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Enhancing genetic evaluations for sheep growth and carcass traits in Ireland and the UK

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University of Edinburgh

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Declaration

I declare that this thesis is my own composition and that the research described in it is my own work, except where acknowledged. The work described has not been submitted for any other degree or professional qualification.

Shauna Fitzmaurice

Peer-reviewed Publications

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Abstract

The use of genetic evaluations within sheep breeding improvement schemes have proved to be valuable to both the Irish and UK industries, with high levels of economic gain achieved through enhanced growth, live body weight and carcass composition traits. Sheep live body weight and carcass composition traits are essential components in determining the profitability of sheep production systems. Previous genetic studies in Ireland have predominantly focused on producing genetic parameters across a multi-breed population rather than on a breed by breed basis. Genetic evaluations have already proven to be of significant economic benefit to the UK sheep industry with over 30 years of genetic selection having taken place. Furthermore, great potential exists for the development of across-country sheep genetic evaluations particularly with the high levels of breeding stock and germplasm being exchanged between Ireland and the UK. These across-country evaluations could in turn lead to more judicious genetic selection and increased levels of genetic gain as well economic benefits for the global sheep industry.

The overall aim of this thesis was to enhance the genetic evaluations for sheep live body weight and carcass composition traits in Ireland and the UK. Specific objectives were to: (i) update the existing within-country genetic evaluations in the two countries, and (ii) examine the feasibility of and develop a joint across-country genetic evaluation system.

Data were obtained from Sheep Ireland (the Irish national database) and AHDB (the UK national sheep breeder database). After all data edits were complete 137,402 records from 50,372 Irish lambs and 132,490 records from 55,155 UK lambs born between 2010 and 2017 spread across 416 and 374 Irish and UK flocks, respectively, remained for further analyses. Data pertained to purebred Texel, Suffolk and Charollais sheep.

Genetic analyses were undertaken on three live body weight traits measured at different growth stages and two carcass composition traits in purebred Irish Texel, Suffolk and Charollais lambs. Variance components were estimated for each trait using mixed linear models separately for each breed. Significant ($P<0.05$) heritability estimates ranged from 0.14 to 0.30 for live body weight traits and from 0.15 to 0.31 for carcass composition traits across the three breeds. Positive genetic correlations were estimated between all traits for each of the three breeds studied. These results showed that significant levels of genetic variation exist both among animals and between breeds which in turn warrants genetic evaluations in Ireland being produced on a within breed basis.

Within breed genetic parameters were derived for the UK sheep population today for Texel, Suffolk and Charollais purebred lambs. Significant ($P<0.05$) heritability estimates for the three aforementioned breeds ranged from between 0.12 to 0.30 for two live body weight traits and from between 0.18 to 0.42 for the two carcass composition traits. As with the previous study on Irish data, strong positive genetic correlations were observed between all traits analysed. These results demonstrated that even after numerous years of selection within the UK population much variation still exists meaning there is still much potential for genetic improvement. In addition to this, genetic parameters differed significantly between breeds particularly for carcass composition traits indicating that within breed analysis should be considered for future genetic evaluation systems in the UK.

The concluding study of this thesis was to produce international genetic evaluations for sheep from both Ireland and the UK. This study firstly determined the level of connectedness between the two countries with common animals to both countries identified. A total of 8,392 Texel parents with progeny in both countries were identified before data edits were applied. Genetic correlations were then estimated between corresponding traits in both countries and ranged from between 0.82 and 0.88. A bivariate analysis was completed to produce EBVs for across-country genetic evaluations. Response to selection was estimated from sire EBVs and results indicated higher rates of genetic gain being achieved when selection was based on across-country evaluations in comparison to within-country evaluations. Rates of genetic gain improved from between 2.59% and 19.63% from selecting animals based on across-country genetic evaluations with the greatest rate of improvement observed for the ultra-sound scan weight trait. Most of the improvement in genetic gain was achieved from the higher selection intensity when records from both Ireland and the UK were pooled together.

In conclusion, current within-country parameters have been updated and demonstrate the merit of conducting genetic evaluations on a breed by breed basis rather than across breed. Results from this thesis also reveal that across-country genetic evaluations will be of significant benefit to the sheep industry in both Ireland and the UK if implemented in the future. There is huge potential in terms of both genetic and economic gain from producing international evaluations. Although the present study focused on live body weight and carcass traits, there is scope to include a range of maternal and other important animal traits as well as incorporating more breeds and countries into these international evaluations and this should be investigated in the future.

Lay Summary

Growth, live body weight measurements during the growth phase and carcass composition (for example muscle and fat depth) are key factors that can determine the profitability of Irish and UK sheep farms. In general, the most profitable lambs on any sheep farm are those that grow quickly and efficiently with sufficient amounts of muscle and fat. There are numerous factors that affect this including, the genetics of the lamb and also the environment the lamb is reared in. In order to increase the profitability of Irish and UK sheep enterprises we need to be able to determine which animals are genetically superior to others and implement informed selection decisions. At present, both Ireland and the UK have their own individual systems of conducting genetic evaluations (estimating the genetic merit of individual animals) meaning that Irish and UK sheep cannot accurately be compared to one another at a genetic level. However, because of the high levels of trade of breeding stock that occurs between these countries it is possible to produce a common international evaluation system across the two countries. This international evaluation system will provide an accurate method of comparing animals to those both in their own country of origin as well as with other foreign breeding stock allowing farmers a wider range of selection candidates to choose from.

National data recorded on farms in both Ireland and the UK was used to produce results for this thesis. Using statistical methods, an updated genetic evaluation system was developed for both Ireland and the UK on a within-country basis as well as a joint across-country evaluation for the two countries. Results from

this thesis show that variation in growth and carcass composition between lambs is dependent on numerous factors; however, the genetic profile of the animal has a large part to play in this with high levels of variation observed within the same breed as well as across different breeds. This means that offspring from two different rams of the same breed could have different levels of performance for the same trait. These within-country evaluations provide an important tool that allows producers to select the top performing animals as future breeding stock. In addition to the updated within-country evaluations, the newly developed international evaluations will be extremely beneficial to sheep farmers as higher levels of genetic gain can be achieved through the use of this selection tool. Not only will this allow breeders to accurately select and compare breeding stock in both countries, it will also greatly increase the number of genetic selection candidates breeders have to choose from. This in turn will lead to faster rates of genetic gain being achieved and increasing levels of performance within the sheep industry in the future.

List of Abbreviations

AHDB	Agriculture & Horticulture Development Board
AI	Artificial Insemination
EBV	Estimated Breeding Value
kg	Kilogrammes
mm	Millimetres
UK	United Kingdom
USA	United States of America

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Chapter 1: General Introduction

1.1 The sheep industry

1.1.1 The international sheep industry

Globally, sheep meat accounts for approximately 3% of total meat consumption (Rancourt and Raoul, 2013). Australia and New Zealand are some of the largest producers of sheep meat in the world accounting for over 90% of worldwide sheep and goat meat exports (GIRA, 2016). Sheep production in these countries is on a different scale to both Ireland and the UK in terms of flock numbers and also highly different breed composition. While breed composition may be different there are still some common breeds, for example Texel and Suffolk that are raised in multiple countries. In Ireland a trial is currently underway to compare Irish and New Zealand genetically elite animals. Animals of high genetic merit from New Zealand were exported to Ireland in order to be able to compare them in a common environment (Teagasc, 2017). This was one of the first steps in generating international genetic comparisons between animals from different countries without having to consider genotype by environment interactions. This will also show us if there is a role for New Zealand genetics in an Irish pasture-based system (Teagasc, 2017).

