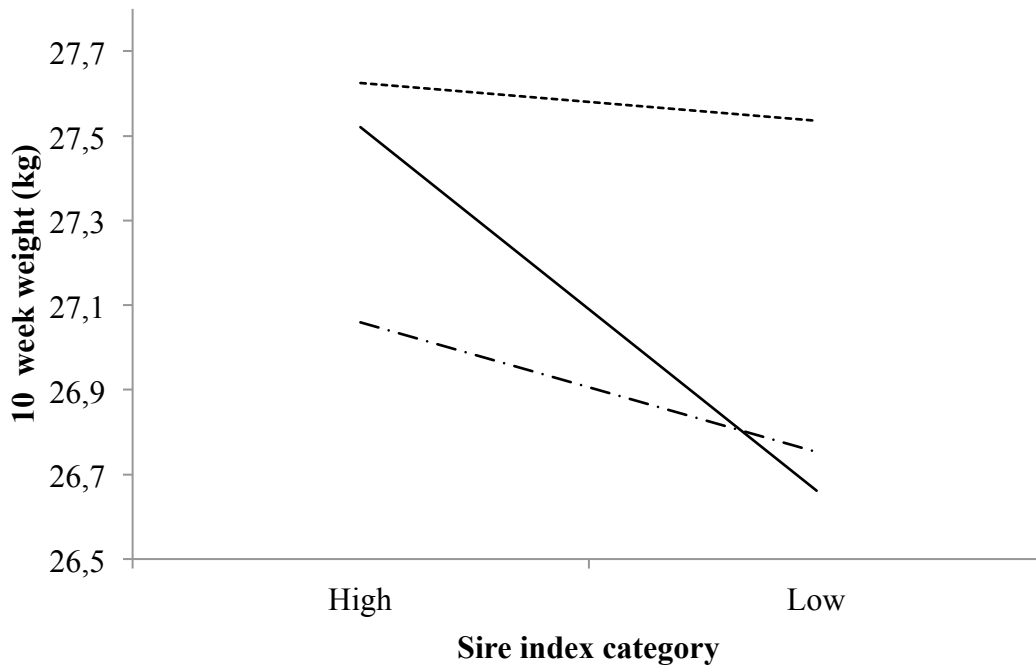


Figure 2.2. Adjusted means for 10 week weight of lambs sired by either high or low index sires of the Charollais (dotted and dashed line), Suffolk (dotted line), and Texel (solid line) breeds.

Chapter 3: Index selection in terminal sires improves lamb performance at finishing

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ABSTRACT

Lamb meat is often perceived by consumers as fatty, and consumption has decreased in recent decades. A lean growth index was developed in the UK for terminal sire breeds to increase carcass lean content, while constraining fat content, at a constant age end point. The purposes of this study were (i) to evaluate the effects of index selection of terminal sires on their crossbred offspring at finishing, and (ii) to evaluate its effectiveness within terminal sire breeds.

Approximately 70% of lambs marketed in the UK have been sired by rams of breeds typically thought of as specialized terminal sires. The most widely used are Charollais, Suffolk and Texel. These breeds participated in sire referencing schemes since the early 1990s by sharing rams among flocks selected on the lean growth index. From 1999 to 2002 approximately 15 ‘high’ and 15 ‘low’ lean growth index score rams were selected from within their sire referencing schemes and mated to Welsh and Scottish Mule ewes. Their crossbred offspring were commercially reared on three farms in the UK. Lambs were finished to an estimated 11% subcutaneous fat by visual evaluation. At finishing, lambs were weighed, ultrasonically scanned and assessed for condition score and conformation. Records were obtained for 6,356 lambs on finishing live weight (FWT), ultrasonic muscle depth (UMD), ultrasonic fat depth, overall condition score (OCS), and conformation of gigot, loin and shoulder. Ultrasonic fat depth was log transformed (logUFD) to approach normality. High index sired lambs were heavier at finishing (1.2 ± 0.2 kg) with thicker UMD (0.7 ± 0.2 mm) and less logUFD (0.08 ± 0.01 mm) ($P < 0.05$). There were no differences in OCS or conformation based on the sire index or breed ($P > 0.08$). Suffolk sired

lambs were heavier than Charollais (1.0 ± 0.3 kg), which were heavier than Texel (0.9 ± 0.3 kg) ($P < 0.001$). Texel sired lambs had thicker UMD than Charollais (0.7 ± 0.2 mm; $P < 0.001$), but were not different than Suffolk. Charollais sired lambs had higher logUFD than both Texel (0.098 ± 0.016 mm) and Suffolk (0.061 ± 0.017 mm) sired lambs ($P < 0.001$). Within a breed, high and low index sired lambs differed in performance with the exceptions of FTW and UMD in Suffolks. Index selection produced heavier and leaner lambs at finishing. Producers have flexibility in choosing the terminal sire that best fits their production system.

Keywords: crossbred lambs, index selection, lamb performance, terminal sire

INTRODUCTION

There has been growing preference among consumers for leaner meats (Woodward and Wheelock, 1990; Webb and O'Neill, 2008). This has particularly impacted the competitiveness of lamb, which has been considered overly fatty. As a consequence, selection programs in terminal sire sheep have focused on reducing excess fatness (Simm et al., 2002).

Lambs from breeds that have historically generated terminal sires account for 70% of the lamb crop in the UK (Pollott and Stone, 2004). The most widely used breeds are Charollais, Suffolk and Texel. Therefore, genetic improvement in these breeds should substantially impact market animals. A lean growth index was adopted by the UK terminal sire sheep industry to improve the lean content of the carcass (Simm and Dingwall, 1989). Although there have been clear benefits within experimental populations (Lewis et al, 1996; Simm and Murphy, 1996; Simm et al. 2002), evidence from commercial settings is more limited (Márquez et al., 2012).

In the UK many terminal sire flocks are managed intensively. This benefits the efficacy of selection by avoiding constraints on growth within that environment. More intensively managed young rams also can be marketed earlier, which lowers production costs and decreases

their generation interval. Commercial lambs, however, are reared at grass, which can be growth limiting. Thus it is necessary to test if genetic improvement in one environment translates to gains in the other.

The objectives of this study were to test: (i) whether index selection within the terminal sire industry has improved the quality of crossbred lambs at finished condition, and (ii) whether any benefits of that selection are consistent within breeds.

MATERIALS AND METHODS

Animal care and use

The Animal Experiment Committees at the Institute of Biological Environmental and Rural Sciences (**IBERS**), the Scottish Agricultural College (**SAC**), and ADAS UK Ltd (**ADAS**) approved all procedures and protocols used in the experiment.

Animal resources

In each of 1998 to 2000, Scottish and Welsh Mule ewes were developed from the matings of Bluefaced Leicester rams with Scottish Blackface and (Welsh) Hardy Speckled Face ewes (van Heelsum et al., 2003, 2006; Mekkawy et al., 2009). Following weaning in each of those years, the ewes were distributed among 3 research farms in the UK: Rosemaund, England; Edinburgh, Scotland; and, Aberystwyth, Wales. The ewes were first bred to terminal sire rams to lamb at approximately 2 years of age.

From 1999 to 2002 the ewes were mated to rams from the Charollais, Suffolk, and Texel breeds. The rams originated from their breeds' sire referencing schemes and were selected according to a lean growth index designed to increase carcass lean growth, while constraining fat growth at a constant age end point (Simm and Dingwall, 1989). The rams used were chosen from

the top and bottom 5% of available rams with index scores, and categorized as ‘high’ and ‘low’ lean growth index categories. Index score of high index rams was 198 ± 8 points higher than that of low index rams, and their EBV for index traits differed. Weight EBV was 6.6 ± 0.5 kg greater, ultrasonic muscle depth (**UMD**) EBV was 2.3 ± 0.2 mm larger, and ultrasonic fat depth (**UFD**) EBV was 0.49 ± 0.12 mm smaller in high versus low index rams (Márquez et al., 2012).

Sires were used for two breeding seasons, and moved between the three farms to create genetic links among farms and years. After their first breeding season, one third of rams stayed at their current farm while two thirds were moved to another farm. This ensured that performance from crossbred lambs born in different locations, and to different dam breeds, could be fairly compared. Both ewe breeds were represented in each farm and year, thus avoiding confounding. Details of the mating design and husbandry were provided by Márquez et al. (2012).

Production and finishing of crossbred lambs

At birth, each lamb had its ancestry, sex, and weight recorded. If a ewe had more than two lambs, any surplus lambs were fostered. Ewes and their lambs were turned out to pasture within 48 h after birth.

Early growth and gain of these lambs was considered previously (Márquez et al., 2012). In this study, from approximately 10 weeks, lambs were scored for fat cover every two weeks. They were harvested upon reaching a target finished condition of 3L fat score, which was assessed subjectively by feel (as for condition scoring) and corresponds to approximately 11% subcutaneous fat (Kempster et al., 1986). This approach was adopted to harvest lambs at comparable levels of physiological maturity. Since lambs of different breed types were being compared, comparisons at fixed maturity levels was deemed more appropriate to evaluate potential differences in body composition.

Once finished, lambs were weighed, scored for condition and conformation, and ultrasonically scanned. Overall condition (**OCS**) was scored on a scale from 1 to 5 in ½ point intervals, where a higher score indicated better condition (fatness). Shoulder (**CONS**), loin (**CONL**) and gigot (**CONG**) conformation were scored on a scale of 1 (poor) to 6 (superior) in ½ point intervals. Muscle depth was ultrasonically measured at the deepest point of the eye-muscle (*m. longissimus lumborum*) at the third lumbar vertebra while UFD was measured at the same position, and at 1 and 2 cm lateral to it and then averaged. Once finished, lambs were processed at a commercial abattoir. Data were available on 6,356 lambs over the four years of the experiment.

Statistical analysis

Weight and ultrasound scanning.

The distribution of the data for finished live weight (**FWT**), UMD, and UFD was investigated. Skewness, kurtosis and normality were evaluated. Significant non-normality was detected only for UFD, and the Box-Cox procedure (Box and Cox, 1964) was applied to define a parsimonious transformation. The log-likelihood was maximum with a log transformation, which was applied. A log transformation also was used previously for this trait (van Heelsum et al., 2001; Husain et al., 2007).

The FWT, UMD, and log transformed UFD (**logUFD**) data were analyzed with SAS software (Version 9.2; Cary, NC) fitting a linear mixed model. Fixed effects were sire index category (high or low) and sire breed (Charollais, Suffolk or Texel), and their interaction, sex (wether or ewe lamb), dam breed (Scottish or Welsh Mule), age of dam (2 to 5 yr), farm and birth year, and their interaction. A combined birth-rearing rank effect was fitted with four categories: single born/single reared, twin or more born/single reared, single or twin born/twin

reared, and triplet or quadruplet born/twin reared. No interaction between sire and dam breed was detected in preliminary analyses and therefore it was omitted from the final model fitted. Random effects were rearing dam, sire nested within breed and index category, and the residual. Variance components were estimated simultaneously in the analysis. The covariates included in the model depended on the trait. For FWT and UMD the estimated subcutaneous fat percentage of the carcass was fitted; it was centered to the target finishing condition of 11% subcutaneous fat cover (Kempster et al., 1986). For logUFD lamb age at measurement was the covariate.

Least squares means were estimated and mean comparisons were conducted with a Tukey-Kramer adjustment for multiple comparisons. Statistical significance of fixed effects was tested using partial sums of squares. Differences between index categories were tested within breeds.

Condition scores.

Condition (OCS) and conformation (CONS, CONL, CONG) scores were subjectively measured ordered categorical variables, and their distributions did not approach normality. Therefore they were analyzed using a generalized linear mixed model. A multinomial distribution was fitted with a logit link function using ASReml (Gilmour et al., 2009). The fixed effects in these models were sire index category and sire breed, along with their interaction, sex, dam breed, age of dam, farm, birth year, and age at measurement as a covariate. The interaction between farm and birth year was not fitted because some scores did not occur in all farm-birth year combinations. Sire nested within index category and breed was fitted as a random effect. Rearing dam was not included as a random effect in this model because a likelihood ratio test indicated it did not define significant variation in any of these scores.

RESULTS

Performance at finished condition

Sire index and breed were significant sources of variation for FWT, UMD, and logUFD ($P < 0.001$). Their interaction was significant for logUFD ($P = 0.02$) and FWT ($P = 0.007$). This interaction in logUFD was due to the difference between lambs sired by high and low index Charollais rams being greater (0.14 ± 0.02) than that in the other two breeds (on average 0.03 ± 0.01 ; Figure 3.1). For FWT, the differences between breeds were greater within low as compared to high index sired lambs. Still, there were no re-rankings among index categories from any breed for any trait.

High and low index sired lambs differed ($P < 0.001$) for FWT, UMD and logUFD, as reported in Table 3.1. High index sired lambs were 1.2 ± 0.2 kg heavier at finishing, with 0.7 ± 0.2 mm greater UMD, and 0.08 ± 0.01 mm lesser logUFD (1.21 mm less UFD). Suffolk rams sired heavier lambs than Charollais (0.96 ± 0.26 kg), which sired heavier lambs than Texel (0.85 ± 0.26 kg) ($P < 0.01$). Suffolk and Texel sired lambs did not differ in either UMD or logUFD. However, Charollais sired lambs had less UMD than Texels (0.66 ± 0.17 mm; $P < 0.001$), and more logUFD than both Texel (0.098 ± 0.016 mm; $P < 0.001$) and Suffolk (0.061 ± 0.017 mm; $P < 0.001$) sired lambs.

Although lambs sired by high index Suffolk rams were numerically heavier with thicker UMD than their low index contemporaries, these differences were not significant. Only for logUFD were significant differences observed ($P = 0.02$), with lambs sired by high as compared to low index Suffolk rams being leaner (-0.056 ± 0.024 mm logUFD). Significant differences between high and low index Suffolk sired lambs were not found in the earlier growth of these lambs either (Márquez et al., 2012). However, in the other two breeds, high and low index sired

lambs differed, with high index sired lambs being heavier with thicker ultrasonic muscle depth and thinner ultrasonic fat depth ($P < 0.01$).

Breed of the dam affected all traits ($P < 0.001$). Lambs from Scottish Mules were heavier at finish, but had less UMD and logUFD than lambs from Welsh Mules (Table 3.1). The age of the dam defined variation in FWT ($P < 0.001$), but not in UMD ($P = 0.7$) or logUFD ($P = 0.6$). The birth-rearing category explained variation in FWT and logUFD ($P < 0.001$), but not in UMD ($P = 0.9$) (results not shown).

An interaction between year and location was observed in all traits ($P < 0.001$). There was no clear pattern to this interaction, although in the first year of the experiment all ewes were primiparous 2-year-olds with the finishing weights of lambs lower than in later years ($P < 0.01$). In general, lambs born in Scotland were heavier at FWT than those born in the other locations.

Finished condition score and conformation

Most lambs (47%) had OCS of 3. The OCS scores did not differ with respect to sire index category ($P = 0.8$), sire breed ($P = 0.08$), or their interaction ($P = 0.9$). However, OCS was affected by farm and birth year of the lamb ($P < 0.001$).

The most common score for all three conformation measures was 4 (CONS: 52%; CONL: 48%; CONG: 44%). Sire breed, index category, and their interaction did not define variation in any of the conformation scores ($P > 0.2$), although the age of the dam and birth year of the lamb did ($P < 0.001$); farm explained variation in both CONS and CONG ($P < 0.001$).

DISCUSSION

Performance at finished condition

Sire index and breed

High index sired lambs performed better than low index sired lambs for FWT, UMD, and logUFD (Figure 3.1), in agreement with previous results. After 9 years of selection with this index, sheep weighed 4.9 kg more, had 1.1 mm less UFD and 2.8 mm thicker UMD at 150 days of age than an unselected line (Simm et al., 2002). Furthermore, these changes in index score have resulted in economically desirable changes in composition: carcasses have proportionally more lean and less fat contents (Lewis and Emmans, 2007).

High and low index Suffolk sired lambs did not differ in FWT or UMD, which was consistent with their earlier growth (Márquez et al., 2012). This was not the case for the other two breeds. We have hypothesized that seasonal or nutritional constraints did not allow these lambs to reach their full genetic potential. Husbandry also may have been more intensive on purebred farms – the source of the rams used in this study – than at the commercial farms on which the crossbred lambs were reared. This may have been more pronounced in the Suffolk breed, with the consequence that their offspring were not able to perform as well as anticipated (Márquez et al., 2012). These results were not expected since persistent differences between a Suffolk line selected on the same index, relative to its control, have been reported (Simm et al., 2001, 2002; Lewis and Emmans, 2007).