1.1.2 UK and Irish Sheep Industry

The main challenges facing the sheep industry are to improve efficiency, safeguard sustainability and increase profitability. These challenges have many contributing factors including the often part-time nature of sheep farming, lack of scale particularly in Ireland, increasing compliance costs that are associated with environmental sustainability, high capital costs associated with management systems, high labour input costs and increasing competition in markets. All these factors have significantly contributed to the low levels of profitability seen on sheep farms, which has led to declining sheep numbers (Byrne *et al.*, 2010). There are currently over 16 million breeding ewes in the UK (AHDB, 2016) and approximately 2.6 million breeding ewes in Ireland (DAFM, 2019). Sheep meat production in the UK is currently at about 300 thousand tonnes per annum (AHDB, 2016) and Irish sheep meat production is currently at 67.5 thousand tonnes per annum (Bord Bia, 2019). There is room for improvement and expansion in both countries in terms of sheep numbers and, more importantly, output per livestock unit. Genetic improvements in the breeding flock will enable both countries to achieve the desired improvements while also tackling the major challenges currently facing the sheep industry.

Profitability is one of the main influencing factors driving the sheep industry in both Ireland and the UK. Genetic improvement has a key role in increasing profitability within the sheep industry and in the UK an economic benefit of £10.7 million annualised has been achieved from genetic improvements alone (Amer *et al.*, 2015). However, the returns realised from the improvement in genetic merit thus far has been substantially below its potential. This has mainly been due to the fact that terminal breeds have increasingly been used to generate replacements for the breeding flock which has had detrimental effects on the maternal performance of the ewe flock (Amer *et al.*, 2015). One of the main drivers of profitability in the sheep industry is the number of lambs slaughtered per breeding ewe. This figure has remained relatively static in Ireland at 1.3 lambs/ewe for the past number of years due to the influence of terminal sires (Europa.eu, 2017); however, there is much scope for improvement. Environmental sustainability can be improved by improving residual feed intake which will reduce emissions and also increase profitability.

However, improving the genetic merit for traits such as this can be slow because of the scarcity of appropriate phenotypic records in large-scale, low heritability and economic competition for progress in other traits (Alcock and Hegarty, 2011). Under the UK Low Carbon Transition plan, the government hopes to cut farming and waste emissions by 6% by 2022 (HM Government, 2009). It has also been suggested that hill sheep farming results in the production of a higher level of greenhouse gas emissions per kg meat produced than lowland sheep farming (Jones, 2014). Increasing the level of output per lamb by increasing individual animal performance will improve efficiency and also have a big impact on improving profitability.

Whilst there have been significant levels of genetic gain achieved in the sheep industry so far, there is great potential within the industry to accelerate the rate of genetic improvement. The economic response to selection in Ireland, in both the maternal and terminal indices (explained below) has been a gain of €0.27 and €0.28 per year, respectively (Santos *et al.*, 2015). Some of the main factors that have been acting as barriers to achieving faster rates of genetic gain include a lack of education, lack of reward from the marketplace, data quantity and quality problems due to the focus on terminal traits, and also socio-economic factors such as the age profile of the farming population. There is a severe lack of education and understanding in the area of genetic selection when it comes to farmers, veterinarians and other industry professionals. This in turn has led to a poor understanding of the key performance indicators which drive profitability on farms. The lack of knowledge within the farming population about genetic evaluations of animals has also led to poor selection decisions when purchasing rams as too much emphasis is placed on the appearance of the animal. This in turn may lead to higher genetic merit animals receiving lower prices at sales which only acts to encourage pedigree breeders to continue focusing on animal phenotypes rather than incorporating genetic evaluations into their breeding programmes as well. Additional factors in terms of the marketplace that have been responsible for the slower pace of genetic gain include the EUROP grading system, subsidies, excessive feeding and management of rams for sale and also the scarcity of objective information at sales. Data quality and quantity has also greatly impacted on the rate of genetic gain achieved. Much of the current data focuses on terminal traits with relatively little focus on maternal traits of economic importance. Other issues with data have also been due to inaccurate recording, absence of automation and lack of technology use as well as a severe scarcity in commercial data (Amer *et al.*, 2015).

1.2 Traditional methods of genetic improvement

Since the domestication of the sheep in 9000 BC, farmers have been making selection decisions based on phenotypes to select for desirable traits (Brito, 2016). This selection based on phenotype alone has greatly slowed down the rate of genetic gain as it is not taking into account the environmental effects which have an impact on the phenotypic measurements. This may lead to selection which does not optimise genetic potential for superior performance (Mofakkarul Islam *et al.*, 2013). Selection on quantitative traits in livestock has allowed for substantial gains to be made in terms of genetic improvement for agricultural productivity (Dekkers and Hospital, 2002). Many of the traits that we select for in sheep production are complex quantitative traits. This means that they are controlled by numerous genes, as well as environmental factors and also that the underlying genes have quantitative effects on the phenotype (Dekkers and Hospital, 2002).

Predicted genetic gain from selectively breeding the best individual animals is primarily a function of the accuracy and intensity of selection as well as the genetic variance of the traits of interest (Woolliams *et al.*, 1999). The accuracy selection reflects the accuracy of the genetic evaluation, which is influenced by the amount of information for each animal and its relatives, the heritability of the trait, the amount of information from correlated traits and strength of these correlations, and the number of animals being compared (Signet, 2014). Selection intensity is the proportion of superior animals being selected from the pool of all potential selection candidates. In order to increase the selection intensity to improve the rate of genetic gain without negative effects such as inbreeding, we need to increase the size of this pool (Genesus, 2017). The heritability of a trait shows how much of the variation in a specific trait is influenced by the animals' genes and also the strength with which these particular traits are inherited (AHDB, 2015). Reproduction and survival traits generally have low heritabilities, whereas growth and carcass composition traits usually have relatively high heritabilities (Signet, 2014). The correlation of two traits describes the direction and strength of association between the two traits. If we only have information on one trait we can still make a prediction based on what we know about the correlation between them which in turn enhances the accuracy (Signet, 2014). In order to achieve genetic improvement in livestock selection programmes we need to define clear breeding objectives for traits that are of high importance. This requires large volumes of accurate data so that genetic evaluations can be carried out on these traits. After we have developed these genetic evaluations, we must then develop a breeding programme to exploit them.

There has already been significant progress in terms of genetic improvement in the sheep industry, particularly in the last 10 to 15 years. However, there is still huge potential within each industry to improve this rate of genetic gain. This is particularly evident when we compare to the dairy and beef cattle industry. In the USA average milk production per cow increased by 5,997 kg between 1957 and 2007 with 56% of this increase being due to genetic improvements (Oltenacu and Broom, 2010). This has been relatively easily achieved in the dairy sector due to the use of artificial insemination as well as intense selection based on progeny testing of bulls and the distribution of semen from high genetic merit bulls for production traits worldwide (Oltenacu and Broom, 2010). However, this is not quite as easy with meat sheep as there is very little use of artificial insemination particularly at a commercial level in the sheep industry; however, there have been good rates of genetic improvement seen in easy to measure traits such as live body weight and growth rate.

Genetic selection methods that are based on quantitative techniques involves the use of statistical analysis of combined phenotypic and pedigree information in order to produce Estimated Breeding Values (EBVs) of individual animals for each breeding goal trait. These EBVs are then used to rank candidate animals for selection, so that only the animals with the highest genetic merit are used for breeding. By using this principle for selection over several generations we achieve genetic improvement for the trait in question (Muir, 2007). Estimated Breeding Values are often calculated by using a computational method known as the best linear unbiased prediction, which involves solving a set of simultaneous equations including the unknowns, the genetic value of each animal and the effects of management and environment on that particular animal's performance. This approach quantifies the unknown genetic component adjusted for all other factors affecting the traits of interest (Signet, 2014). The improvement of genetic merit in livestock is cumulative, permanent and cost effective, and this is attained by selecting animals we want to use as breeding stock based on the EBV ranking system (Simm, 1998).

1.3 Factors affecting live body weight and carcass composition traits

1.3.1 Genetic factors

In order for a selective breeding programme to succeed it is vital that genetic variation exists and is known for economically important traits that constitute the breeding goal (Fogarty, 1995). Numerous studies have produced heritability estimates and genetic correlation estimates for live body weight and carcass composition traits and a review of these parameter estimates was produced by Safari and Fogarty (2003) highlighting the high levels of variation that exists within these traits in numerous different sheep populations worldwide. Traditionally genetic parameters were produced using small research flocks (Wolf *et al.,* 1981; Mousa *et al.,* 1999) or sire referencing schemes (Simm *et al.,* 2001; Simm *et al.,* 2002); however, these were not always representative of the entire population (Safari and Fogarty, 2003). In addition, more recent studies using crossbred animals have been used to determine genetic parameters for live body weight, carcass composition and meat quality traits through a combination of performance and slaughter records

(Brito *et al.*, 2017; Massender *et al.*, 2019) with some studies also incorporating video image analysis technology as well (Rius-Vilarrasa *et al.*, 2008). While slaughter records are an extremely useful way of measuring carcass composition traits in sheep, this is not an option for breeding stock which means that alternative ways of measuring carcass composition such as ultrasound scanning and CT scanning (Bünger *et al.*, 2011) must be used.

Although numerous methods are used to collect data for generating genetic parameters for live body weight and carcass composition traits, heritability estimates tended to be relatively mixed with both high and low heritability estimates observed for these traits regardless of the method used, with the breed and sample reference population appearing to be more of an influencing factor. Safari and Fogarty (2003) produced a comprehensive report of heritability estimates from the literature worldwide for all sheep production traits. Heritability estimates for live body weight traits ranged from 0.01 for pre weaning weight (Notter and Hough, 1997) to 0.89 for weaning weight (Aslaminejad and Roden, 1997) and heritability estimates for carcass composition traits ranged from 0.01 for fat depth in Poll Dorset sheep (Gilmour *et al.*, 1994) to 0.59 for muscle depth in French meat sheep (Bibe *et al.*, 2002). In addition to this variation that was observed among traits, there is also much variation observed between breeds for the same trait (Maxa *et al.*, 2007; Zishiri *et al.*, 2014). Strong genetic correlations between live body weight and carcass composition traits have also widely been reported in the literature (Safari and Fogarty, 2003) with genetic correlations of up to 0.98 reported between live body weight traits, namely, weaning weight and post weaning weight (Snyman *et al.*,

1998) and genetic correlations of up to 0.82 between live body weight and fat depth recorded at the same time point (Lee *et al.*, 2002).

Genetic improvement in live body weight and carcass composition traits in sheep is vital in the aim to improve both profitability and production efficiency on sheep farms worldwide. The phenotypes of these traits expressed by the animals are highly influenced by genetic factors. The high levels of variation generally reported for live body weight and carcass composition traits in the literature indicate that more informed selection decisions could lead to huge improvements being achieved for these traits across a multitude of breeds.

1.3.2 Management factors

Live body weight and carcass composition traits are not only influenced by genetic factors but also by environmental and management factors at a flock level. Numerous environmental factors affect live body weight gain and carcass composition in lambs including: diet, the rearing type of the lamb (whether the lamb is reared as a single, twin or triplet), and also the sex of the lamb as male lambs tend to grow faster than female and wether lambs (Crouse *et al.*, 1981; Hanrahan, 1999). Carcass value can be determined by carcass weight, fatness and conformation (Jones *et al.*, 2004a), all of which can be influenced by management factors. Reducing the number of days required for a lamb to reach its target slaughter weight is one of the key drivers of on farm profitability (Byrne *et al.*, 2010) and lamb nutrition is one of the key management factors that affect this. There is currently significant emphasis being placed on sensory and health qualities of meat and there is evidence to suggest that altering a lambs diet can have positive effects on lamb meat quality (Ponnampalam *et* *al.*, 2016) and meat tenderness (Ramírez-Retamal and Morales, 2014). Different lamb diets have an impact on carcass weight in comparison to live body weight at slaughter and also on carcass fat levels (De Brito *et al.*, 2017). Lambs that are fed on a grass only diet tend to grow slower and have leaner carcasses than those fed on a high concentrate or forage crop diet (De Brito *et al.,* 2017). The inclusion of concentrates in the diet of pasture based lambs can have a positive impact not only on improving the growth rate of lambs but it also allows lambs to be slaughtered at lighter weights in comparison to grass only fed lambs due to having a greater carcass weight and a better carcass yield (Priolo *et al.*, 2002). Feeding concentrates, however, comes at a cost and although this may be cost effective for some farmers, other factors of the management system at farm level can also have an impact on profitability.

Other management factors that can influence profitability on farm include stocking rate and prolificacy potential with a higher output per hectare significantly increasing farm profitability (Bohan *et al.*, 2018). Although a higher weaning rate and stocking rate will tend to reduce live body weight gain in a grass based system, the increase in profitability, even with the inclusion of concentrates into the lambs diet, was still significantly greater than the less intensive systems evaluated by Bohan *et al.* (2018). This increase in profitability achieved could also be improved upon by selecting for more efficient animals through the use of performance recording on farms. Ideally, all farmers should be performance recording all animals on farm in order to improve production levels; however, this is not a realistic option for the majority of sheep farmers. The extensive nature of hill sheep farming combined with the fact that many sheep farms are currently managed on a part time basis, have resulted in a lack of time and resources being available for on farm recording of important live body weight and carcass composition traits among others. Through a combination of improved on farm management and the use of genetic selection tools there is huge potential for increased profitability and efficiency on farm through the improvement of live body weight and carcass composition traits.