Lambs in this study were finished to a constant fatness to compare them at similar degrees of physiological maturity. Since the lambs differed in genetic background, reflecting crosses of several sire and dam breed-types, this approach avoided inferring differences in body composition among them simply as an artifact of differences in mature size. Furthermore,

although other endpoints are also used commercially (e.g., age, weight), a target fat level is by far the most common within UK systems.

Although the differences between high and low index sired lambs were relatively small in an absolute scale, they were observed and would translate to increased profits for producers. Forming predictions of the performance of crossbred offspring of purebred rams is difficult. The purebred rams used in this experiment were selected on criteria measured at a fixed age, with high index rams allowed to reach heavier (mature) weights. Their crossbred offspring were finished to a constant fatness, with progeny of high index rams being heavier. Even if it were possible to account for nutritional and other environmental differences between purebred and crossbred farms, it is not clear what the exact translation between purebred selection and their crossbred progeny performance should be.

No interaction between sire and dam breed was identified for any measure, which suggests that our results may apply to other terminal sire breed crosses. This lack of an interaction agrees with most previous literature (Cameron and Drury, 1985; Freking and Leymaster, 2004; Hopkins et al., 2007). However, Kempster et al. (1987) did identify such an interaction, although they considered more diverse sire and dam breeds in their study. The absence of sire-dam interaction may not be surprising for traits measured in lambs after weaning, as maternal effects wane. Maternal heritabilities for UMD and UFD have been generally found to be low and in some cases not different from zero (Larsgard and Olesen, 1998; Husain et al., 2007).

Environment.

Environmental contributions to finishing characteristics are important, but their explicit cause often is difficult to identify. However, there are exceptions. Often, primiparous ewes will rear

smaller offspring, as was the case here, and in the growth from birth to 10 weeks of these lambs (Márquez et al., 2012). Conington et al. (1998) suggested that differences between locations may be greater than those between years, but that both significantly affect finishing traits.

Ultrasonic measurements

Ultrasound provides a way to predict carcass characteristics prior to slaughter, which then can be used to delineate genetic differences in carcass merit among animals (Wilson, 1992). This tool has been successfully used in sheep, at relatively low cost (e.g., Kvame and Vangen, 2007; Emenheiser et al., 2010). Kvame and Vangen (2007) obtained genetic correlations of 0.70 ± 0.13 between UMD and carcass lean muscle content, and of 0.82 ± 0.10 between UFD and carcass fat content. In our case, index selection resulted in lambs with thicker UMD and thinner UFD, which, according to these correlations, would translate into increased lean and reduced fat contents of the carcass. This was the goal of the index, and provides economic benefit to producers.

Finished condition score and conformation

Conformation at marketing is evaluated subjectively, but is important in determining the value of lamb. The lack of differences in the conformation of high and low index sired lambs indicates that selection for lean growth will, at least, not adversely affect conformation avoiding potential discounts at harvest. Live conformation score depends on both muscling and fat (Lewis et al., 1996; Jones et al., 1999; Navajas et al., 2008). Positive genetic correlations have been found between logUFD, UMD, and OCS, indicating that selection for UMD may improve conformation, but selection against logUFD could lead to a decrease in conformation score (van Heelsum et al., 2001). These antagonisms were not apparent from the index selection characterized in this experiment, nor were breed differences observed.

Conformation should be predictive of carcass composition but this correlation was found to be low (Jones et al., 1999). Van Heelsum et al. (2003) reported that live conformation of sires was uncorrelated to the lean and fat contents of their crossbred offspring's carcasses. Similarly, Mekkawy et al. (2009) estimated a heritability of 0.11 (95% confidence region of 0.02 to 0.19) for the conformation scores in the dams of lambs in this study. Although conformation is one of the measures used for determining the price of lambs in the UK, it is likely not a good indicator of carcass composition.

Overall condition score at finishing also is measured subjectively, and is intended to reflect differences in fatness alone. It has been found to be correlated with subcutaneous and intermuscular fat in the lumbar region (phenotypic correlation of 0.76; Frutos et al., 1997), but an inaccurate predictor of body composition generally (Frutos et al., 1997; Lambe et al., 2008). Mekkawy et al. (2009) estimated a moderate heritability (0.24; 95% confidence region of 0.12 to 0.37) for condition score pre-mating for the dams of lambs in this study. Selection on the lean growth index did not change the OCS of lambs, which may be due to the constant fatness endpoint used in this experiment. Other studies have found that ultrasonic measures and FWT are better indicators of carcass quality than condition or conformation scores (e.g., Lambe et al., 2008), and ultrasonic measures may be even better. Although conformation and condition scores are primary measures upon which lambs are selected to be slaughtered, other objective measures may be more reflective of actual carcass quality.

In conclusion, the results of this study indicate that selection in terminal sire breeds for lean growth rate improves finishing characteristics in their crossbred progeny. Differences in the performance of crossbred lambs sired by purebred high and low index rams were less than anticipated based on differences in the EBV of their sires. This justifies re-evaluation whether

current breeding programs are optimal for improving crossbred progeny performance at grass. However, forming clear expectations is challenging: beyond inheriting only one half of their sires' genes, crossbred lambs are reared under different conditions and are evaluated (harvested) at different endpoints. Still, differences among sire breeds in weight and ultrasound measures exist, indicating that producers have flexibility in choosing the terminal sire breed that best suits their production system. No differences were found among sire breeds or index category in conformation or condition score; relative to weight and ultrasound, their value in characterizing differences in carcass composition seems equivocal. Therefore, selection decisions based on objective evaluation of lean growth, as captured in the lean growth index, provides a more reliable approach for improving carcass quality in lamb.

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Table 3.1. Adjusted least squares means for finishing traits in crossbred lambs by sire index and breed, and dam breed¹

	No. ²	FWT ± SE, kg	UMD ± SE, mm	logUFD ± SE, mm
Sire breed				
Charollais	2282	41.3 ± 0.2 ^b	24.3 ± 0.1 ^b	1.41 ± 0.01 ^a
Suffolk	1968	42.2 ± 0.2 ^a	24.6 ± 0.1 ^{ab}	1.35 ± 0.01 ^b
Texel	2106	40.4 ± 0.2 ^c	24.9 ± 0.1 ^a	1.31 ± 0.01 ^b
Sire index				
High	3170	41.93 ± 0.2 ^a	25.0 ± 0.1 ^a	1.32 ± 0.01 ^b
Low	3186	40.73 ± 0.2 ^b	24.3 ± 0.1 ^b	1.40 ± 0.01 ^a
Dam breed				
Scottish Mule	3020	42.1 ± 0.2 ^a	24.9 ± 0.1 ^b	1.35 ± 0.01 ^b
Welsh Mule	3336	40.5 ± 0.2 ^b	25.5 ± 0.1 ^a	1.37 ± 0.01 ^a

^{a-c}Within a column, means without a common superscript differ ($P < 0.05$).

¹FWT = finishing weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth.

²No of lambs within each category.

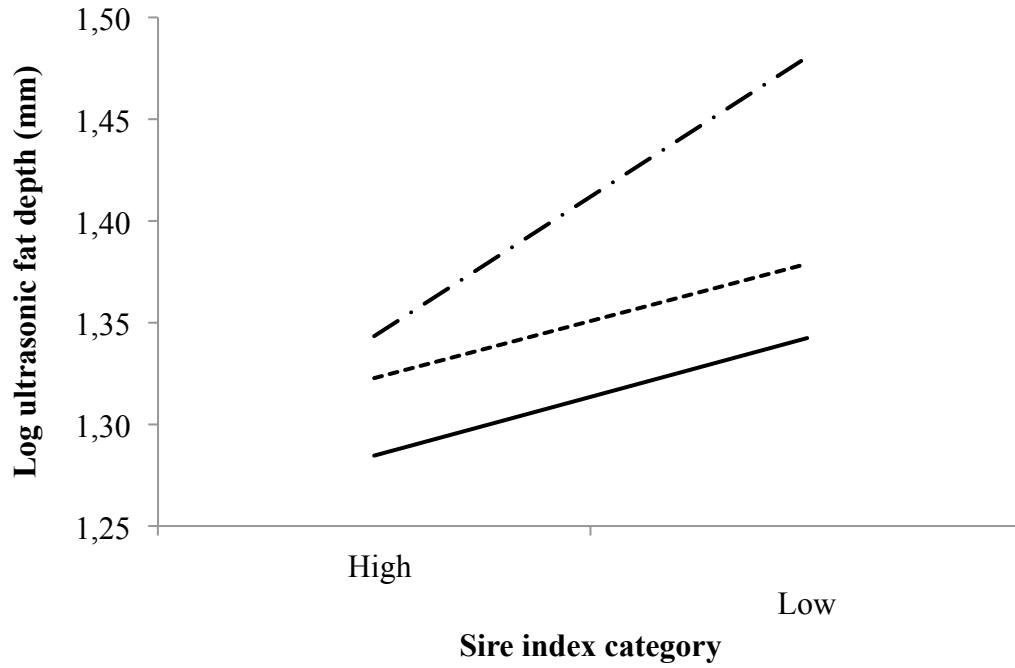


Figure 3.1. Adjusted means for logarithmic ultrasonic fat depth of lambs sired by either high or low index sires of the Charollais (dotted and dashed line), Suffolk (dotted line), and Texel (solid line) breeds.

Chapter 4: Genetic evaluation of days to harvest in crossbred lambs

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ABSTRACT

Days to harvest (**DTH**) is the number of days a lamb is fed before reaching a target level of fatness. Although economically relevant, this trait has not been thoroughly evaluated in sheep. Most lambs harvested in the UK are crossbreds sired by purebred terminal sires, with Charollais, Suffolk and Texel most commonly used. Sires from these breeds were selected on an index designed to increase lean growth while constraining fat. The purpose of this research was to (i) evaluate the effects of index selection in terminal sires on DTH, and (ii) evaluate the feasibility of incorporating DTH into genetic evaluation programs. Charollais, Suffolk, and Texel sheep had participated in sire referencing schemes, where genetic links among flocks were established by sharing rams. Rams with high or low index scores were chosen from these schemes, and mated to crossbred ewes at 3 farms in the UK. Lambs were harvested at a target 11% subcutaneous fat. Records on DTH from 6,350 lambs were analyzed in two ways: (i) as time to harvest fitting a survival model; and, (ii) as a normally distributed variable in a bivariate analysis with weight at harvest. The survival analysis was stratified by rearing type (single/twin). In both approaches, sires were fitted using a multivariate normal distribution with a relationship matrix. Regardless of model fitted, sire index did not affect DTH ($P > 0.10$). However, Texel-sired lambs reached harvest faster ($P < 0.01$) than either Charollais- or Suffolk-sired lambs, although DTH in those two breed-types did not differ ($P > 0.1$). Ewe lambs reached harvest faster than wethers ($P < 0.01$). Lambs from older ewes were harvested faster ($P < 0.001$). The heritability of DTH was 0.21 from the survival model, and 0.20 from the bivariate model. Rank correlation of sire EBV

between methods was 0.9 suggesting strong agreement. The use of high or low index sires did not extend DTH in lambs harvested at a target fatness. Importantly, there is no antagonism between improving carcass merit and extending the grazing season. Furthermore, DTH is moderately heritable. If economically justified within a breeding program, it could be reduced through genetic selection.

Keywords: crossbred lambs, days to harvest, genetic evaluation, index selection, survival analysis.

INTRODUCTION

Days to harvest is an economically relevant trait (Golden et al., 2000) that measures how many days a lamb is fed before reaching a target level of fatness. Longer finishing periods often can increase costs because of the need to provide supplementary feed after the end of the normal grazing season. Given that this trait may substantially affect the efficiency of production systems, a thorough investigation and genetic analysis of DTH is appropriate. Although growth rate has been extensively studied in sheep (e.g., Safari et al., 2005) and influences DTH, DTH has not been evaluated.

We investigated two approaches to genetic evaluation of DTH. In our first approach, our intent was to quantify the risk, or probability, that a lamb would be harvested at a given time. Survival analysis (Kalbfleish and Prentice, 2002) provides a method for doing so. By considering DTH as a time to an event, we determined whether the probability that lambs were harvested at a given age differed among sires. Survival analysis has been used previously in sheep to model traits such as lamb survival time (e.g., Leeds et al., 2012), but not time to a harvest end-point. Thus, this application is unique.

However, there are disadvantages to survival analysis. It is difficult to conduct a multivariate analysis to account for correlations with other traits and potential bias from selection for those traits. For this reason, our second approach was to fit a bivariate model of DTH, in which it was assumed to be normally distributed, and weight at harvest.

Given the likely economic importance of DTH, the objectives of this study were twofold: (i) to evaluate the effects of index selection and terminal sire breed on DTH; and, (ii) to ascertain whether genetic evaluation of DTH is feasible in terminal sire sheep using either survival analysis or bivariate methods.

MATERIALS AND METHODS

The Animal Experiment Committees at the Institute of Biological Environmental and Rural Sciences, the Scottish Agricultural College, and ADAS UK Ltd approved all procedures and protocols used in the experiment.

Data description

Lambs were reared on pasture and from 10 weeks of age were assessed for harvest condition every two weeks. The DTH was defined as the number of days between a lamb's birth and its harvest at a subjective target condition score of 3L, corresponding to approximately 11% subcutaneous fat by visual evaluation (Kempster et al., 1986). To score for body condition, lambs were restrained and assessed for fatness by palpation of the vertebral process and ribs. Lambs were reared to a common fatness level in order to compare them at the same physiological maturity. Further details of husbandry and mating have been given previously (Márquez et al., 2012, 2013).

Records of DTH were obtained on 6,350 lambs born from 1999 to 2002. Lambs were from matings of Scottish and Welsh Mule ewes with Charollais, Suffolk, and Texel terminal sires, as previously described (van Heelsum et al., 2003; Márquez et al., 2012). Terminal sire breeding accounts for 70% of lambs harvested in the UK, and the most widely used breeds are Charollais, Suffolk, and Texel (Pollott and Stone, 2004). The rams used were obtained from their breed's sire referencing schemes (Simm et al., 2001). Selection was based on a lean growth index designed to increase carcass lean growth, while constraining fat growth at a constant age end point (Simm and Dingwall, 1989). After approximately a decade of sire referencing, rams from the top and bottom 5% of these schemes were chosen. High index rams differed by 198 ± 8 index points (4.6 SD) from low index rams, and had higher live weight and ultrasonic muscle depth EBV, and lower ultrasonic fat depth EBV than low index rams (Márquez et al., 2012). Most rams were used for 2 breeding seasons and were moved between 3 farms in the UK (in England, Scotland and Wales). Genetic links among farms and years were created by relocating rams to different farms after 1 breeding season. In total, 94 rams were used for mating, approximately half from each index category. Each of the 3 terminal sire breeds contributed approximately one third of the rams.

Statistical modeling

The distribution of DTH was highly skewed, and no suitable transformations were found to approximate normality. We attempted to fit a generalized linear model to these data using Weibull, Gamma, and Poisson distributions. In all cases, based on the Anderson-Darling goodness of fit test (Anderson and Darling, 1952), the fit was poor ($P < 0.01$). This finding was confirmed by visual assessment of the fit of these distributions. A zero inflated Poisson

regression, setting the earliest DTH as zero, was also attempted; the fit was again poor ($P < 0.01$).

Underlying these distributional issues was the fact that single- and twin-reared lambs differed substantially in DTH (Figure 4.1). Single-reared lambs reached harvest fatness earlier than twin-reared lambs, but over a wider age range. There were 1,274 lambs reared as singletons and 5,076 lambs reared as twins.

Survival analysis

The DTH is a measure of time to an event (harvest), which can be analyzed using a survival model. Formally, the survival function is the probability that an animal i survives to time t (Kachman, 1999). We estimated the survival function with a Kaplan-Meier survival curve (Kaplan and Meier, 1958), which quantifies the probability of surviving to a point in time given the cumulative probability of surviving in the preceding time intervals. It also accounts for censoring. However, since all lambs had a harvest date, there was no censoring in these data.

The hazard can be modeled in several ways, although the Cox (Cox, 1972) and Weibull (Kalbfleish and Prentice, 2002) proportional hazards models are most commonly used. The Cox model is semi-parametric: it makes no distributional assumption on the hazard function. The Weibull model assumes that the hazard function has a Weibull distribution. We investigated the appropriateness of the Weibull model and found that the fit to the data was poor. Therefore all analyses were performed using the Cox proportional hazards model.