1.4 Current genetic evaluations in Ireland and the UK

1.4.1 Irish Genetic Evaluations

Ireland began genetically evaluating sheep in the 1990's (Murphy *et al.*, 1999) although this was largely ineffective and a significant move away from sheep farming saw the national sheep flock decline in numbers from its peak at 4.8 million in 1992 to its lowest number at 2.35 million in 2010 (Keady and Hanrahan, 2016). A new breeding strategy was implemented by the Irish Cattle Breeding Federation and Sheep Ireland aiming to increase maternal efficiency and also reduce costs to improve profitability (AbacusBio, 2017). Sheep Ireland now runs all of the Irish genetic evaluations for sheep. This incorporates the EBVs with the economic value of the trait to give a value of how profitable a breeding animal's progeny will be in comparison to the average animal. Within sheep Ireland the breeding objective is developed through the terminal and maternal index (Pabiou *et al.*, 2014). The terminal index ranks animals based on their ability to produce lambs with high growth rates, survivability and lambing ease and the maternal index ranks animals based on their ability to produce daughters with strong maternal characteristics as well as taking terminal traits such as growth rate into account (Pabiou *et al.*, 2014).

Each trait is weighted based on its economic value and the traits of greater importance are given a higher emphasis based on this economic value and this is shown in Figure 1.1. For example, days to slaughter which is part of both the terminal and maternal indices has the highest relative emphasis in the terminal index at 47.37% (Bohan *et al*., 2019). This, however, is not surprising considering the relative emphasis that is placed on production traits in both the terminal and maternal index at 62.56% and 41.65%, respectively (Bohan *et al.,* 2019). In the maternal index emphasis on traits is much more evenly spread with the highest emphasis being placed on number of lambs born with a relative emphasis of 18.19% (Bohan *et al*., 2019).

Originally, Sheep Ireland had all the evaluations contained in one index but in 2013 the decision was made to split the Sheep Value Index that was already present into two indices. These new indices are known as the Terminal Index and the Replacement Index. The terminal index ranks animals based on growth and carcass traits such as growth rate, days to slaughter and lambing difficulty. The Replacement index ranks animals based their expected maternal performance and looks at traits such as: milk yield, lamb survivability and lambing ease. Both of these indices measure the genetic ability of an animal’s progeny to generate profit at farm level (Sheep Ireland, 2017). Genetic values are expressed according to the Eurostar rating system on a scale from 1 to 5 with each unit representing an interval containing 20% of the breeding population (ICBF, 2013).

Sheep Ireland is currently working with data recorded from both pedigree sheep breeders and commercial sheep breeders. The pedigree data is in the

LambPlus scheme in which there were 600 flocks being recorded in 2015 with this number steadily increasing as time goes on. Commercial data is analysed through the central progeny test schemes. Flocks within these schemes use artificial insemination (AI) on all of the ewes and each flock uses a number of different rams in order to evaluate as many new sires as possible every year while also creating linkage between new bloodlines and improving already existing bloodlines as much as possible. In 2016, 32 rams of 6 different breeds were successfully used for AI across 5 participating flocks comprising of over 2,880 ewes (Sheep Ireland, 2017).

LambPlus has expanded from 87 breeders in 2009 to currently over 600 pedigree breeders participating in the scheme with approximately 22 different breeds including: Texel, Suffolk, Charollais, Vendeen, Belclare, Bluefaced Leicester, Border Leicester, Galway, Easy Care, Lleyn, Blackface Mountain, Rouge de l'Ouest, Mayo Connemara, Beltex, Ile de France, Hampshire Down, Cheviot, Dorset, Lanark, Primera, and Shropshire. However, 10 of these breeds have 5 or less breeders involved which is severely limiting the effect that genetic evaluations are having on these breeds (Sheep Ireland, 2017). This large increase in uptake from breeders shows that sheep farmers are now beginning to see the potential of genetic evaluations in terms of flock improvement.

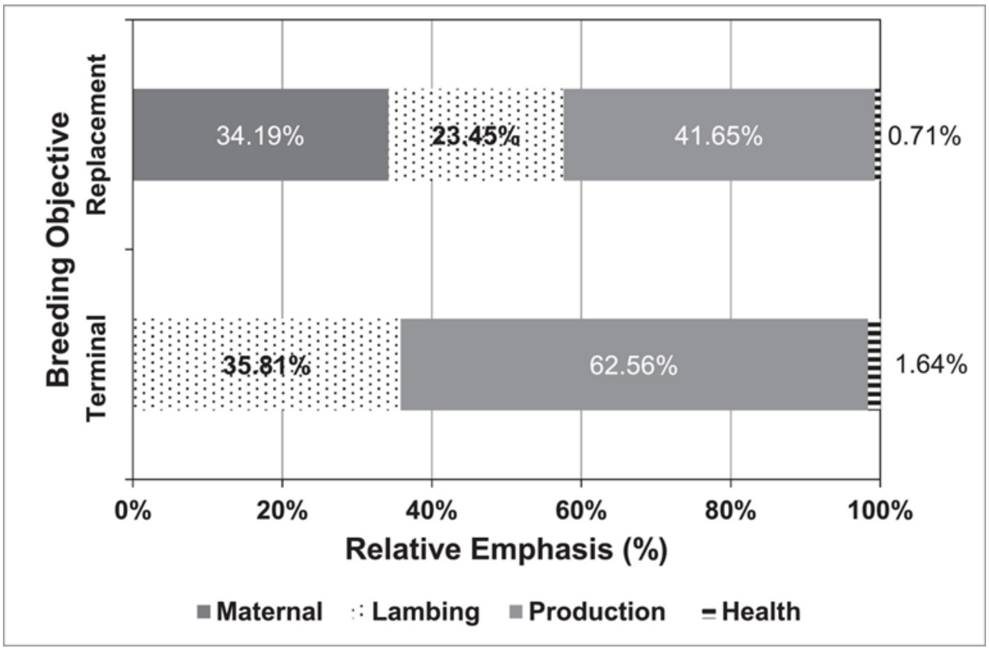

Figure 1.1 Relative emphasis based on the economic contribution for each trait group (maternal, lambing, production and health) in the national terminal and replacement breeding objective (Bohan *et al*., 2019).

1.4.2 UK National Genetic Evaluations

Initially UK national genetic evaluations of sheep were solely based on terminal sires for traits such as carcase and growth characteristics. This was done by using the Terminal Sire Index selection index which had been developed for the main terminal breeds such as the Charollais, Texel and Suffolk. This index was designed to increase lean meat yield while trying to reduce levels of associated fat yields (Simm and Dingwall, 1989). Although significant levels of genetic gain were achieved, selecting solely for genetic improvement in these terminal traits had a negative impact on the genetic merit of the maternal traits e.g. milk production and prolificacy (AHDB, 2015). Another selection index known as the Hill Index attempts to incorporate both maternal and production traits for common hill breeds such as the Scottish Blackface and the North Country Cheviot. This index includes traits such as the maternal ability of the ewe, the number of lambs reared to weaning per ewe, and lamb performance traits (Conington *et al.*, 2001).