The Cox proportional hazards models were fitted with the Survival Kit v6.0 (Ducrocq et al., 2010). The model fit was:

$$h(t, X, Z) = h_{0_g}(t) \exp(\mathbf{X}'\beta + \mathbf{Z}'u)$$

where X is an incidence matrix for fixed effects, β are fixed effects coefficients, Z is an incidence matrix for random effects, and u is a vector of random coefficients. The baseline hazard, $h_{og}(t)$, was stratified by rearing type (the o subscript designates the baseline hazard and g designates the rearing type, single or twin). This was done because baseline hazards of each group were different, as evident from their distributions (Figure 4.1).

Fixed effects in the model were sire index category, sire and dam breed, age of dam, sex of lamb, birth year, farm, and birth year-farm interaction. Both dam breeds were represented in all farms, avoiding confounding of dam breed with farm. Estimated subcutaneous fat percentage at harvest, based on condition score, was fitted as a covariate. Other two-way interactions, including sire breed by index category, were tested but were unimportant ($P > 0.1$).

Sire was fitted as a random effect with a multivariate normal distribution with mean zero and variance $A\sigma_s^2$, where σ_s^2 is the sire variance and A is the relationship matrix among sires. The pedigree used to form the relationship matrix included the 94 sires of the crossbred lambs, along with 75 paternal grandsires and 94 paternal granddams. There was no relatedness between sires of different breeds; within a breed, sires of different index categories also were not related. The A matrix therefore was comprised of disconnected subpopulations characterizing the genetic relatedness within the 6 breed-index category sire groups.

The feasibility of combining the sire index-breed groups was evaluated with a likelihood ratio test. The 6 groups formed independent samples, and were analyzed separately with the proportional hazard model described earlier to obtain their log-likelihood. The sum of the 6 log-likelihoods was tested against the log-likelihood of the combined analysis. No difference was found ($P > 0.1$), indicating that the combined analysis was equivalent to separate analyses of

each index-breed group. Furthermore, the estimates of sire variances for each subset were similar to that obtained from the combined analysis. We therefore combined the data.

The inclusion of rearing dam as a random effect was tested with a likelihood ratio test, which suggested that it should be added to the model. Rearing dam was assumed to follow a log-gamma distribution, with shape and scale parameter taken to be equal. The use of the log-gamma distribution is mathematically convenient, and tends to a log-normal distribution when parameter estimates are large (Ducrocq, 1997).

Estimates of moments of the posterior distributions of random effects (mean, standard deviation, and skewness) were obtained according to Ducrocq and Casella (1996). An approximate estimate of the heritability (h^2) on a non-logarithmic scale was obtained according to Yazdi et al. (2002) as:

$$h^2 = \frac{4\sigma_s^2}{\sigma_s^2 + \sigma_d^2 + 1},$$

where σ_d^2 is the variance due to rearing dam, calculated as the tri-gamma function evaluated at the posterior mode of the variance of the rearing dam effect. This heritability can be interpreted similarly to heritabilities in standard linear mixed models (Yazdi et al., 2002).

Estimates of sire effects (\hat{s}) were obtained and approximate accuracies (acc) were calculated as:

$$acc = \sqrt{\frac{n}{(n + (4 - h^2)/h^2)'}}$$

where n is the number of observations on a sire. Estimated breeding values of sires were first expressed as a hazard ratio (HR), which is obtained by exponentiating the sire solution. The HR can be thought of as the risk of an event to occur for a certain level of a fixed effect, compared to another level of that fixed effect. A higher HR indicates higher risk of an event occurring, in this

case harvest of the lamb. In addition, EBV were expressed as genetic standard deviations units (\hat{s}/σ_s , where σ_s is the square root of the sire variance), and as expected median DTH of progeny.

Expected survival curves for sires with different EBV were calculated (HR of 0.8 to 1.2, at 0.1 increments). Median days to harvest were obtained for all permutations of fixed effects for each HR, and then averaged. This approach provided expected median DTH for progeny of sires with different EBV.

Bivariate model

Our second approach was to fit a bivariate linear-linear model. The response variables were weight at harvest (**HWT**) and DTH. Lamb's HWT was used as the response even though rams were selected on the lean growth index, because the index is not routinely computed for commercial crossbred lambs. The HWT is a component of the lean growth index, therefore they are highly correlated. Both traits were considered to be normally distributed, and the peculiarity in distributions of single- and twin-reared lambs were ignored.

The fixed effects fitted for both traits were the same as that for the survival model with the addition of rearing type. Subcutaneous fat depth was also still included as the covariate. Similar to the survival model, random effects were sire, rearing dam and residual. The model was fitted and (co)variance parameters were estimated with ASReml (Gilmour et al., 2009). Convergence was assumed when the log-likelihood changed less than 0.002 times the current iteration number, and the estimates of variances changed by less than 1 percent.

Solutions from the survival and bivariate model were compared by obtaining rank correlations between sire EBV obtained from the two methods.

RESULTS

The raw means of DTH for different categories of interest are shown in Table 4.1. The overall mean of DTH was 178 (SD 57) d, and the median DTH was 175 d; the minimum and maximum DTH were 69 and 325 d, respectively. The wide range of DTH was due in part to the long-tailed distribution of single-reared lambs. Table 4.1 and Figure 4.1 show that twin- and single-reared lambs reached DTH following different trajectories, which were not proportional (i.e., not constant over time). The median DTH (estimated from Kaplan Meier survival curve) was 112 for single- and 182 d for twin-reared lambs (Figure 4.2). Seventy-five percent of single- and twin-reared lambs were harvested by 181 and 224 d, and 90% by 241 and 256 d, respectively.

Survival analysis

Design variables hazard ratios

For the survival analysis, differences between groups were estimated in terms of HR. In our study a higher HR is favorable because those animals reached harvest condition in fewer days than the others. Table 4.2 shows estimates of HR for categories of interest. There were no differences in HR for lambs sired by high versus low index sires ($P = 0.5$). Suffolk-sired lambs were chosen as the reference level for sire breed. Texel-sired lambs had a greater hazard than Suffolk- and Charollais-sired lambs ($P < 0.001$), and therefore reached harvest condition earlier than lambs of the other breeds. There was no difference between Charollais- and Suffolk-sired lambs in DTH.

Lambs from Scottish or Welsh ewes did not differ in DTH ($P = 0.8$; Table 4.2). Lambs from younger ewes took longer to reach harvest condition, but there were no differences between lambs from 4- and 5-year-old dams ($P > 0.1$). Ewe lambs reached harvest condition earlier than

wether lambs ($P < 0.001$). There was a strong farm by birth year interaction but no clear pattern was observed to disentangle its likely cause.

Variance component estimates

The mean and the mode of the posterior distribution of the sire variance were 0.065 and 0.061, respectively. Its SD was 0.014. The rearing dam variance component was calculated as the trigamma function evaluated at the estimated shape-scale of the log-gamma distribution. The mean and mode were 0.137 and 0.138, respectively. Its SD was 0.017. The heritability of DTH was estimated as 0.21.

The mean HR for sires with EBV in the top and bottom 10% of the population was 1.17 and 0.84, respectively, which corresponded with genetic standard deviation units of 2.41 and -2.68. For a HR of 1.17, the expected median DTH for single-reared lambs was 114 d and for twin-reared lambs was 167 d. For a HR of 0.84, these values were 123 and 178 d. Approximate accuracies ranged from 0.26 to 0.92.

As an illustration of the consequence of sire genetic differences in survival rate, expected survival curves for Suffolk and Texel sires were calculated. These are shown for twin ewe offspring from a contemporary group born in 2003 to Scottish Mule dams in Scotland (Figure 4.3). Sire hazard ratios of 0.8, 1.0 and 1.2 were assumed. As expected, DTH decreased with increasing sire HR. The median DTH for Suffolk sires with a HR of 0.8 was 159 d, with a HR of 1 was 151 d, and with a HR of 1.2 was 145 d. For Texel rams, the median DTH was 147 d with a HR of 0.8, 139 d with a HR of 1.0, and 133 d with a HR of 1.2.

Bivariate model

Design variable solutions

In the bivariate model there were no differences between high- and low- index sired lambs for DTH ($P = 0.17$). Index differences were observed for HWT, with high index sired lambs being 0.46 kg heavier than low index sired lambs. There were no differences between Suffolk and Charollais sired lambs in DTH ($P > 0.10$), although Texel-sired lambs reached harvest condition on average 12 d faster than Suffolk- or Charollais- sired lambs ($P < 0.01$). At finishing, Suffolk-sired lambs were heavier than Charollais- and Texel-sired lambs. Charollais-sired lambs were heavier than Texel-sired lambs. These results are similar to those reported in Márquez et al. (2013) for the same data.

Breed of dam defined a significant amount of variation for both traits, with Scottish mules rearing lambs on average 2.2 kg heavier than Welsh mules. Lambs from Scottish mules reached harvest 1.6 d later than those from Welsh mules. The age of the dam also influenced both traits, with older ewes rearing heavier lambs in fewer days ($P < 0.01$).

Variance component estimates. The genetic correlation between DTH and HWT was 0.58 ± 0.10 , and the residual correlation was 0.45 ± 0.01 . The heritability of DTH was 0.20 ± 0.04 , and for HWT 0.19 ± 0.04 . The rank correlation between sire EBV for DTH obtained from the survival and bivariate analyses was 0.9. Among the 5 highest ranking rams (approximately 5%), 4 were the same in both methods.

DISCUSSION

Model selection

Modeling DTH data was challenging because of its highly skewed and non-normal distribution. Attempts were made to transform and to fit alternative distributions to these data (e.g., Gamma, zero inflated Poisson). All of these provided a very poor fit. Because DTH reflects a time to an event (harvest), a survival model was deemed appropriate. Still, there are drawbacks of survival analysis. There are larger computation requirements, which make fitting large animal models difficult. It is not straightforward to include maternal additive effects in the model fitted, or to do multivariate analyses.

In order to account for possible selection for a correlated trait, an alternative to the survival model was to fit DTH as a normally distributed variable in a bivariate analysis. A drawback to this approach is that differences in the distributions of DTH in single- and twin-reared lambs was not intimately modeled.

The non-normality in the distribution of DTH stemmed from the differences between single- and twin-reared lambs (Figure 4.1). There are biological reasons for these differences: single-reared lambs have more resources from their dams, while twins have to compete for these resources to grow. Previous studies (e.g., Tosh and Kemp, 1994) have identified litter size as a factor affecting growth: competition between multiple-reared lambs keeps them from realizing their full genetic potential prior to weaning. Therefore, single-reared lambs have an advantage in growth over twin-reared lambs. There was a wide range of DTH in these lambs, as can be observed from the long tail in the distribution of DTH for single-reared lambs. This result suggests that some single-reared lambs either lacked the genetic potential to take advantage of their favorable environment or simply were unthrifty. This skewness was not year or site

specific, but general for all lambs. The distribution of DTH for twin-reared lambs more nearly approached normality, but still exhibited some skewness.

Index and breed comparisons

Lambs were finished to a fixed fat level so they would be at comparable physiological maturity at harvest. Ideally, animals should be compared at a fixed maturity level because different body tissues grow at different rates (Butterfield, 1988). Under non-limiting conditions, animals will follow a genetically determined path towards maturity: growth rates of bone tissue, followed by lean tissue, would be higher earlier in this trajectory. After reaching maturity, the animals primarily are depositing fat tissue (Lewis et al., 2002a). Therefore, comparing animals at fixed levels of physiological maturity, as approximated by fatness, is more equitable than comparisons at fixed ages or weights (Parks, 1982).

The lack of differences in DTH between lambs sired by high and low index rams in either evaluation model is favorable. Rams were selected on an index that constrained fat growth (Simm and Dingwall, 1989). Therefore it could be expected that lambs sired by leaner (high index) rams would require more time to reach a fixed harvest fatness level than those sired by fatter (low index) rams. Because this was not the case, terminal sire breeders selecting on the lean growth index do not have to be concerned about deleterious consequences on DTH. Likewise, selection for improved carcass merit does not extend the grazing period or potentially require additional feeding after grazing is exhausted, with risk of increasing production costs. This selection index has been used in the UK with favorable results in growth and carcass traits (Lewis et al., 1996; Lewis et al., 2002b).

In both models, Charollais- and Suffolk-sired lambs did not differ in DTH, while Texel-sired lambs reached harvest fatness earlier than either. At harvest, Suffolk- and Texel-sired

lambs did not differ in ultrasonic fatness while Charollais-sired lambs were fatter; in the bivariate analysis, Suffolk-sired lambs were heaviest, followed by Charollais and then Texel-sired lambs, similar to results in Márquez et al. (2013). Some research (Cameron and Drury, 1985; Kempster et al., 1987) suggests that breeds with lighter mature weights tend to reach a level of subcutaneous fat more quickly.

Ewe breed did not define variation in DTH in the survival model. Although significant when DTH was considered normally distributed in the bivariate model, the difference between ewe breeds was small (1.6 d). Such small differences between ewe breeds in DTH is favorable. Maternal heritabilities for growth at and after weaning have been found to be low (Safari et al., 2005), indicating a waning maternal influence at harvest. However, Fogarty et al. (2000) found that the breed of dam is influential in determining the age at which lambs reach harvest condition. That study used Merino and Merino cross ewes, and the authors hypothesized that this reflects the differences in the sizes of the ewes. Our results indicate that UK sheep producers likely have flexibility in choosing Mule (crossbred) ewe types to mate to terminal sires, particularly with regards to DTH.

Genetic evaluation

Our estimates of genetic parameters using either model show that there is variation in DTH. Heritability estimates were moderate, which was expected since it effectively resembles growth rate, with heritability estimates of a similar magnitude. The estimates were also very similar between the two analytical approaches: 0.21 for survival analysis and 0.20 for the bivariate analysis. Safari et al. (2005) reviewed estimates of genetic parameters of sheep and reported heritabilities for weight gain of 0.17 ± 0.01 . These results indicate that there is potential for genetic improvement if DTH was incorporated into a selection program.

Genetic variation in DTH exists among sire breeds, as evidenced by the differences in median DTH of different breeds (Figure 4.3) and, in the survival model, by the HR of sire breeds (Table 4.2). There was a difference of 14 days between median DTH of sires with HR of 0.8 and 1.2, indicative of a range in the finishing period depending on the sire's breeding value. The ranking of sire breeds in DTH was similar in the bivariate analysis, substantiating that differences in harvest periods could be expected across breed-types.

The method used for genetic evaluation of DTH influenced sire solutions. The rank correlation of sire EBV of 0.9 obtained from the survival and bivariate analyses indicated that re-rankings of sires will be present, although they may not be substantial. Both methods have advantages and drawbacks. Survival analysis may better account for differences in rearing types of lambs but is currently restricted to univariate applications. Although less able to model distributional differences between rearing types, multivariate evaluations of normally distributed traits is common in genetic evaluations. Although any selection bias was likely small in these data – all lambs were harvested – it can be addressed with a multivariate approach. Linear models are known to be robust to departures from normality stemming from the central limit theorem. Given the size of these data, the large correlation between EBV may reflect that robustness.

Economic relevance

A considerable amount of the cost associated with finishing an animal is related to the days it spends on feed to reach a desired harvest endpoint. Golden et al. (2000) suggest that DTH is an economically relevant trait in beef cattle, and that genetic evaluation in terms of EBV for this trait would simplify comparing the costs of finishing progeny of different sires (Garrick and

Enns, 2003). Still, an economic evaluation of the profitability of selecting for reduced DTH in sheep systems is needed, given that this has not been done previously.

Days to harvest EBV have been developed for beef cattle, and could be developed for sheep breeding programs. The justification for doing so, however, depends on this trait's economic relevance with respect to other traits affecting growth and harvest attributes. Still, if warranted, the best way to incorporate a DTH EBV would be as part of a selection index that considers these and other components of the breeding objective. The different harvest endpoints used in commercial production would need to be considered in the design of such an index. In the USA, the Gelbvieh beef breed publishes a carcass value index that incorporates estimates of genetic merit for carcass weight, DTH, marbling and rib eye area. These are adjusted to a constant fat endpoint (American Gelbvieh Association, 2011).