Currently Signet, which is part of the Agriculture and Horticulture Development Board (AHDB) beef and lamb sector, provides genetic evaluations to livestock producers in the UK. The genetic analyses are provided by the Edinburgh Genetic Evaluation Services. Signet currently produces 5 breeding indices. Breeding indices allow for each trait to be individually weighted according to its economic importance within the index in order to meet a specific or set of breeding objectives. The indices currently being used are the Terminal Sire Index, the Maternal Index, the Longwool Index, the Welsh Index/ Carcase + Index and the Hill 2 Index. The traits that are currently being measured across all sheep breeds are 8-week weight, mature size, litter size, maternal ability, scan weight, muscle depth and fat depth. In some breeds there are also EBVs available for faecal egg counts for both strongyles and nematodirus and a combination of both, as well as traits such as birth weight and lambing ease. A small number of sheep from specific breeds have also undergone CT scanning and so have EBVs for CT fat, CT lean and CT muscularity. An overall EBV index across all the traits is available (Signet, 2014).

1.4.3 International Genetic Evaluations

International genetic evaluations based on pooled data from multiple countries have proven to be feasible in dairy and beef cattle; however, there has been very little work done in terms of across-country genetic evaluations in sheep. Access to international evaluations on relevant breeds between countries will allow farmers to make more informed decisions when selecting breeding stock which will result in increased levels of genetic gain and increased profits (Wickham and Durr, 2011). This is particularly important when there is a high level of trade of pedigree breeding stock across-country borders, as is the case between Ireland and the UK. By expanding genetic evaluations internationally, we can increase the size of the breeding population for comparison with larger progeny group sizes which could lead to more accurate EBVs and increased rates of genetic gain.

There are numerous issues to consider when addressing international genetic evaluations including data accessibility, handling and validation, genotype by environment interaction, genetic connectedness between populations in different countries and model selection (Fouilloux *et al.*, 2006). To alleviate some of these issues, previous studies in dairy cattle focused on the combination of existing national genetic evaluation results (Schaeffer, 1994), which is the method currently used by the International Bull Evaluation Service (Interbull, 2020). This also allows us to preserve the knowledge and data quality control at a national level (Phocas *et al.*, 2005).

International genetic evaluations are currently also being successfully calculated in beef cattle through the Interbeef initiative (ICAR, 2020), based on individual animal records from multiple countries. Interbeef produces international genetic evaluations for live body weight and carcass traits across 12 different countries for purebred Charolais, Limousin, Simmental, Aberdeen Angus and Hereford cattle (ICAR, 2020). The feasibility of a joint genetic evaluation of beef cattle by pooling individual animal data from Ireland and the UK has also been demonstrated by Englishby (2018).

The sheep industry is relatively similar to the beef industry in terms of the importance and emphasis that is placed on the improvement of terminal traits and the development of international genetic evaluations for sheep could follow that of beef. Currently no international genetic evaluations exist for sheep for globally used breeds. The results from the work conducted within this PhD could initiate the development of an international genetic evaluation system across multiple countries and breeds worldwide.

1.5 Objectives and thesis outline

The overall aim of this thesis was to enhance the genetic evaluations for sheep live body weight and carcass composition traits in Ireland and the UK. Specific objectives were to:

1. Update the existing within-country genetic evaluations in the two countries.
2. Examine the feasibility of and develop a joint across-country genetic evaluation system.

Chapter 2 of the thesis addresses the first objective and provides estimates of genetic parameters and breeding values for a range of live body weight and carcass composition traits for purebred Texel, Suffolk and Charollais sheep raised in Ireland. This Chapter determines whether it would be beneficial to produce genetic parameters on a within breed basis for purebred Irish sheep, which in turn could lead to more accurate genetic evaluations within-country.

Chapter 3 also addresses the first objective by quantifying the genetic variation present in key live body weight and carcass composition traits within the same sheep breeds as Chapter 2 raised the UK. The study establishes whether genetic variation still exists within the UK sheep population after over 30 years of genetic selection and assesses models for future genetic evaluations.

Chapter 4 addresses the second objective of the thesis. This study draws on outcomes from the previous two Chapters and assesses the feasibility and potential benefits that an across-country genetic evaluation system could produce in terms of increasing the rate of genetic gain for live body weight and carcass composition traits in Ireland and the UK.

Chapter 2: Genetic analysis of live body weight and carcass composition traits in purebred Irish Texel, Suffolk and Charollais lambs

2.1 Chapter Introduction

Live body weight and carcass composition data are routinely collected to produce genetic evaluations for popular terminal sheep breeds in Ireland. At present genetic parameters used in current evaluation systems have been estimated collectively for all breeds in the national population. This Chapter determines differences between breeds in estimates of genetic parameters and breeding values for three live body weight and two carcass composition traits within purebred Irish Texel, Suffolk and Charollais lambs. This Chapter has been published in the Journal of Animal Science (https://doi.org/10.1017/S1751731119002908) and the results address the first objective of this thesis. All work conducted related to this Chapter was completed by the PhD candidate under guidance from supervisors and in collaboration with all listed co-authors of the manuscript.

2.2 Manuscript

Genetic analyses of live body weight and carcass composition traits in purebred Texel, Suffolk and Charollais lambs

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Short title: Genetics of lamb weight traits

Abstract

Lamb live body weight is one of the key drivers of profitability on sheep farms. Previous studies in Ireland have estimated genetic parameters for live body weight and carcass composition traits using a multi breed population rather than on an individual breed basis. The objective of the present study was to undertake genetic analyses of three lamb live body weight and two carcass composition traits pertaining to purebred Texel, Suffolk and Charollais lambs born in the Republic of Ireland between 2010 and 2017, inclusive. Traits (with lamb age range in parenthesis) considered in the analyses were: pre weaning weight (20 to 65 days), weaning weight (66 to 120 days), post weaning weight (121 to 180 days), muscle depth (121 to 180 days) and fat depth (121 to 180 days). After data edits, 137 402 records from 50 372 lambs across 416 flocks were analysed. Variance components were derived using animal linear mixed models separately for each breed. Fixed effects included for all traits were contemporary group, age at first lambing of the dam, parity of the dam, a gender by age of the lamb interaction and a birth type by rearing type of the lamb interaction. Random effects investigated in the pre weaning and weaning weight analyses included animal direct additive genetic, dam maternal genetic, litter common environment, dam permanent environment and residual variances. The model of analysis for post weaning, muscle and fat depth included an animal direct additive genetic and litter common environment effect only. Significant direct additive genetic variation existed in all cases. Direct heritability for pre weaning weight ranged from 0.14 to 0.30 across the three breeds. Weaning weight had a direct heritability ranging from 0.17 to 0.27 and post weaning weight had a direct heritability ranging from 0.15 to 0.27. Muscle and fat depth heritability estimates ranged from 0.21 to 0.31 and 0.15 to 0.20, respectively. Positive direct correlations were evident for all traits. Results revealed ample genetic variation among animals for the studied traits and significant differences between breeds to suggest that genetic evaluations could be conducted on a per breed basis.