From these results we conclude that selection on the lean growth index does not have negative effects on the number of days required for lambs to reach a target level of fatness. Differences between terminal sire breeds exist and can be exploited by producers to select the best rams for their production system. These and previous results (Márquez et al., 2012; Márquez et al., 2013) lead us to recommend wider uptake of index-based selection as a permanent and cost effective way to improve sheep in the UK and elsewhere.

Furthermore, genetic evaluation of DTH using either survival analysis or a bivariate model is computationally feasible. Heritability estimates were similar in both methods and the correlation between sire EBV was high. We are better able to model non-normality and differences in the distribution of single- and twin-reared lambs with the survival analysis. However, if there is selection for other traits, biases cannot be directly addressed. It therefore

may be more pragmatic to include DTH as a normally distributed variable in genetic evaluation programs.

Since DTH was moderately heritable, improvement through genetic selection can be expected. If economically justified, DTH could be incorporated into an index to facilitate reducing the costs of finishing lambs in pasture-based systems.

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Table 4.1. Mean days to harvest of different categories

	No.	Days to harvest \pm SE	Median	Minimum	Maximum
Sire index					
High	3167	179.3 \pm 1.0	179	69	325
Low	3183	176.1 \pm 1.0	173	73	325
Sire breed					
Charollais	2276	181.9 \pm 1.6	181	75	314
Suffolk	1968	181.1 \pm 1.3	178	75	319
Texel	2106	169.9 \pm 1.3	164	69	325
Dam breed					
Scottish Mule	3020	176.0 \pm 1.1	173	69	325
Welsh Mule	3330	179.2 \pm 1.0	177	73	319
Rearing type					
Single	1274	143.1 \pm 1.7	113	69	325
Twin	5076	186.4 \pm 0.7	183	81	325

Table 4.2. Hazard ratios under Cox proportional hazards model of different categories

	Hazard ratio	95% confidence interval		<i>P</i> -value
		Lower	Upper	
Sire index				
Low versus high	0.958	0.850	1.080	0.5
Sire breed				
Charollais versus Suffolk	1.020	0.876	1.187	0.8
Texel versus Suffolk	1.440	1.242	1.671	<0.001
Dam breed				
Scottish versus Welsh	1.054	0.989	1.124	0.1
Sex				
Ewe versus wether	1.130	1.070	1.194	<0.001
Age of dam (yr)				
3 versus 2	1.291	1.193	1.397	<0.001
4 versus 2	1.310	1.182	1.452	<0.001
5 versus 2	1.374	1.188	1.589	<0.001
Subcutaneous fat	1.025	0.976	1.125	0.4

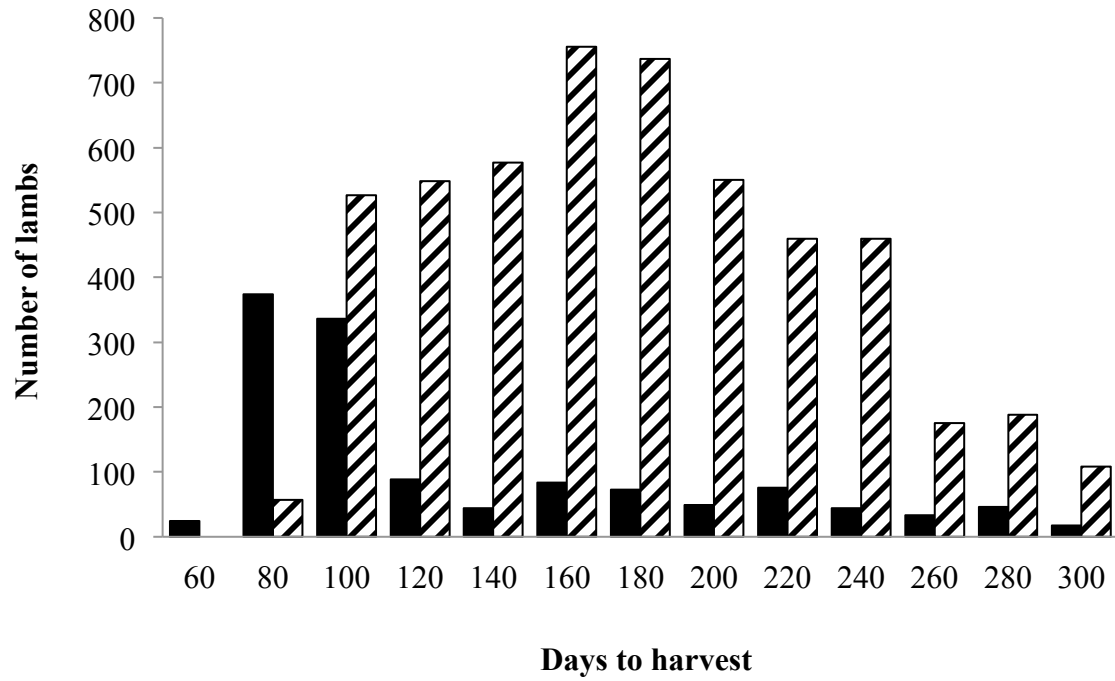


Figure 4.1. Histogram of days to harvest in single- and twin-reared lambs. Twin-reared lambs are represented by dashed black bars, and single-reared lambs by solid black bars.

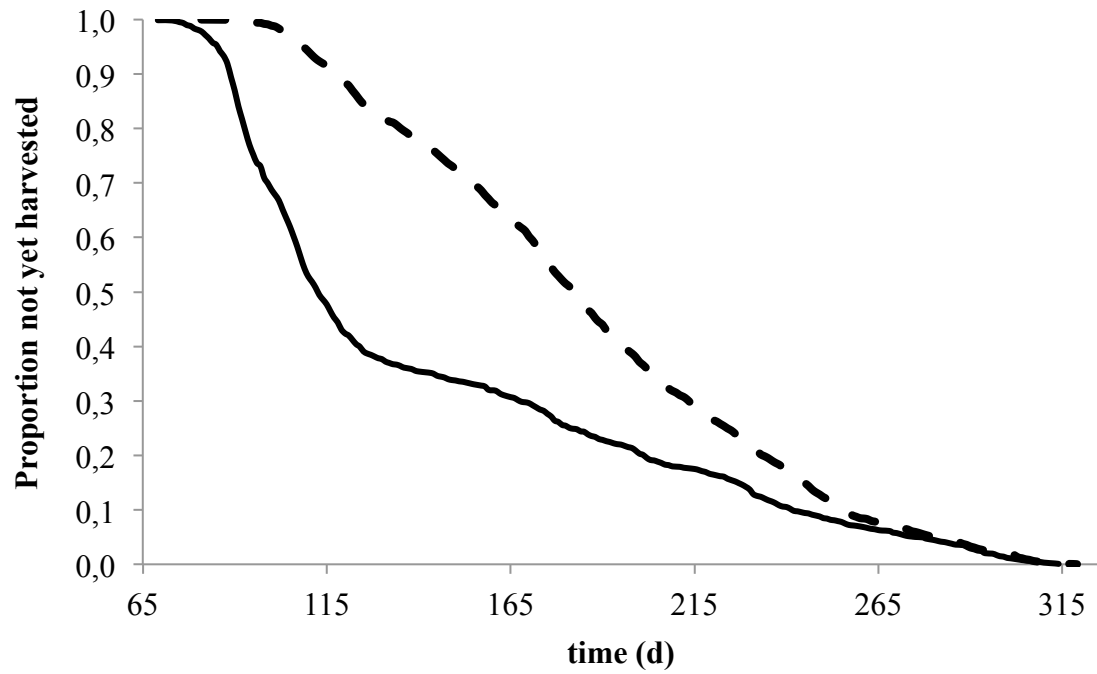


Figure 4.2. Kaplan-Meier estimate of survival function. Twin-reared lambs are represented by the dashed black line. Single-reared lambs are represented by the solid black line.

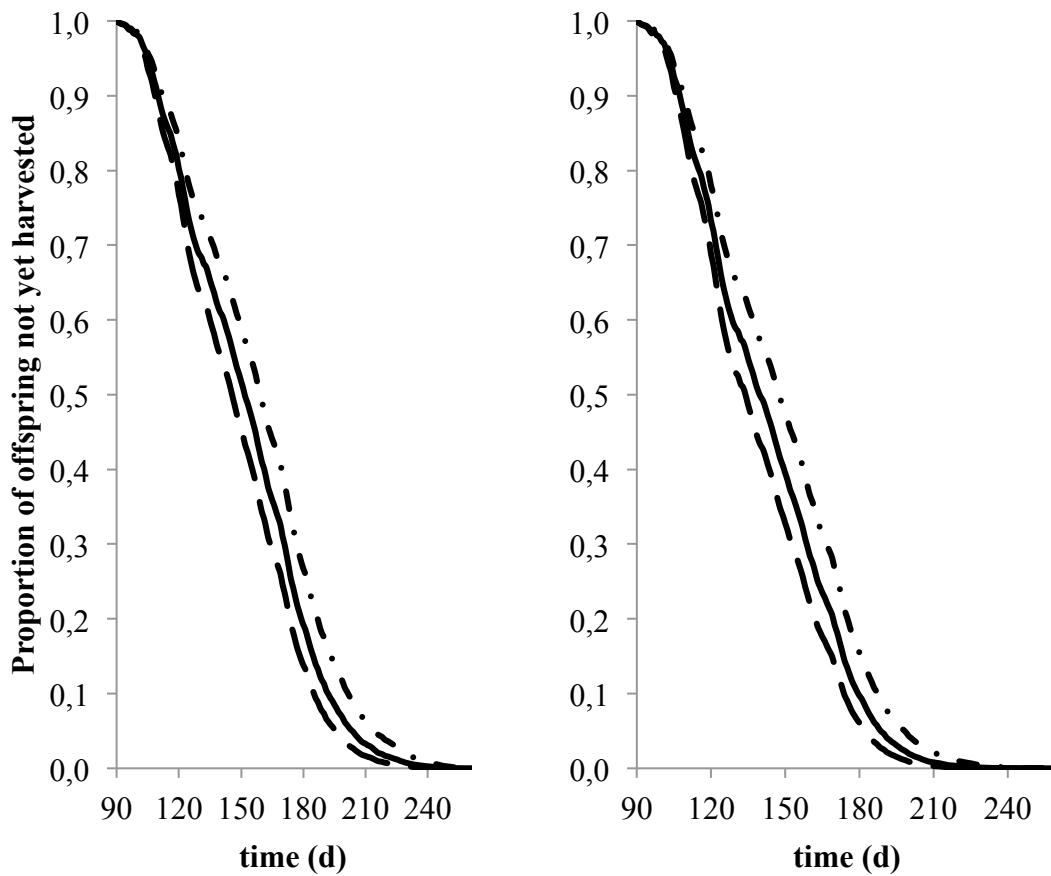


Figure 4.3. Expected survival curves of Suffolk (left) and Texel (right) sires with hazard ratios of 1.2 (dashed line), 1 (solid line), and 0.8 (dashed and dotted line). The illustrations are for twin ewe offspring of these sires from a contemporary group born in 2003 to Scottish Mule dams in Scotland.

Chapter 5: Heterogeneous variances and genetics by environment interactions in genetic evaluation of crossbred lambs

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ABSTRACT

Accounting for environmental heteroscedasticity and genetics by environment interaction (GxE) in genetic evaluation is important because animals may not perform predictably across environments. The objectives of this study were to evaluate the presence and consequences of heteroscedasticity and GxE on genetic evaluation. The population considered was crossbred lambs sired by terminal sires and reared under commercial conditions in the UK. Data on 6,325 lambs sired by Charollais, Suffolk, and Texel rams were obtained. The experiment was done between 1999 and 2002 on three farms located in England, Scotland, and Wales. There were 2,322, 2,137 and 1,866 lambs in England, Scotland and Wales, respectively. A total of 89 sires were mated to 1,984 ewes of two types (Welsh and Scottish Mules). Most rams were used for two breeding seasons with some rotated among farms to create genetic links. Lambs were reared on pasture and had their parentage, birth, 5 wk, 10 wk, and harvest weights recorded. Lambs were harvested at a constant fatness, at which they were ultrasonically scanned for fat and muscle depth. Heteroscedasticity was evaluated in two ways. Firstly, data were separated into three subsets by farm. Within farm variance component estimates were then compared to those derived from the complete data (Model 1). Secondly, the combined data were fitted, but with a heterogeneous (by farm) environmental variance structure (Model 2). To investigate the GxE, a model with a random farm by sire (FxS) interaction was used (Model 3). The ratio of the FxS variance to total variance was a measure of the level of GxE in the population. Heterogeneity in

environmental variability across-farms was identified for all traits ($P < 0.01$). Rank correlations of sire EBV between farms differed for Model 1 for all traits. However, sires ranked similarly (rank correlation of 0.99) for weight traits with Model 2, but less so for ultrasonic measures. Including the FxS interaction (Model 3) improved model fit for all traits. However, the FxS term explained a small proportion of variation in weights (less than 2%) although more in ultrasonic traits (at least 10%). We conclude that heteroscedasticity and GxE were not large for these data, and can be ignored in genetic evaluation of weight but, perhaps, not ultrasonic traits. However, before incorporating heteroscedasticity and GxE into routine evaluations of even ultrasonic traits, their consequences on selection response in the breeding goal should be evaluated.

Keywords: crossbred lambs, genetics by environment interaction, heterogeneous variances, sheep

INTRODUCTION

An animal's phenotype reflects a combination of its genetics and environment. Selection often takes place among animals that are reared in different environments, and animals (and their progeny) may not perform uniformly across environments. Genetic evaluation programs often assume that animals will perform consistently, and that environments will have similar levels of variability. There is a wealth of evidence to show that this is not so, and ignoring it will have unfavorable consequences on genetic evaluation schemes (Robert-Graniè et al., 1999; Mulder and Bijma, 2005).

Differences in phenotypic variances across flocks can arise from differences in production conditions such as management, nutrition, and climate. Such environmental heteroscedasticity (sub-populations having different variances) has been found in several livestock species for a multitude of traits (SanCristobal-Gaudy et al., 2001; Rowe et al., 2006; Nakaoka et al., 2007).

Variable performance levels across flocks can also arise from sensitivities of genotypes to their environmental circumstances (Falconer and Mackay, 1992). Such genotype by environment interactions (**GxE**) have been observed in sheep and other species (e.g. Maniatis and Pollott, 2002; Pollott and Greeff, 2004; Steinheim et al., 2008).

Ignoring environmental heteroscedasticity and GxE can hinder the robustness of genetic evaluations. Accuracy of selection can be affected, leading to decreases in genetic response (Mulder and Bijma, 2005). Variance components may be poorly estimated and EBV biased, leading to re-rankings of animals (Hill, 1984; Garrick and Van Vleck, 1987). These effects can be greater when animals are selected on EBV derived from individual phenotypes, which is the norm in livestock species, rather than on family mean performance (Hill and Zhang, 2004).

In the UK, 70% of the lamb crop has terminal sire breeding, and the predominant breeds are Charollais, Suffolk, and Texel (Pollott and Stone, 2004). Environments in which lambs are reared differ, and by testing sires with progeny in several environments we can better estimate heteroscedasticity, any GxE, and their consequences. Such were the objectives of this study using a population of terminal-sire cross lambs reared under commercial conditions.

MATERIALS AND METHODS

Animal care and use

The Animal Experiment Committees at the Institute of Biological Environmental and Rural Sciences (**IBERS**), the Scottish Agricultural College (**SAC**), and ADAS UK Ltd (**ADAS**) approved all procedures and protocols used in the experiment.

Animal resources

Data on 6,325 crossbred lambs sired by Charollais, Suffolk, and Texel rams were obtained. There were a total of 89 rams, which came from their breed's sire referencing schemes. These are cooperative breeding schemes where reference rams are shared among flocks to create connectedness and facilitate within breed genetic evaluation. The rams were selected according to a lean growth index designed to increase carcass lean growth, while constraining fat growth at a constant age end point (Simm and Dingwall, 1989). Sires were chosen from the top and bottom 5% of available rams based on index score and categorized as 'high' or 'low' lean growth index. High vs. low index rams differed in their EBV: in high index rams, harvest weight (**HWT**) EBV were 6.6 ± 0.5 kg greater, ultrasonic muscle depth (**UMD**) EBV were 2.3 ± 0.2 mm thicker, and ultrasonic fat depth EBV were 0.49 ± 0.12 mm thinner, than in low index rams (Márquez et al., 2012).

Lambs in this study came from mating of the terminal sires to Scottish or Welsh Mules. The Mule ewes were developed from the matings of Bluefaced Leicester rams with Scottish Blackface and (Welsh) Hardy Speckled Face ewes (van Heelsum et al., 2003; Mekkawy et al., 2009). Matings between Mule ewes and terminal sires took place between 1999 and 2002 on three farms in the UK (one each in England, Scotland, and Wales). Most sires were used for two breeding seasons and were physically moved between farms to create genetic links among farms and years (Márquez et al., 2012; Márquez et al., 2013).

All lambs had parentage, along with their birth (**BWT**), 5-wk (**5WT**), and 10-wk (**10WT**) weights recorded. From the time lambs were approximately 10 weeks old they were evaluated for finishing condition every two weeks. They were harvested upon reaching a subjective target fatness score of 3L (approximately 11% subcutaneous fat (Kempster et al., 1986)). Lambs were

finished to a constant fatness so they could be compared at equitable levels of physiological maturity. Upon finishing, lambs' weights (HWT) were obtained, and they were ultrasonically scanned for muscle and fat depth. Their UMD was measured at the deepest point of the eye muscle (longissimus lumborum) at the third lumbar vertebra. Ultrasonic fat depth was measured at the same location and at 1 and 2 cm lateral to it and averaged. When finished, lambs were processed at a commercial abattoir. Further details of design and husbandry are provided by Márquez et al. (2012; 2013).

Genetic groups

A pedigree was assembled, which consisted of 1,325,736 animals. There were six distinct (unrelated) breed types in the pedigree. Each breed type was fitted as a genetic group: one for each terminal sire breed (the sires of the lambs), one for each Mule ewe breed types (the dams of the lambs), and one for the Bluefaced Leicester (the maternal grandsires of lambs). By fitting groups, differences in genetic means among breed types were accounted for, thereby reducing bias in the evaluation (Van Vleck, 1990). All analyses in this study were performed using ASReml (Gilmour et al., 2009).

Heteroscedasticity

The traits investigated were BWT, 5WT, 10WT, HWT, UMD and log transformed ultrasonic fat depth (**logUFD**). Ultrasonic fat depth was transformed to approximate normality. Analyses of the effects of index selection on these traits have been reported previously (Márquez et al., 2012; 2013).

Within farm.

Heteroscedasticity due to farm was tested by creating three subsets of data based on where lambs were born and reared. There were 2,322, 2,137, and 1,866 lambs born in England, Scotland, and Wales, respectively. The model fitted was:

$$y_i = \mathbf{X}_i\beta_i + \mathbf{Z}_{a_i}a_i + \mathbf{Z}_{d_i}d_i + e_i \quad [\text{Model 1}]$$

where y_i is a vector of observations, β_i is a vector of fixed effects coefficients, a_i is a vector of additive animal effects, d_i is a vector of rearing dam effects, and e_i is a vector of random residual effects. The \mathbf{X}_i , \mathbf{Z}_{a_i} , and \mathbf{Z}_{d_i} matrices are incidence matrices relating to observations in β_i , a_i and d_i , respectively. The i subscript refers to data from each of the three farms. Fixed effects were an overall mean, lamb sex (ewe or whether), age of dam (2 to 5-yr), and birth year (2000-2003). For all traits except BWT, a birth-rearing rank effect was fitted with four categories: single born/single reared, twin or more born/single reared, single or twin born/twin reared, and triplet born/twin reared. For BWT, birth rank (single, twin, or triplet) was fitted. Covariates for all traits except HWT and UMD were age at measurement. For HWT and UMD, the covariate was estimated subcutaneous fat percent at harvest. The (co)variance structure of this model was:

$$\text{var} \begin{bmatrix} a_i \\ d_i \\ e_i \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_{a_i}^2 & 0 & 0 \\ 0 & \mathbf{I}\sigma_{d_i}^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_{e_i}^2 \end{bmatrix} \quad [\text{Model 1}]$$

where \mathbf{A} is the numerator relationship matrix among animals in the pedigree and \mathbf{I} is an identity matrix of appropriate dimensions, $\sigma_{a_i}^2$ is the additive genetic variance, $\sigma_{d_i}^2$ is the environmental rearing dam variance, and $\sigma_{e_i}^2$ is the residual environmental variance. Genetic groups were considered in \mathbf{A} . A likelihood ratio test revealed that for harvest traits (HWT, UMD, logUFD) rearing dam did not explain a substantial amount of variation ($P > 0.2$), and therefore for these

traits the rearing dam random effect was omitted. We were unable to fit a maternal additive effect because the pedigree of the dams was limited due to the absence of pedigree recording of Scottish Blackface and Hardy Specked Face hill breeds, the dam breeds of the Mule ewes.

For each trait, log likelihoods for data from each farm were obtained. These are independent samples, and therefore the log likelihoods were summed and compared against a model fitted to the combined data. In the combined model, additional effects of farm and farm by birth year interaction were included. In the absence of heteroscedasticity, the sum of the log likelihoods from the independent samples and the log likelihood from the combined data would be expected to be equal. We used a likelihood ratio test with 2 degrees of freedom. Rank correlations of EBV obtained from the combined and within farm data were obtained to investigate any consequences of variance heterogeneity. Not all sires had progeny on all farms, but for those who did, re-rankings of sires were investigated, and correlations between EBV in the different farms were obtained.

Across farm

The second method to test variance heterogeneity was by fitting heterogeneous residual (farm) variances (Model 2). In this model, the combined data were used, but separate residual variances were estimated for each farm. The fixed effects of Model 1, in addition to farm, and farm by year interaction, were fitted to all the data with a modified (co)variance structure. The (co)variance matrix remained the same as in Model 1, except:

$$\text{var} \begin{bmatrix} a \\ d \\ e_1 \\ e_2 \\ e_3 \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 & 0 & 0 & 0 \\ 0 & I\sigma_d^2 & 0 & 0 & 0 \\ 0 & 0 & I\sigma_{e_1}^2 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_{e_2}^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_{e_3}^2 \end{bmatrix} \quad [\text{Model 2}]$$

where σ_e^2 ($i = 1,2,3$) is the residual variance of farm i . The log likelihood for this model was obtained for each trait, and was tested against a null model with a single residual variance component. We used a likelihood ratio test with 2 degrees of freedom. The consequences of heteroscedasticity were investigated by obtaining rank correlation of EBV calculated assuming either heterogeneous or homogeneous environmental variances.

Genotype by environment interaction

To investigate the presence of GxE we fitted an animal model with a random farm by sire (Fxs) interaction term. Fixed effects were the same as in Model 1. Random effects were animal, farm, Fxs and a random residual. A random rearing dam was fitted for BWT, 5WT, and 10WT.

The (co)variance structure for this model was:

$$\text{var} \begin{bmatrix} a \\ f \\ fxs \\ d \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 & 0 & 0 & 0 \\ 0 & I\sigma_f^2 & 0 & 0 & 0 \\ 0 & 0 & I\sigma_{fxs}^2 & 0 & 0 \\ 0 & 0 & 0 & I\sigma_d^2 & 0 \\ 0 & 0 & 0 & 0 & I\sigma_e^2 \end{bmatrix} \quad [\text{Model 3}]$$

where \mathbf{A} is the numerator relationship matrix, σ_a^2 , σ_f^2 , and σ_{fxs}^2 are the variance components associated with animal, farm, and Fxs, respectively. Other variance components are defined as in Model 1 and Model 2. The Fxs interaction component gives an indication of the amount of GxE in a population (Dickerson, 1962). To test for its significance, a likelihood ratio test was performed by comparing it to a model without the random Fxs interaction term. The ratio of Fxs to total variance was calculated to quantify the extent of GxE in the population.

To investigate whether any GxE was caused by heterogeneous phenotypic variances, traits were standardized to their within-farm variance, and Model 3 was again fitted. Large

differences in variance component estimates and re-ranking of sires in standardized as compared to unstandardized data would indicate the importance of variance heterogeneity.

Connectedness

The study was designed to establish sound genetic links, or connectedness, among farm locations within and across terminal sire breeds and index categories. The strength of those connections was quantified through the use of prediction error correlations (Lewis et al., 2005; Kuehn et al., 2007; 2008), also known as connectedness correlations.

As a point of reference, prediction error (co)variances of EBV for 5WT were derived as in Kuehn et al. (2009). The mixed linear animal model fitted included farm-year combination, sex-birth rearing type combination, and age of dam as fixed effects. The connectedness

correlation (r_{ij}) of Lewis et al. (2005) was derived for farm i and j as:
$$r_{ij} = \frac{PEC(\widehat{\mu}_i, \widehat{\mu}_j)}{\sqrt{PEV(\widehat{\mu}_i)PEV(\widehat{\mu}_j)}}$$

where $\widehat{\mu}_{i.(j)}$ is the mean EBV of all animals in farm $i(j)$, $PEC(\widehat{\mu}_i, \widehat{\mu}_j)$ is the prediction error covariance between these means, and $PEV(\widehat{\mu}_i)$ and $PEV(\widehat{\mu}_j)$ are the prediction error variances of the mean EBV for farms i and j . The same approach was adopted to derive connectedness correlations among breed-index categories. Animals evaluated on the same farm, or connected through common pedigree ties, have a positive prediction error covariance, resulting in higher values of r_{ij} . A heritability of 0.20 was used to calculate the prediction error (co)variances.

RESULTS

Heteroscedasticity

Within farm

When the data were separated by farms, likelihood ratio tests indicated the presence of heterogeneity in the environmental variance for all traits ($P < 0.01$). However, the estimates of total variance and heritability were similar for the combined data, and for within each subset of farm data (Table 5.1).

Rank correlations between lamb EBV with the full data and farm subsets ranged from: 0.77-0.81 for BWT; 0.55-0.93 for 5WT; 0.57-0.74 for 10WT; 0.71-0.82 for HWT; 0.70-0.83 for UMD; and, 0.76-0.95 for logUFD. There were no clear patterns among farms. These rank correlations among lamb EBV were higher than those among sire EBV, likely reflecting the fewer numbers of sires than lambs on individual farms.

Across farm

Allowing for heterogeneous environmental variances among farms (Model 2) provided a better fit to the data for all traits ($P < 0.01$). However, when comparing the additive genetic variances and heritabilities obtained from models with heterogeneous vs. homogenous variance structures, they were within the standard error for most traits (except HWT and UMD) (Table 5.2).

Rank correlations between EBV obtained from the homogenous and heterogeneous variance models were 0.99 for all weight traits (both animals and sires), and 0.88 and 0.84 for UMD and logUFD, respectively, among sires. These results indicate that re-ranking only would

be observed for ultrasonic traits, and likely would not be very substantial. Estimates of heritabilities were similar to the within farm heritabilities of Model 1.

Genotype by environment interaction

For all traits, including a random FxS interaction in the model resulted in a better fit ($P < 0.001$, except $P = 0.02$ for HWT). Heritabilities were similar to those estimated in Models 1 and 2. The proportion of the FxS variance to total variance was small for weight traits, but more pronounced for ultrasonic measures (Table 5.3). Standardizing traits to a common within farm variance did not have an effect on variance components or rankings (results not shown).

Connectedness

Among farm locations, connectedness correlations were between 0.61 and 0.67. Between the high and low index category within a breed, these correlations ranged from 0.44 for the Suffolk to 0.53 for the Charollais breeds. Values between breeds were only slightly lower (0.40). Kuehn et al. (2008) found that correlations of 0.10 and above indicated strong connectedness among contemporary groups. Although there were only 8 sires shared between Wales and Scotland, 14 between Wales and England, and 13 between Scotland and England, the rotation of rams among farms generated the well-connected design intended.

DISCUSSION

Variance heterogeneity

Heteroscedasticity was present in this population, especially for ultrasonic traits. In the combined data, the additive genetic variance was similar to that estimated within farms (Model

1). These estimates changed little when fitting Model 2. Such was the case even when a homogeneous farm variance was assumed.

For both weight and ultrasound traits, accounting for heterogeneous variances improved model fit. However, for the weight traits, rank correlations between EBV obtained with homogenous and heterogeneous variances were near one. This suggests that any consequences of heteroscedasticity are not pronounced for weight traits, in agreement with previous results (Canavesi et al., 1995). Sire re-ranking was more evident for UMD and logUFD, suggesting heteroscedasticity would more likely affect genetic evaluation of ultrasound traits.

Ignoring heterogeneous variances in genetic evaluation has risks. As observed in this study, animals may be incorrectly ranked resulting in lower selection response. Accuracies of EBV may also be affected. By fitting a heterogeneous variance model, EBV are scaled, lessening the impact of inaccuracies in the estimation (Gianola, 1986). Given the presence of heterogeneous variances, several livestock breeds have developed genetic evaluation models that account for heteroscedasticity (Wiggans and VanRaden, 1991; Nakaoka et al., 2007).

An effective way to mediate bias in EBV due to heterogeneous variances is to test progeny in different environments. In progeny testing of dairy cattle, ranking of bulls was not greatly affected by heteroscedasticity when their daughters were randomly distributed among farms with high and low variances (Winkelman and Schaeffer, 1988). Sire referencing schemes, such as those from which the rams used in this study were drawn, provide another way of distributing genetics of sires to many flocks. It has been reported that assumptions of homogeneity may not lead to substantial decreases in selection response when heritabilities are higher in more variable populations (Garrick and Van Vleck, 1987). No such pattern was found in these data.

There is previous evidence for heterogeneity of variances within individual sheep breeds. San Cristobal-Gaudy et al. (2001) found that selecting for increased litter size lead to increases in variability of the trait, and that using a heterogeneous variance model resulted in increased selection response. In a study comparing different breeds, Tosh and Kemp (1994) found variable estimates of heritability for weights up to 100 d in 3 breeds (Hampshire, Polled Dorset, and Romanov). They also report heterogeneous breed variances and suggested that taking into account breed specific variance estimates may be necessary when comparing different breeds in an across-breeds genetic evaluation.

Genetics by environment interactions

The FxS variance component and ratio to total variance are indicative of the presence and influence of GxE within a population (Dickerson, 1962; Meyer, 1987). For weight traits, this explained approximately 1% of the total variation. For ultrasonic traits, this percentage was greater (10 – 13%), indicating that GxE has a larger influence on such body composition traits. For weight traits, our results are similar to Maniatis and Pollott (2002), also in sheep; however, they report a lower proportion of variance due to FxS in ultrasonic traits than in the current study.

In our case, including the FxS effect in the analyses decreased estimates of heritability. This is similar to Maniatis and Pollott (2002). Here, as in their study, ignoring FxS led to inflated estimates of additive genetic variance. They hypothesized that some of the additive variance was being partitioned into the FxS variance component, yielding downwardly biased heritabilities. Shrunk additive variances were also found by Hagger (1998) for ADG in sheep when fitting an FxS effect. Therefore levels of GxE in production traits appear to be low but real in sheep populations.

Misztal (1990) suggests that an explanation for a significant FxS interaction is poor representation of sires across-flocks, where genetic evaluations are more severely regressed. In our study, sires were well represented across flocks, with a proportion of sires having progeny in two of the three farms. The connectedness among farms was also strong. Another reason for the FxS interaction may be preferential treatment of some half-sib groups (Meyer, 1987), but given the design of this experiment, with management intentionally standardized across farms, such would not be anticipated.

Ultrasonic traits had greater indication of heteroscedasticity than weight traits, and also had a higher proportion of variation explained by the FxS interaction. Dickerson (1962) and Canavesi et al. (1995) found that FxS interaction may be caused by, or at least inflated by, heterogeneous variances. When we standardized variances across farms, the variance component estimates, and the proportion of FxS interaction variance to total variance, did not change. This is similar to Notter et al. (1992) and Maniatis and Pollott (2002).

Effects on genetic evaluation

Weight at harvest reflects an animal's growth to a certain end point, such as a target level of fatness. As such, it is a combination of the bone, fat, lean, and other tissues deposited in an animal as it grows (Brody, 1945). We did not observe evidence of heterogeneity and GxE in HWT, or in earlier weights, but we did in ultrasonic traits. Ultrasonic measures are indicative of fat and lean tissue deposition in an animal (Emenheiser et al., 2010), and therefore can be thought of as components of HWT. Perhaps, when considering the components rather than the culmination of growth, heterogeneity and GxE become more apparent. Our findings indicate that accounting for heterogeneity and GxE in genetic evaluation of ultrasonic measures, at least in progeny of terminal sires, will likely reduce such bias.