Keywords: sheep, Ireland, parameters, growth, muscle

Implications

This study demonstrated the existence of genetic variation between different breeds of sheep for the three main live body weight and two carcass composition traits in the Irish sheep production system suggesting that genetic evaluations should be conducted on a per breed basis. This would allow for more informed and accurate selection decisions on farm, resulting in superior productivity and profitability within Irish sheep flocks.

Introduction

Lamb live body weight and the rate at which the animal grows have been defined as the key drivers of profitability in Irish (Byrne *et al.*, 2010) and international (Cocks *et al.*, 2002; Jones *et al.*, 2004a; Conington *et al.*, 2004) sheep production systems. In Ireland, for example, each additional day a lamb requires to reach its target slaughter weight results in an economic loss of €1.41 per lamb per day (Byrne *et al.*, 2010). In addition to the live body weight traits, carcass composition also has an impact on the profitability of sheep production systems with one increase on the EUROP scale for muscle depth leading to an economic gain of €0.35 per lamb and an increase of one point on the fat scale leading to an economic loss of -€0.52 per lamb (Byrne *et al.*, 2010). Lamb live body weight, weight gain and carcass composition have been shown to vary greatly not only across the various stages of a lambs growth period, such as pre and post weaning (Leymaster and Jenkins, 1993; Djemali *et al.*, 1994; Leeds *et al.*, 2012) but also across a plethora of breeds including meat (Osorio-Avalos *et al.*, 2012), wool (Safari *et al.*, 2007) and dual purpose (Dixit *et al.*, 2001) breeds.

Previous research has shown considerable variability across both pre and post weaning lamb growth rates not only at a phenotypic level (Dixit *et al.*, 2001) but also at a genetic level (Safari *et al.*, 2005; Thiruvenkadan *et al.*, 2011), with heritabilities for lamb live body weight at different ages ranging from 0.15 to 0.41 (Safari *et al.*, 2005). Such studies, however, have tended to focus on small sample sizes, which may not accurately represent the whole sheep population. Furthermore, although some studies have shown that genetic variability exists among breeds (Freking and Leymaster, 2004; Osorio-Avalos *et al.,* 2012), genetic parameters and sheep genetic evaluations in Ireland to date have been developed within a multi-breed population context (Pabiou *et al.*, 2014a) and heretofore the genetic variation within individual breeds has not been considered.

The objective of the present study therefore was to estimate genetic parameters and breeding values for a range of lamb live body weight and carcass composition traits within three breeds commonly recorded in Ireland namely Texel, Suffolk and Charollais. Results from the present study would determine differences between breeds in the genetic evaluations of sheep in Ireland.

Materials and Methods

Data

A full database was extracted across three breeds, namely Texel, Suffolk and Charollais, from Sheep Ireland, the Irish national database (http://www.sheep.ie). Records pertaining to years 2010 to 2017, inclusive, were retained for analyses. Only purebred lambs (as defined by the data records) of the three aforementioned breeds (i.e., Texel, Suffolk and Charollais) were considered in the present study.

In Ireland lamb live body weights are recorded at three time points post lambing by Irish producers using weigh-scales: pre weaning, at weaning and post weaning, the latter coinciding with muscle and fat ultrasound scanning. Based on the editing criteria used for the national genetic evaluations pre weaning weight was defined as live body weight taken between 20 and 65 days of age; only records of lambs weighing between 12.00 and 32.00 kg were retained in the present study. Weaning weight was defined as the live body weight recorded between 66 and 120 days of age and weighing between 20.00 and 55.00 kg. Post weaning weight was defined as live body weight measured between 121 and 180 days of age; only lambs with live body weight records between 25.00 and 75.00 kg were considered for further analysis. Across all live body weight measurements average daily gain was calculated for each lamb with a known birth and weigh date at either of the three weight points; only average daily gains between 100 and 650 g/d were retained for each live body weight measurement (261 lambs with an erroneous average daily gain were omitted from subsequent analyses). Muscle and fat depth traits were recorded on the same day as post weaning weight in all lambs. Only muscle depth measurements within the range of 10 to 44 mm and fat depth measurements ranging within 1 to 23 mm were retained.

Live body weight and carcass composition measurement records were discarded if flock of birth, sire, dam or maternal grandsire were unknown. Dams with no known parity number or a parity number >10 were discarded; parity number was subsequently categorised as 1, 2, 3, 4, or ≥ 5. Age at first lambing was defined based on the age of the ewe at first lambing; ewes were either defined as lambing for the first time as ewe lambs (between 8 and 18 months of age) or those that lambed for the first time as hoggets (between ≥18 and 28 months of age). Birth type was defined as the number of lambs born per lambing event; only birth types between 1 (singles) and 4 (quadruplets) were retained. Rearing type was defined as the number of lambs reared per litter; only rearing type between 1 and 3 were retained for analysis. Lambs that were recorded as artificially reared or reared by a non-genetic dam were not included for further analysis.

For all traits, each lamb was allocated to a contemporary group of breed-by-flock-by-week of weighing. Only contemporary groups containing at least 5 records were retained for analysis. Following all edits described above, 33 721 pre weaning weight records, 32 623 weaning weight records, 28 140 post weaning weight records, 21 468 muscle depth records and 21 442 fat depth records were retained for genetic analysis; the breakdown of records per breed is shown in Table 2.1.

Genetic Analysis

Variance components were estimated for each lamb live body weight trait (i.e., pre weaning, weaning and post weaning weight) and each carcass composition trait (i.e., muscle depth and fat depth) using linear mixed animal models in ASReml (Gilmour *et al.*, 2009) separately for each breed. The model employed was:

$$Y = CG + AFL + Parity + Gender * Age + Birth\ type * Rearing\ type$$
$$+ Animal + Dam + DamPE + Litter + e$$

where Y = lamb live body weight or carcass composition record, CG = contemporary group, AFL = age at first lambing of the dam, Parity = parity of the dam, Gender*Age = the interaction between the gender and age of the lamb, Birth type*Rearing type = the interaction between the birth type and rearing type of the lamb, Animal = random animal direct additive genetic effect, Dam = random maternal genetic effect, DamPE = random dam permanent environmental effect associated with multiple lambing records of the same dam, Litter = common environmental effect reflecting the non-genetic covariance among members of the same litter, and e = random residual effect.

Each model was progressively built up from including just a residual effect to include a direct genetic, maternal genetic, dam permanent environmental and litter common environmental effect. In the case of post weaning weight, muscle and fat depth the model included a direct genetic and a litter common environmental effect only as there was no significant dam effect. A log likelihood ratio test was used to determine if the additional random terms improved the fit of the data (Ferreira *et al.,* 1999). Whilst the maternal genetic and dam permanent environmental effect were not always significant, these effects were kept in the model as the log likelihood ratio test suggested it was the model of best fit.