In selection regimes, where animals are often reared in environments that differ, ignoring GxE when estimating variance components in genetic evaluation leads to reductions in selection response (Garrick and Van Vleck, 1987; Mulder and Bijma, 2006). Mulder and Bijma (2005) found that progeny testing schemes were more robust to GxE than sib-testing schemes: when including information on progeny, in the presence of any GxE, the rate of genetic change was greater. The current data derive from a progeny testing scheme. We therefore anticipate less of an impact of any GxE than otherwise.

In the presence of GxE, the breeding objective of selection programs in different environments may differ. The construction of selection tools may also differ because genetic (co)variances between traits may vary across environments. With the presence of GxE, a way to optimize selection programs is to have an overall breeding goal yet test progeny in more than one environment, as done in the current study.

Conclusions

The consequences of heteroscedasticity or GxE on genetic evaluation programs need to be carefully evaluated before their formal incorporation. The limited extent of environmental heteroscedasticity observed in this study may justify it being ignored even for ultrasonic traits. Re-ranking of sires when presuming variances were homogeneous was trivial.

Accounting for any GxE in the genetic evaluation of ultrasonic traits may be more important: the FxS random component explained at least 10% of the variation in these traits. This would alleviate bias and increase accuracy. Still, to robustly estimate the FxS effect, the number of offspring per sire needs to be large enough. Connectedness among offspring of sires in different environments also needs to be sufficient. Such was certainly the case in this study but may not be so in industry breeding schemes.

Even where heteroscedasticity or GxE may be important, incorporating them into genetic evaluation schemes is complicated. Firstly, environments must be delineated. In the current study this was straightforward; by its design, lambs were reared in three distinct locations within the UK. However, in genetic evaluation schemes, environments may be less easily distinguished, and may overlap. In the current study environments were conveniently defined by country (England, Scotland and Wales). However, this is not likely to be suitable on a wider 'real world' scale since environments vary gradually across geographic regions and climates. Furthermore, environmental conditions also are not static over time, even on individual farms.

Another consideration is the efficacy of running genetic evaluations. In fitting models with more random effects, solutions may be more difficult to obtain. Furthermore, the amount of data in routine genetic evaluation is large, with computational time a constraint. Therefore the costs of accounting for heteroscedasticity and GxE in routine, particularly multivariate, genetic evaluations need to be considered.

The aim of genetic evaluation programs is to assist livestock industries achieve defined breeding goals. The presence of environmental heterogeneity or GxE may hinder progress toward these goals. However, before incorporating such factors into routine genetic evaluations, their extent and consequence on reaching breeding goals need to be carefully evaluated.

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Table 5.1. Within farm and combined estimates of additive and environmental variance and heritability for growth and harvest traits.

	Trait					
	BWT ¹	5WT	10WT	HWT	UMD	logUFD
Additive						
Combined	0.11 ± 0.023	0.69 ± 0.15	1.68 ± 0.36	5.29 ± 0.64	1.33 ± 0.15	0.019 ± 0.003
England	0.094 ± 0.034	0.59 ± 0.24	2.01 ± 0.63	5.86 ± 0.95	1.31 ± 0.23	0.027 ± 0.004
Scotland	0.097 ± 0.033	1.25 ± 0.37	1.81 ± 0.63	6.46 ± 1.18	1.43 ± 0.24	0.015 ± 0.003
Wales	0.094 ± 0.034	0.67 ± 0.26	1.32 ± 0.53	4.39 ± 0.98	1.60 ± 0.29	0.027 ± 0.005
Environmental						
Combined	0.27 ± 0.02	3.61 ± 0.12	8.07 ± 0.26	10.67 ± 0.47	2.67 ± 0.11	0.046 ± 0.002
England	0.29 ± 0.01	2.89 ± 0.17	5.84 ± 0.41	7.61 ± 0.66	2.69 ± 0.18	0.035 ± 0.003
Scotland	0.26 ± 0.02	2.54 ± 0.21	5.73 ± 0.41	11.79 ± 0.89	1.96 ± 0.17	0.046 ± 0.003
Wales	0.29 ± 0.02	4.20 ± 0.23	9.73 ± 0.51	11.76 ± 0.81	3.19 ± 0.23	0.046 ± 0.003
Heritability						
Combined	0.22 ± 0.04	0.13 ± 0.03	0.14 ± 0.03	0.33 ± 0.04	0.33 ± 0.04	0.30 ± 0.04
England	0.18 ± 0.06	0.12 ± 0.05	0.19 ± 0.06	0.43 ± 0.06	0.33 ± 0.05	0.43 ± 0.06
Scotland	0.20 ± 0.06	0.26 ± 0.07	0.17 ± 0.06	0.35 ± 0.06	0.42 ± 0.06	0.24 ± 0.05
Wales	0.18 ± 0.05	0.12 ± 0.05	0.10 ± 0.04	0.27 ± 0.06	0.33 ± 0.05	0.38 ± 0.06

¹BWT= birth weight; 5WT = five week weight; 10WT = ten week weight; ¹HWT = harvest weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth

Table 5.2. Additive and environmental variances and heritabilities for homogeneous and heterogeneous variance models for growth and harvest traits.

	BWT ¹	5WT	10WT	HWT	UMD	logUFD
Additive						
HOM ²	0.12 ± 0.03	0.91 ± 0.18	2.11 ± 0.41	6.01 ± 0.67	1.50 ± 0.16	0.024 ± 0.003
HET	0.13 ± 0.02	0.94 ± 0.19	2.14 ± 0.42	6.00 ± 0.67	1.34 ± 0.15	0.020 ± 0.003
Environmental						
HOM	0.27 ± 0.01	3.16 ± 0.12	6.87 ± 0.26	10.22 ± 0.49	2.58 ± 0.12	0.0044 ± 0.002
England	0.28 ± 0.02	2.88 ± 0.16	5.85 ± 0.32	12.44 ± 0.66	2.02 ± 0.13	0.0046 ± 0.002
Scotland	0.24 ± 0.02	2.73 ± 0.15	5.98 ± 0.32	7.72 ± 0.53	2.69 ± 0.14	0.0041 ± 0.002
Wales	0.30 ± 0.02	3.96 ± 0.19	9.03 ± 0.43	10.82 ± 0.64	3.41 ± 0.17	0.053 ± 0.003
Heritability						
HOM	0.24 ± 0.04	0.17 ± 0.03	0.18 ± 0.03	0.37 ± 0.04	0.36 ± 0.03	0.34 ± 0.04
England	0.24 ± 0.04	0.19 ± 0.04	0.20 ± 0.04	0.33 ± 0.03	0.39 ± 0.04	0.30 ± 0.04
Scotland	0.26 ± 0.05	0.20 ± 0.04	0.20 ± 0.04	0.44 ± 0.04	0.33 ± 0.03	0.33 ± 0.04
Wales	0.23 ± 0.04	0.16 ± 0.03	0.15 ± 0.03	0.35 ± 0.04	0.28 ± 0.03	0.27 ± 0.03

¹BWT= birth weight; 5WT = five week weight; 10WT = ten week weight; ¹HWT = harvest weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth

²HOM = homogeneous variances model; HET = heterogeneous variances model

Table 5.3. Variance components estimates for genetics by environment interaction model for weights up to ten weeks.

	BWT ¹	5WT	10WT	HWT ¹	UMD	logUFD
Additive	0.18 ± 0.03	1.02 ± 0.023	2.31 ± 0.53	6.60 ± 0.74	1.41 ± 0.20	0.026 ± 0.003
FxS ²	0.009 ± 0.004	0.09 ± 0.04	0.19 ± 0.09	0.22 ± 0.14	0.47 ± 0.11	0.013 ± 0.002
Heritability	0.30 ± 0.05	0.15 ± 0.05	0.15 ± 0.05	0.37 ± 0.04	0.30 ± 0.04	0.28 ± 0.05
GxE	0.015 ± 0.007	0.013 ± 0.007	0.012 ± 0.007	0.012 ± 0.008	0.10 ± 0.02	0.13 ± 0.03

¹BWT= birth weight; 5WT = five week weight; 10WT = ten week weight; ¹HWT = harvest weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth

²FxS = sire by farm interaction; GxE = FxS variance as a proportion of total variance

Chapter 6: Genetics by environment interaction in sheep affects genetic evaluation

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ABSTRACT

Genetics by environment interaction (GxE) affects genetic evaluation because animals may not perform predictably across environments. The purpose of this study was to evaluate and quantify GxE in a population of crossbred lambs using a multivariate approach and reaction norms. Data consisted of 6,325 crossbred lambs sired by Charollais, Suffolk, and Texel rams. The experiment was performed on three farms located in England, Scotland, and Wales. In total, 89 sires were mated to 1,984 ewes of two types (Welsh and Scottish Mules). Most rams were used for two breeding seasons and were physically rotated among farms to create genetic links. Lambs were reared on pasture and had their birth, 5 wk, 10 wk, and harvest weights recorded. Lambs were ultrasonically scanned for fat and muscle depth (UMD) at harvest at a constant fatness. The GxE was first assessed by fitting traits as separate but correlated by farm of origin. Low correlations between traits in farms indicate presence of GxE. For most traits genetic correlations between farms were high (above 0.8). The second approach was to fit reaction norms of sires. For weight traits and UMD, sires had positive slopes for their reaction norm (were environmentally sensitive), which were of similar values (were parallel). That is, the performance of a sire's progeny improved with improving environment. For ultrasonic fat depth, reaction norms had slopes ranging from negative to positive, indicating GxE for this trait. There was evidence of genetic variation in sensitivity of sires; therefore, they could be selected to be more or less sensitive depending on economic considerations. Although GxE was limited for most traits,

genetic sensitivities do exist and can be incorporated into selection strategies using reaction norms.

Keywords: crossbred lambs, genetics by environment interaction, reaction norms

INTRODUCTION

The phenotypic expression of a trait can differ depending on the environment. This genetics by environment interaction (**GxE**) is common in sheep and other livestock (Maniatis and Pollott, 2002; Pollott and Greeff, 2004; Steinheim et al., 2008; Santana et al., 2013). In genetic evaluation, a trait measured in different environments is usually considered to be the same trait. Therefore, the evaluation of a sire with offspring across multiple environments does not necessarily reflect his merit in a particular environment, but the average of his performance across environments. The consequence of this is that offspring of sires may not perform as predicted in every environment.

One way to deal with GxE is with a multitrait evaluation, where a trait in different environments is regarded as different but correlated. This approach is advantageous when environments can be classified discreetly, and gives separate estimates of heritability and EBV by environment. One problem with this method is the difficulty in classifying environments. When many environments are defined, the number of (co)variance parameter estimates grow as well.

Reaction norms may be a better way to deal with GxE in cases where defining discrete environments is difficult. Reaction norms describe GxE by fitting the phenotype as a continuous function of the environment. This model is able to account for gradual and continuous changes in the environment, and quantify the environmental sensitivity of an animal. Therefore, the objectives of this study were to evaluate and quantify GxE in a crossbred lamb population by

fitting a multivariate model and reaction norms. The respective merits of these two approaches were then compared.

MATERIALS AND METHODS

Animal care and use

The Animal Experiment Committees at the Institute of Biological Environmental and Rural Sciences (**IBERS**), the Scottish Agricultural College (**SAC**), and ADAS UK Ltd (**ADAS**) approved all procedures and protocols used in the experiment.

Animal resources

Performance data on 6,325 crossbred lambs sired by Charollais, Suffolk, and Texel rams were obtained. There were a total of 89 rams, which came from their breed's sire referencing schemes. The rams were selected according to a lean growth index designed to increase carcass lean growth, while constraining fat growth at a constant age end point (Simm and Dingwall, 1989). These sires were chosen from the top and bottom 5% of available rams based on index score and categorized as 'high' or 'low' lean growth index. High vs. low index rams differed in their EBV: at approximately 21-wk, weight EBV of high index rams was 6.6 ± 0.5 kg greater, ultrasonic muscle depth (**UMD**) EBV was 2.3 ± 0.2 mm larger, and ultrasonic fat depth EBV was 0.49 ± 0.12 mm smaller than low index rams (Márquez et al., 2012). Terminal sires were mated to Scottish and Welsh Mules to produce the lambs considered in the study. Most sires were used for two breeding seasons and moved between farms to create genetic links among farms and years. This design ensured that connectedness among farms and breeds was high (Márquez et al., 2014). The Mule ewes originated from matings of Bluefaced Leicester rams

with Scottish Blackface and (Welsh) Hardy Speckled Face ewes (van Heelsum et al., 2003; Mekkawy et al., 2009).

Matings took place between 1999 and 2002 on three farms in the UK (in England, Scotland, and Wales). The environments of the three farms differed. In England, the altitude ranged from 75 to 105 m above sea level, and the mean annual rainfall was 660 mm with average temperatures ranging from 3 to 22°C. In Scotland, the altitude ranged from 150 to 200 m, rainfall was 1,000 mm, and average temperatures ranged from 7 to 26°C. In Wales the altitude ranged from 10 to 70 m above sea level, with annual rainfall of 1,170 mm and average temperatures of 3 to 20°C. Topography also differed on the three farms. Furthermore, mean rainfall varied within farm in the years of the experiment (Figure 1), although temperatures were relatively stable (Met Office, UK).

Lambs were finished to a constant fatness level to ensure comparisons were made at the same maturity level. The birth weight (**BWT**), 5-wk weight (**5WT**), and 10-wk weight (**10WT**) of lambs were recorded. From approximately 10 wk on, lambs were evaluated for finished condition (fatness) bi-weekly. Lambs were harvested when they achieved a target fatness score of 3L, which corresponds to approximately 11% subcutaneous fat (Kempster et al., 1986). Finishing lambs to a constant fatness is common practice and ensures that lambs are harvested at comparable physiological maturity levels. Once finished, harvest weights (**HWT**) were obtained, and lambs were ultrasonically scanned for muscle and fat depth. Lamb's UMD was measured at the deepest point of the eye muscle (*longissimus lumborum*) at the third lumbar vertebra. Fat depth was measured at this location and at 1 and 2 cm lateral to it; these measures were then averaged. Lambs were processed at commercial abattoirs. Further details of design and husbandry are in Márquez et al. (2012, 2013).

Genetic groups

A pedigree was assembled with 127,833 animals. Six unrelated breed-types appeared in the pedigree, and each was fitted as a genetic group. One was fitted for each of the three terminal sire breeds (the sires of the lambs), one for each of the two Mule ewe types (the dams of the lambs), and one for the Bluefaced Leicester (the maternal grandsires of the lambs). Genetic groups were fitted because there were no relationships among animals in the six groups. By fitting genetic groups we account for different genetic means of animals and reduce bias in their evaluation due to their differing genetic backgrounds (Van Vleck, 1990). All analyses in this study were performed using ASReml (Gilmour et al., 2009).