Direct heritability was calculated as the ratio of the direct additive genetic variance to the observed total phenotypic variance. Maternal heritability was estimated as the ratio of the maternal genetic variance to the total phenotypic variance. Common environmental effect was calculated as the ratio of the litter variance to the total phenotypic variance. Dam repeatability was calculated as the ratio of maternal genetic variance plus permanent environment to the total phenotypic variance. The correlation between the direct additive and maternal genetic effects was also estimated where applicable. Genetic correlations between the studied traits were estimated pairwise using the model previously described in a series of bivariate analyses. Estimated breeding values (EBV) were calculated for each trait and genetic trends were produced from these results by estimating the slope of the average ram EBV per year of birth. Genetic trends were only produced for sires with at least 10 progeny and ranged from 3 to 61 sires per year across all traits and breeds.

Table 2.1 Number of lambs (n), trait mean (μ), standard deviation (SD), coefficient of variation (CV), corresponding mean lamb age, and number of sires, dams, maternal grandsires (MGS), flocks and contemporary groups (CGs) by trait and breed.

Trait (units of measurement)	Breed	n	μ (SD)	Age	CV	Sires	Dams	MGS	Flocks	CGs
Pre Weaning Weight (kg)	Texel	11 891	20.86 (4.70)	46.59	22.53%	804	5 359	1 093	162	480
	Suffolk	8 783	22.32 (4.85)	45.12	21.73%	541	3 816	759	110	329
	Charollais	13 047	20.58 (4.58)	46.20	22.25%	602	4 965	919	139	456
Weaning Weight (kg)	Texel	12 388	36.69 (7.63)	96.92	20.80%	847	5 688	1 176	161	508
	Suffolk	7 839	40.93 (7.87)	96.31	19.23%	542	3 625	774	107	308
	Charollais	12 396	37.09 (7.40)	96.65	19.95%	607	4 820	913	139	449
Post Weaning Weight (kg)	Texel	12 074	48.70 (9.47)	144.76	19.45%	847	5 746	1 179	161	422
	Suffolk	6 819	56.42 (10.79)	147.24	19.12%	508	3 411	753	96	281
	Charollais	9 247	51.92 (9.91)	148.99	19.09%	567	4 106	844	129	354
Muscle Depth (mm)	Texel	8 810	32.59 (4.09)	146.57	12.55%	662	4 259	916	108	280
	Suffolk	5 589	34.11 (5.01)	151.28	14.69%	402	2 792	621	69	204
	Charollais	7 094	33.23 (3.97)	151.81	11.95%	455	3 344	714	96	252
Fat Depth (mm)	Texel	8 782	6.10 (2.70)	146.63	44.26%	661	4 250	916	108	281
	Suffolk	5 556	8.50 (4.00)	151.42	47.06%	399	2 784	618	69	205
	Charollais	7 087	8.10 (3.80)	151.82	46.91%	455	3 346	712	97	253

Results

Phenotypic values and data structure

Edited data used in the genetic analyses are shown in Table 1. The Suffolk breed proved to be heaviest at all three live body weight measurements although they were slightly younger at both pre weaning and weaning weights. The Suffolk breed also had the highest muscle and fat depth among the three breeds studied although this may be attributed partly to the higher weight at scanning. Overall the Texel breed had the highest number of records across all five traits and they also had the highest number of flocks. Judging on the coefficient of variation, the greatest variability was observed in fat depth and the least variability was observed for muscle depth, and this was true across all breeds.

Genetic Parameters

Variance components were estimated (Table 2.2) and heritability estimates were subsequently derived for each trait and breed. All estimates of genetic standard deviation and direct heritability were statistically greater than zero ($P<0.05$) as shown in Table 2.3. All traits studied apart from pre weaning weight were most heritable in the Texel breed. Pre weaning weight was most heritable in the Suffolk breed. Maternal heritability was significantly greater than zero for all weight traits in the Texel breed, pre weaning weight in Suffolks and weaning weight in Charollais. The litter common environmental effect accounted for the majority of the total phenotypic variance for most live body weight traits and a significant proportion for the carcass composition traits.

Negative correlations were estimated between direct additive and maternal genetic effects within trait for all breeds (Table 2.3). This is an antagonistic correlation suggesting that animals with genetically superior direct additive genetic effect are expected to be maternally inferior. Significant (P<0.05) positive genetic correlations between the direct additive genetic effects on pre weaning and subsequent weights for each of the three breeds were calculated (Table 2.4). Direct genetic correlations between live body weight traits and the two carcass composition traits were also strongly positive reaching a maximum of 0.72 (± 0.04) between weaning weight and muscle depth for the Texel breed (Table 2.4).

Table 2.2 Lamb direct genetic variance (V_g^d), maternal genetic variance (V_g^m), variance due to common environmental effect (C_m) and variance due to maternal repeatability (PE_m) per trait and breed; model of analyses of post weaning weight, muscle and fat depth did not include a maternal effect; SE=standard error of estimate.

	Breed	V_g^d (SE)	V_g^m (SE)	C_m (SE)	PE_m (SE)
Pre Weaning Weight	Texel	1.57 (0.27)*	0.58 (0.18)*	2.98 (0.19)*	0.57 (0.19)*
	Suffolk	2.44 (0.40)*	0.56 (0.22)*	3.39 (0.24)*	0.12 (0.23)
	Charollais	1.39 (0.25)*	0.20 (0.13)	3.54 (0.18)*	0.06 (0.16)
Wean Weight	Texel	6.89 (0.81)*	0.98 (0.39)*	6.55 (0.48)*	0.43 (0.43)
	Suffolk	4.79 (1.03)*	0.84 (0.55)	7.85 (0.73)*	0.26 (0.64)
	Charollais	5.77 (0.79)*	0.87 (0.39)*	6.01 (0.45)*	0.18 (0.41)
Post Weaning Weight	Texel	11.94 (1.10)*		8.99 (0.62)*	
	Suffolk	7.42 (1.48)*		11.55 (1.09)*	
	Charollais	6.79 (1.03)*		8.73 (0.74)*	
Muscle Depth	Texel	2.76 (0.28)*		1.39 (0.18)*	
	Suffolk	2.05 (0.35)*		1.48 (0.26)*	
	Charollais	1.70 (0.25)*		1.51 (0.18)*	
Fat Depth	Texel	0.01 (0.00)*		0.01 (0.00)*	
	Suffolk	0.01 (0.00)*		0.02 (0.00)*	
	Charollais	0.01 (0.00)*		0.01 (0.00)*	

*Estimates significantly different ($P < 0.05$) from zero.

Table 2.3 Lamb direct heritability (h^2_d), maternal heritability (h^2_m), proportion of phenotypic variance due to the common environmental effect (**C²m**), maternal repeatability (R_m), and the correlation between direct and maternal genetic effects (CORR d/m) per trait and breed; model of analyses of post weaning weight, muscle and fat depth did not include a maternal effect; SE=standard error of estimate.