Statistical analysis

Multivariate approach

The first approach to test the extent of GxE in this population was to form subsets of the data according to the lamb's farm of origin. For a given trait, data from the three subsets were fitted as separate but correlated traits in a trivariate analysis. The traits studied were BWT, 5WT, 10WT, HWT, UMD and a log transformed ultrasonic fat depth (**logUFD**). The model fitted for this analysis was:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 & 0 \\ 0 & \mathbf{X}_2 & 0 \\ 0 & 0 & \mathbf{X}_3 \end{bmatrix} \begin{bmatrix} \beta_1 \\ \beta_2 \\ \beta_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{a1} & 0 & 0 \\ 0 & \mathbf{Z}_{a2} & 0 \\ 0 & 0 & \mathbf{Z}_{a3} \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{d1} & 0 & 0 \\ 0 & \mathbf{Z}_{d2} & 0 \\ 0 & 0 & \mathbf{Z}_{d3} \end{bmatrix} \begin{bmatrix} d_1 \\ d_2 \\ d_3 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

where y_i is a vector of observations in farm i ($i = 1, 2$ or 3 for England, Scotland and Wales, respectively), β_i is a vector of fixed effects coefficients, a_i is a vector of animal additive effects, d_i is a vector of rearing dam effects, and e_i is a vector of random residual effects. The \mathbf{X}_i , \mathbf{Z}_{a_i} , and \mathbf{Z}_{d_i} matrices are incidence matrices relating to observations in β_i , a_i and d_i , respectively. Fixed

effects were an overall mean, lamb sex (ewe or wether), age of dam (2- to 5-yr old), and birth year. For BWT, birth rank (single through triplet) was fitted, and for all other traits a birth-rearing rank effect was fitted with four categories: single born/single reared, twin or more born/single reared, single or twin born/twin reared, and triplet born/twin reared. Ewes with triplets or quadruplets were only allowed to rear twins, and the other lambs were fostered by other ewes. Covariates were age at measurement for all traits except HWT and UMD, where subcutaneous fat at harvest was fitted as the covariate. The (co)variance structures for this model were:

$$\text{var} \begin{pmatrix} a_1 \\ a_2 \\ a_3 \end{pmatrix} = \mathbf{A} \otimes \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_{1,2}} & \sigma_{a_{1,3}} \\ \sigma_{a_{2,1}} & \sigma_{a_2}^2 & \sigma_{a_{2,3}} \\ \sigma_{a_{3,1}} & \sigma_{a_{3,2}} & \sigma_{a_3}^2 \end{bmatrix}$$

for the random animal additive effect, where \mathbf{A} is the relationship matrix among animals; and

$$\text{var} \begin{pmatrix} d_1 \\ d_2 \\ d_3 \end{pmatrix} = \mathbf{I} \otimes \begin{bmatrix} \sigma_{d_1}^2 & 0 & 0 \\ 0 & \sigma_{d_2}^2 & 0 \\ 0 & 0 & \sigma_{d_3}^2 \end{bmatrix}$$

for the rearing dam effect, where \mathbf{I} is an identity matrix of appropriate dimensions. The random rearing dam effect was only fitted for BWT, 5WT, and 10WT because likelihood ratio tests indicated it did not improve the fit of the model for traits at finishing ($P > 0.10$); and

$$\text{var} \begin{pmatrix} e_1 \\ e_2 \\ e_3 \end{pmatrix} = \mathbf{I} \otimes \begin{bmatrix} \sigma_{e_1}^2 & 0 & 0 \\ 0 & \sigma_{e_2}^2 & 0 \\ 0 & 0 & \sigma_{e_3}^2 \end{bmatrix}$$

was the (co)variance structure for the random residual effect. A genetic maternal effect was not fitted because pedigree information on dams of lambs was not extensive.

The estimates of genetic correlations between performances in the different farms are indicators of the presence of GxE. In the absence of GxE, sire performance would be similar

across farms and this correlation would be expected to be above 0.8 (Robertson, 1959).

Consequences of GxE were further investigated by obtaining rank correlations between sire EBV in the three farms.

Reaction norms

The second approach used to investigate GxE was by using reaction norms (Lynch and Walsh, 1998). These relate the mean phenotypic response of a genotype to changes in the environment. Reaction norms are fitted through a random regression model, where a random sire intercept is fitted along with a random slope of the regression of sire on environmental means. The environment was defined as the mean performance in a farm and year (as a deviation from the overall mean). Therefore there were 12 continuous points on the environmental scale.

In a reaction norm model, the estimated intercept is the sire's EBV and the random slope is a measure of environmental sensitivity. The model fitted was:

$$y = X\beta + \mathbf{1}s_{intercept} + X_{fy}s_{slope} + Z_d d + e$$

where $X, \beta, Z_d d$, and e are as in the multivariate model, y are the traits, $s_{intercept}$ is a vector of random sire intercepts, X_{fy} is an incidence matrix relating to mean performance of a trait for a farm-year combination, and s_{slope} is the random sire slope. The (co)variance model was:

$$var \begin{bmatrix} s_{intercept} \\ s_{slope} \end{bmatrix} = A \otimes \begin{bmatrix} \sigma_{int}^2 & \sigma_{int,slope} \\ \sigma_{slope,int} & \sigma_{slope}^2 \end{bmatrix} = A \otimes G$$

Separate sire variances were estimated for each environment as:

$$\hat{\sigma}_{s|X}^2 = VGV'$$

where $V = [1 \ W]$, and W is the mean for an environment and, as in a standard sire model, the heritability in each environment is:

$$h^2|W = \frac{4\hat{\sigma}_{s|W}^2}{\sigma_p^2}$$

A model with a quadratic polynomial term was fitted but did not improve the log-likelihood over that for a linear reaction norm model.

Reaction norms indicate GxE in different ways. In a plot of reaction norms, parallel lines indicate lack of GxE. Lines that do not cross but are not parallel indicate GxE due to scale, and in this case there is no re-ranking of sires in different environments. If the lines cross, this indicates re-ranking of sires in different environments, and is of most concern (Lynch and Walsh, 1998).

To investigate the effects of the definition of environment on the fit of the reaction norm model, traits were re-evaluated by defining the environments as deviations from the three farm means (years were ignored). Parameter estimates and reaction norms with environments defined in these two ways were compared.

RESULTS

Multivariate model

Table 6.1 shows the estimates of variance components and heritabilities for each trait in each farm. Between farms estimates of additive variances and heritabilities were within the standard error of each other, except for UMD and logUFD. Residual variances followed the same pattern.

For most farm pairs, genetic correlations between farms were greater than 0.8. Such was the case in all farms for BWT, HWT, and logUFD. However, these genetic correlations were lower than 0.8 between Scotland and Wales for 5WT (0.58 ± 0.36). Such was also the case between England and Wales for 5WT (0.78 ± 0.37), 10WT (0.76 ± 0.39), and UMD ($0.77 \pm$

0.23). The rank correlations estimates of sire EBV among the three farms were all greater than 0.80, indicating low levels of re-rankings.

Reaction norms

Estimates of variance components for intercept, slope, covariance and correlations of the reaction norm models are in Table 6.2. Estimates for slopes were not different from zero for BWT but were for all other traits. Slopes greater than zero indicate that performance was generally better in environments with higher environmental means. There was no clear pattern of rankings of environments in the different farms or years.

The correlation between sire intercept and slope was only different from zero for 10WT and HWT, as their SE exceeded the estimated value. These results indicate that there is little to no relationship between sire performance and sensitivity for most traits. For 5WT and 10WT all sires had positive estimated slopes, indicating that performance improved in better environments (Figure 2 for 10WT, Figure 3 for HWT, and Figure 4 for logUFD). For 5WT and HWT, Suffolk and Charollais sires had, generally, larger EBV estimates than Texel sires. There was no clear pattern for the other traits.

Plots of reaction norms of sires for weight traits (Figures 2 and 3) show that while slopes are positive, most lines are parallel or near parallel (i.e., slopes were similar). This indicates that sires would rank similarly across different environments, so GxE may not be very pronounced. The only trait where this was not clear was logUFD (Figure 4), where reaction norms cross and re-ranking of sires in different environments is expected.

Heritabilities calculated in different environments followed similar patterns for all traits (Figure 5 for logUFD). Heritabilities were higher in environments where mean performance was more extreme (low or high) than when it was moderate. This variation in heritability was due to

changing sire variances across environments. Heritabilities from the reaction norm model were similar to those estimated from the multivariate model.

Genetic parameter estimates were similar regardless of how the environment was defined for weight traits, but had greater effect on ultrasound traits. When the environment was defined only as farm, the estimates for the intercept and slope were 0.68 ± 0.14 and 1.51 ± 0.86 , respectively, for UMD, and 0.19 ± 0.04 and 5.01 ± 3.99 , for logUFD, respectively. For the 3 environments, the estimated correlations between intercept and slope were 0.05 ± 0.19 and -0.37 ± 0.14 for UMD and logUFD, respectively, which are within the standard errors for the estimates of the same correlations obtained with the 12 environments. Defining environments more explicitly than simply by farm, such as by farm-year combination, allowed for better description of a gradually and continually changing environment.

DISCUSSION

Multivariate model

Genetic correlations between traits in different environments were generally higher than the 0.8 proposed by Robertson (1959) as the lower threshold for significant GxE. However, that was not always the case. Most of the genetic correlations below 0.8 were between England and Wales. Still, in this experiment, we attempted to standardize management among the three farms and thus opportunity for GxE was likely small.

A consequence of low genetic correlations for a trait among environments is that the genetic determination of the trait may differ across them. Thus, selection in one environment may not be optimal in another (Wei and van der Werf, 1995; Mulder and Bijma, 2005). In most sheep production circumstances, progeny of sires are expected to perform in a variety of environments. The presence of GxE can therefore hinder uniform performance. Genetic

correlations below 0.8 were observed for a few traits in these data. Even in those cases, rank correlations between sire EBV were high, suggesting re-ranking of sires whose progeny perform in similar lowland environments will be minimal. Such was also found by Márquez et al. (2014) in these same data.

For the multivariate model, heritability estimates for BWT were higher than other estimates in terminal sire breeds (Maxa et al., 2007). Estimates for harvest traits were similar to those observed by Jones et al. (2004) in these same breeds in the UK. The higher heritability for BWT may be due to not accounting for a genetic dam effect, which was not possible given the available pedigree information.

In our multivariate analyses, we did not observe constant heritabilities across environments. This was most pronounced for ultrasound traits. It has been reported that heritabilities can be higher in poorer environments, and decrease as the environment improves (Pollott and Greeff, 2004). This was not the case in our experiment, where there were no clear patterns in the relationship between the mean environment in a farm and the heritability.

Reaction norms

A weakness of the multivariate approach is in defining discrete environments. In our study this was straightforward: lambs were produced from a designed experiment and were reared in three defined environments (farms). However, that is not the norm. Farm environments vary spatially and temporally within livestock industries. Reaction norms describe a genotype's phenotypic response as a function of a continuous environment, and are therefore useful when phenotypes change gradually and continually over environmental gradients (Lynch and Walsh, 1998).

The criteria used to describe environments are important when estimating reaction norms. They must capture salient features of the breeding goal, and be sufficiently large in terms of animal numbers to avoid unreliable estimates of subclass means (Fikse et al., 2003). For ultrasound measures, we found that the categorization of environments influenced parameter estimates. Such has also been found in other species and traits (Fikse et al., 2003; Pégolo et al., 2009). We believe that our choice of environmental category – namely the combination of farm and year – captured the climatic and geographic features of our experimental sites, which was not the case when using farm alone.

Reaction norms offer a way to quantify GxE and select animals in terms of their EBV (intercept) and environmental sensitivities (slope) for a trait. Given evidence of GxE, there has been interest in applying reaction norms to sheep populations (Pollott and Greeff, 2004; Santana et al., 2013). Defining the environment as a continuous variable also lessens the number of parameters that must be estimated as compared to a multivariate model. With these types of models, separate heritabilities and EBV can be estimated across environmental values straightforwardly. This can be a valuable tool for producers who need to select the best rams for their particular environments.

For weight traits and UMD, sires had better performance in superior environments. This has implications for management of lambs: if they are provided with a favorable environment, they will likely do better than their counterparts in poorer environments. However, given that slopes of sires were similar, we do not expect re-rankings when their offspring are reared in environments of varying quality. That is, there was not no appreciably GxE for weight traits. This is in contrast to Lewis et al. (2004) and Macfarlane et al. (2004), who did find genetics by nutrition interactions for ADG and feed efficiency (defined as ADG/daily intake). In their

experiments, when Suffolk lambs were fed under non-limiting conditions, they were able to achieve their genetic potential, but were otherwise unable to do so. Santana et al. (2013), using reaction norms in Santa Ines sheep found evidence of GxE in weights up to 180 d, with effects being more severe in 60 and 180 d weights.

The pattern in slopes was slightly different for logUFD (Figure 4). There was more evidence of GxE in this trait, and we expect re-ranking of sires in different environments. We have previously reported GxE for logUFD (Márquez et al., 2014), although this size of interaction was larger than that found by Pollott and Greeff (2004).

As with the multivariate analyses, heritabilities varied with contemporary group: they were higher in the more extreme environments. Similar patterns in heritabilities have been observed before (Pollott and Greeff, 2004; Pégolo et al., 2009), where heritabilities were estimated to be smaller in the mean environments.

Environmental sensitivity

Phenotypes can differ with changes in the environment. Genotypes that are sensitive to changes in the environment (have non-zero slopes) are said to be plastic, while robust genotypes are those that are not sensitive to environmental changes (have zero slopes). Our estimates of genetic variance of reaction norm slopes are greater than zero for some traits (5WT, 10WT, logUFD), indicating variability in sensitivities and opportunities for selection. Kolmodin et al. (2003) showed, in simulation, that plasticity increased in a selection scheme where GxE was present. Therefore opportunities to select for plasticity or robustness in these sheep are present.

The decision to select for plasticity or robustness depends on breeding goals. Some authors have suggested that ideal animals are those that not only have high EBV but also are robust. Including robustness in the breeding objective is particularly important when sires are

evaluated in favorable settings with the expectation their offspring will perform similarly well in industry settings (Knap, 2005). In our case, robust lambs would be those that have high production potential and are resilient. However, there are risks in focusing selection on robust animals, in that they may not be able to adapt as well to abrupt environmental changes. In extensive sheep production systems, maintaining plasticity may be important for future adaptability, and breeding for robustness may eliminate genetic variation that is important to adaptation to unforeseen environments.

The genetic basis of traits expressed in favorable and unfavorable environments may be different. Other studies have found that in unfavorable environments the genetic variability of traits was higher than in favorable environments, implying that some animals have the genetic ability to cope with poor conditions better than others (Lewis et al., 2004; Macfarlane et al., 2004; Pollott and Greeff, 2004). Conversely, in favorable environments genetic variation was lower and genotypes responded similarly to environmental conditions.

In this study, genetic variability in environmental sensitivity was identified in UK terminal sire breeds. Reaction norm models can be used in genetic evaluation to characterize these sensitivities, which would provide producers with additional information for sire selection. If economically justified, this would allow selection for plasticity or robustness to be incorporated into the breeding goal.

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Table 6.1. Estimates of additive genetic variance and heritability in the three farms when traits were fitted as separate but correlated

	Traits ¹					
	BWT	5WT	10WT	HWT	UMD	logUFD
Additive						
England	0.15 ± 0.05	0.96 ± 0.34	2.21 ± 0.67	5.03 ± 0.83	1.13 ± 0.22	0.024 ± 0.004
Scotland	0.15 ± 0.04	1.20 ± 0.34	1.49 ± 0.51	5.84 ± 1.05	1.32 ± 0.22	0.012 ± 0.003
Wales	0.12 ± 0.04	0.75 ± 0.28	1.60 ± 0.60	4.52 ± 0.97	1.28 ± 0.26	0.024 ± 0.005
Dam						
England	0.13 ± 0.02	1.45 ± 0.17	2.59 ± 0.34	-	-	-
Scotland	0.11 ± 0.02	0.88 ± 0.14	3.14 ± 0.36	-	-	-
Wales	0.11 ± 0.02	0.73 ± 0.16	1.64 ± 0.36	-	-	-
Residual						
England	0.26 ± 0.03	2.69 ± 0.21	5.75 ± 0.42	8.11 ± 0.36	2.78 ± 1.07	0.037 ± 0.003
Scotland	0.23 ± 0.04	2.56 ± 0.21	5.91 ± 0.36	12.20 ± 0.16	2.02 ± 0.98	0.048 ± 0.003
Wales	0.30 ± 0.02	4.15 ± 0.23	9.59 ± 0.51	11.68 ± 0.09	3.39 ± 0.30	0.058 ± 0.004
Heritability						
England	0.27 ± 0.08	0.19 ± 0.06	0.21 ± 0.06	0.38 ± 0.05	0.29 ± 0.05	0.39 ± 0.06
Scotland	0.31 ± 0.08	0.25 ± 0.07	0.14 ± 0.05	0.32 ± 0.05	0.39 ± 0.06	0.20 ± 0.05
Wales	0.23 ± 0.07	0.13 ± 0.05	0.12 ± 0.04	0.28 ± 0.05	0.27 ± 0.05	0.34 ± 0.06

¹BWT= birth weight; 5WT = 5-week weight; 10WT = 10-week weight; HWT = harvest weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth.

Table 6.2. Estimates of variance, covariance and correlation components from reaction norm models

	Traits ¹					
	BWT	5WT	10WT	HWT	UMD	logUFD
Intercept	0.012 ± 0.003	0.19 ± 0.05	0.59 ± 0.15	1.14 ± 0.02	0.47 ± 0.08	0.005 ± 0.001
Covariance	0.005 ± 0.005	0.008 ± 0.018	0.005 ± 0.004	-0.005 ± 0.052	0.005 ± 0.03	-0.002 ± 0.002
Slope	0.011 ± 0.021	0.05 ± 0.02	0.006 ± 0.002	0.017 ± 0.023	0.01 ± 0.02	0.011 ± 0.015
Correlation	0.44 ± 0.61	0.08 ± 0.19	0.28 ± 0.19	-0.03 ± 0.01	0.07 ± 0.47	-0.28 ± 0.32

¹BWT= birth weight; 5WT = 5-week weight; 10WT = 10-week weight; HWT = harvest weight; UMD = ultrasonic muscle depth; logUFD = log ultrasonic fat depth.

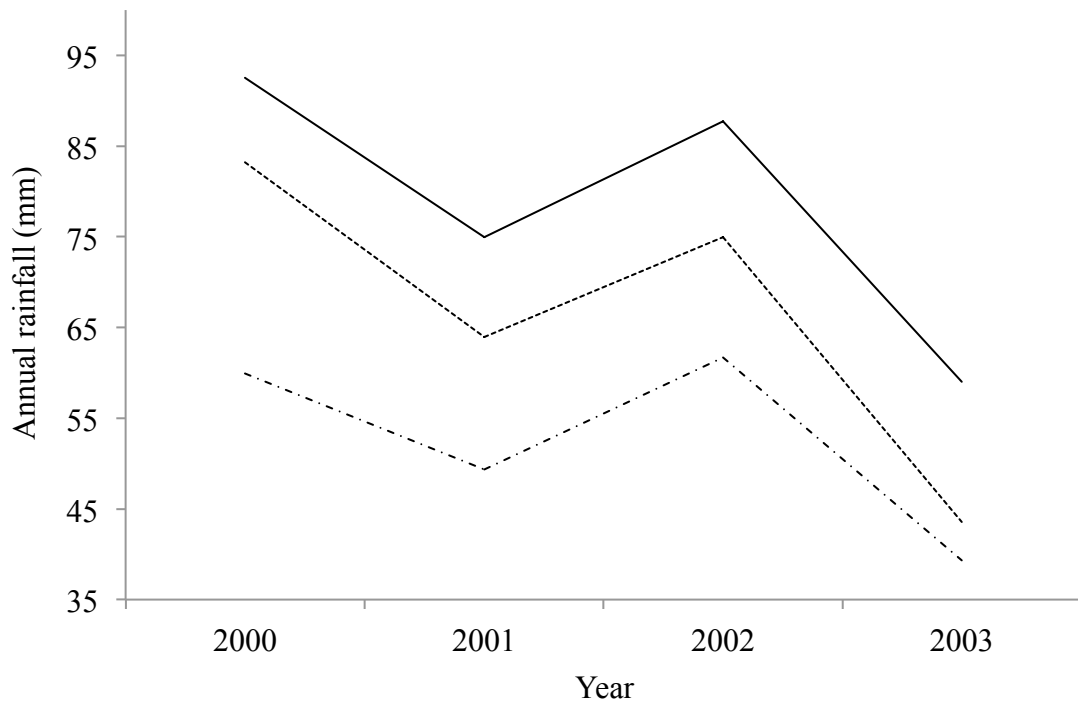


Figure 6.1. Plot of annual rainfall in England (dotted line), Scotland (dashed and dotted line) and Wales (solid line) (Met Office, UK).

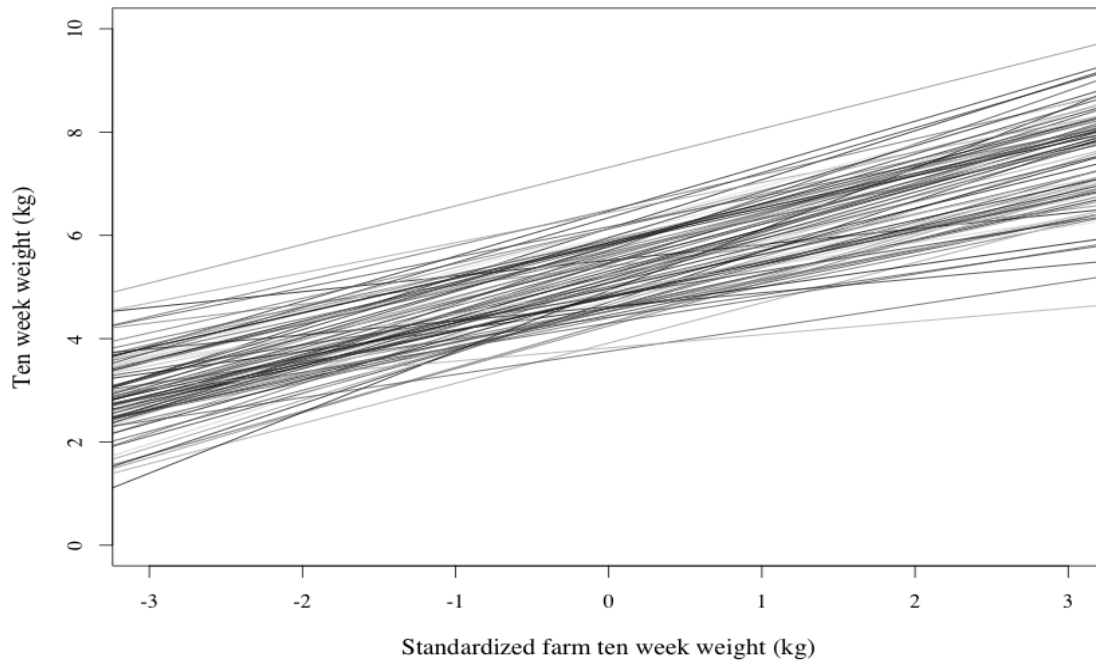


Figure 6.2. Reaction norms of sires for ten 10-week weight. Each line represents a sire.

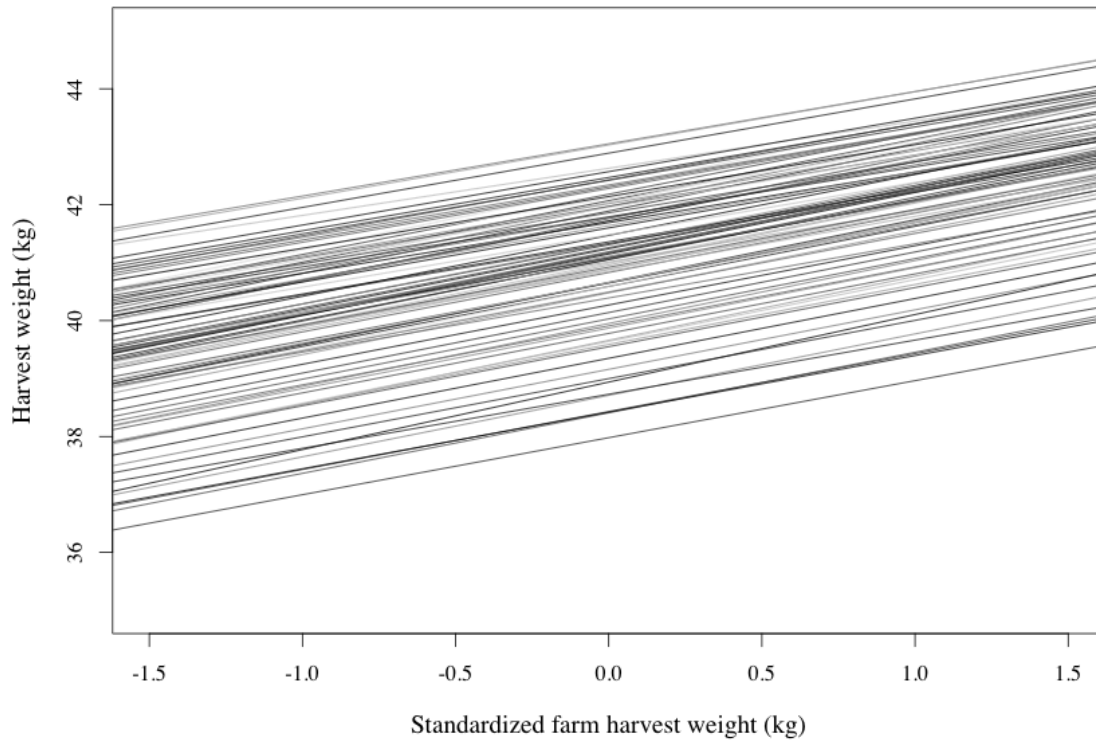


Figure 6.3. Reaction norms of sires for harvest weight. Each line represents a sire.

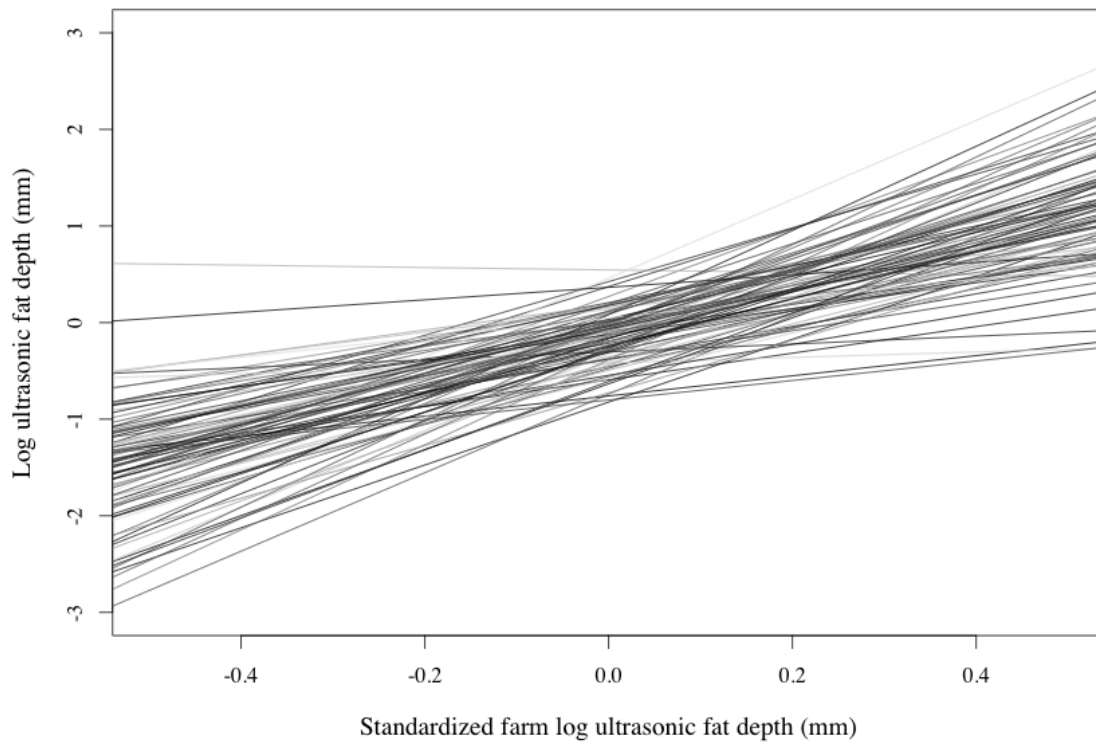


Figure 6.4. Reaction norms of sires for ultrasonic fat depth. Each line represents a sire.

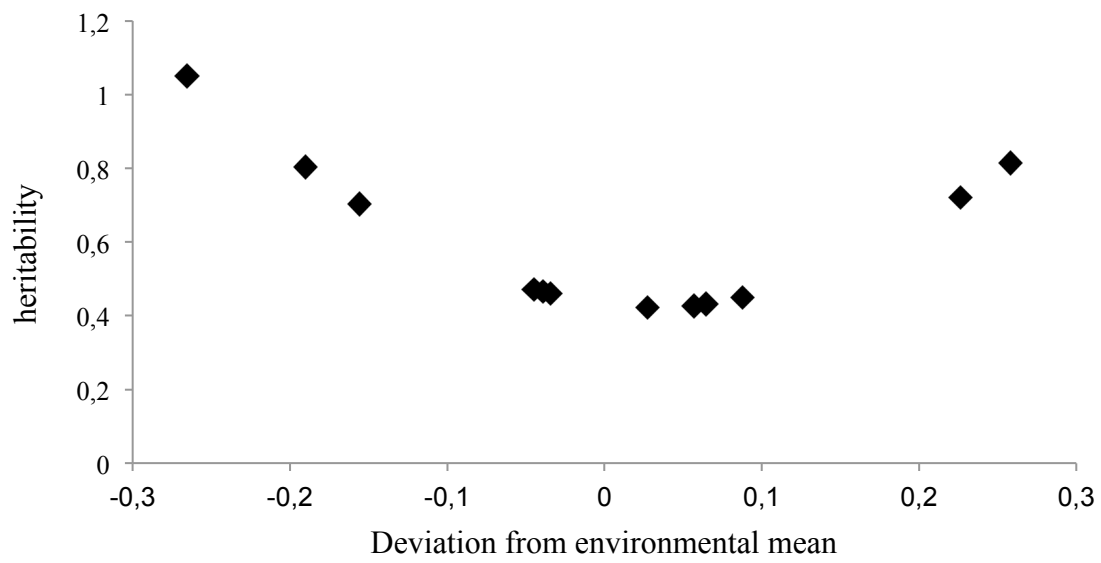


Figure 6.5. Estimated heritabilities in different environments for logarithmic ultrasonic fat depth.

Chapter 7: Conclusions

Selection of terminal sires based on the lean growth index translates to improvements in growth and finishing of their commercial crossbred lambs. Terminal sires have a large influence on the genetics of market lambs in the UK, and therefore index selection is a cost effective way of improving production. Differences between high and low index sired lambs were observed for all weights except at birth. For harvest weight and ultrasonic traits, differences between high and low index sired lambs were less than expected given the sire's EBV. Forming expectations of how much high vs. low index sired lambs should differ based on their sire's EBV is challenging. Only half of their genes come from the sire, and they are reared in environments that differ substantially.

One particularly important result from this work is that days to harvest were unchanged in rams selected for high index score, which implies that leaner lambs do not take longer to reach the same fatness level. One of the criticisms of the lean growth index has been that lambs of leaner sires would take longer to reach harvest fatness. This would imply that they would need to be fed for longer amounts of time, increasing costs. This proved not to be the case in this study.

An important advantage of index selection is that changes are permanent, cumulative, and cost effective. The wider uptake of index selection is recommended to improve sheep production systems. Selection on this index offers an objective evaluation of lean growth, and offers a reliable approach to improve lamb's carcass quality. Differences among terminal sire breeds are also important. Some breeds may be more suited to a particular production circumstance, and producers have flexibility in choosing the most appropriate one.

The presence of environmental heterogeneity and GxE biases genetic evaluation. Variance heterogeneity was not large in the present study, although more pronounced for

ultrasonic traits than weight traits. Genetics by environment interactions were also more pronounced for ultrasonic traits. The decision of incorporating variance heterogeneity and GxE into commercial genetic evaluation is a complicated one. Improvements in the genetic evaluations must be balanced against additional requirements needed to fit more complicated models.

Reaction norms offer a way to evaluate both the EBV and environmental sensitivity of sires. Some variation was present in reaction norm slopes, indicating that sensitivities could be selected for. This approach could offer a way to incorporate GxE into genetic evaluation, and producers would know whether a sire is sensitive or not. Incorporating robustness or sensitivity into breeding goals may be appropriate depending on the traits considered, and on correlations with other traits.

Final conclusions

Addition research into incorporating results like the current ones into across breeds genetic evaluation is needed. In these production circumstances, market lambs are crossbreds, and their performance information is not incorporated into the genetic evaluations of sires. A valuable source of information is thus lost. Including crossbred lamb's information into genetic evaluation could be achieved by treating offspring and sire phenotypes as correlated, or by running a genetic evaluation that incorporates all data and accounts for breed percentages or the like. Across breeds genetic evaluation is routinely performed for other species and would likely improve evaluation of UK lambs.

Further investigation of the effects of GxE with the data used for routine evaluation is also needed. Our data, although well designed to estimate genetic parameters, is small compared

to industry data. Data across more environments and years, as routinely collected, will offer more insight into the presence and consequences of GxE.

In designing breeding programs, economic considerations need to be taken into account. At the time this research was performed, decreasing fatness in the carcass was of paramount importance. The lean growth index offers a reliable way to select for leaner, faster growing, more profitable lambs under this paradigm. Currently, incorporating other traits into the breeding objective may be important. Traits related to the environment and consumer perceptions of production are increasing in importance and will affect profits.

There will be shifts in breeding goals and market needs, and the ability to adapt to these changes is important to maintain a successful industry. Changes in industry structure, with terminal sires used more widely all the time also need to be thought of when designing future breeding programs. The use of index selection, and genetic evaluation that incorporates crossbred offspring information could be a very valuable, and as of yet underutilized tool for producers.