	Breed	h²d (SE)	h²m (SE)	C²m (SE)	Rm (SE)	CORR d/m (SE)
Pre Weaning Weight	Texel	0.16 (0.03)*	0.06 (0.02)*	0.30 (0.02)*	0.12 (0.02)*	-0.65 (0.07)*
	Suffolk	0.22 (0.03)*	0.05 (0.02)*	0.31 (0.02)*	0.06 (0.02)*	-0.77 (0.06)*
	Charollais	0.14 (0.02)*	0.02 (0.01)	0.35 (0.02)*	0.03 (0.01)	-0.84 (0.05)*
Wean Weight	Texel	0.27 (0.03)*	0.04 (0.02)*	0.26 (0.02)*	0.06 (0.02)*	-0.61 (0.07)*
	Suffolk	0.17 (0.03)*	0.03 (0.02)	0.27 (0.02)*	0.04 (0.02)	-0.68 (0.09)*
	Charollais	0.23 (0.03)*	0.03 (0.02)*	0.24 (0.02)*	0.04 (0.01) *	-0.71 (0.06)*
Post Weaning Weight	Texel	0.32 (0.03)*		0.24 (0.02)*		
	Suffolk	0.16 (0.03)*		0.25 (0.02)*		
	Charollais	0.18 (0.03)*		0.23 (0.02)*		
Muscle Depth	Texel	0.31 (0.03)*		0.16 (0.02)*		
	Suffolk	0.21 (0.03)*		0.15 (0.03)*		
	Charollais	0.21 (0.03)*		0.19 (0.02)*		
Fat Depth	Texel	0.20 (0.03)*		0.20 (0.02)*		
	Suffolk	0.15 (0.03)*		0.17 (0.03)*		
	Charollais	0.17 (0.03)*		0.17 (0.02)*		

*Estimates significantly different ($P < 0.05$) from zero.

Table 2.4 Lamb genetic correlations (standard error in parentheses) between the direct additive genetic effects for each trait (below the diagonal) and the maternal genetic effects for each trait (above the diagonal) by breed; model of analyses of post weaning weight, muscle and fat depth did not include a maternal effect.

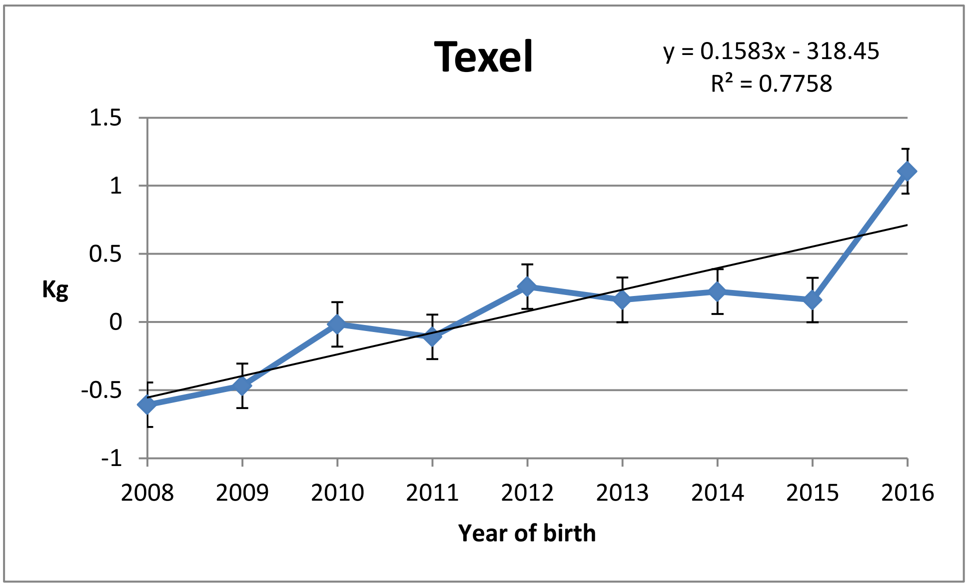
		Pre weaning	Weaning	Post weaning	Muscle depth
Texel	Pre weaning		0.95 (0.03)*		
	Weaning	0.76 (0.04)*			
	Post weaning	0.65 (0.07)*	0.94 (0.02)*		
	Muscle depth	0.57 (0.06)*	0.72 (0.04)*	0.69 (0.03)*	
	Fat depth	0.31 (0.08)*	0.49 (0.07)*	0.45 (0.06)*	0.42 (0.06)*
Suffolk	Pre weaning		0.80 (0.06)*		
	Weaning	0.61 (0.09)*			
	Post weaning	0.76 (0.08)*	0.77 (0.07)*		
	Muscle depth	0.41 (0.09)*	0.23 (0.15)	0.61 (0.07)*	
	Fat depth	0.36 (0.11)*	0.27 (0.16)	0.29 (0.12)*	0.48 (0.09)*
Charollais	Pre weaning		0.97 (0.04)*		
	Weaning	0.55 (0.07)*			
	Post weaning	0.63 (0.07)*	0.90 (0.04)*		
	Muscle depth	0.51 (0.08)*	0.63 (0.07)*	0.54 (0.06)*	
	Fat depth	0.18 (0.10)	0.27 (0.10)*	0.26 (0.09)*	0.41 (0.08)*

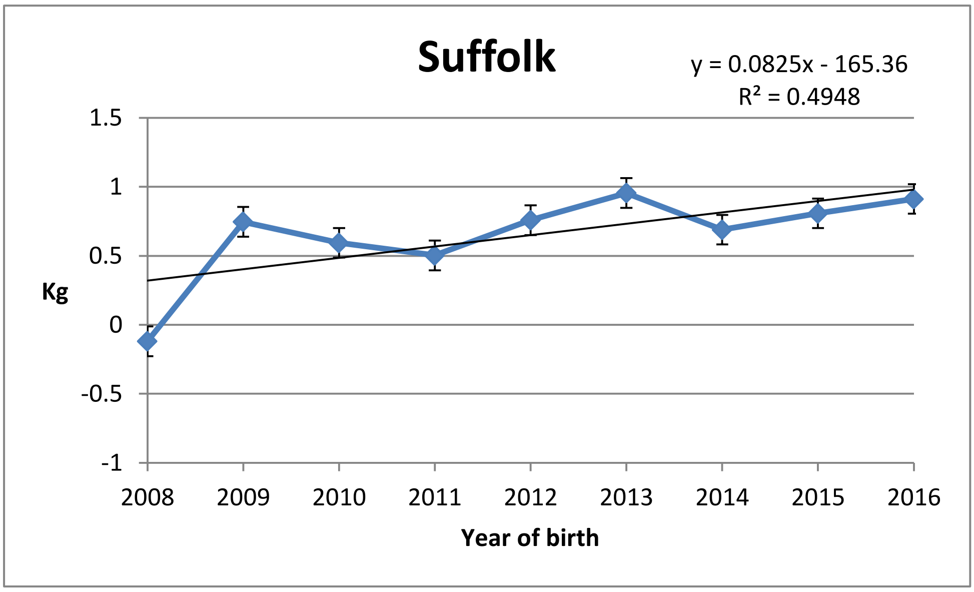
*Estimates significantly different ($P < 0.05$) from zero.

Genetic Trends

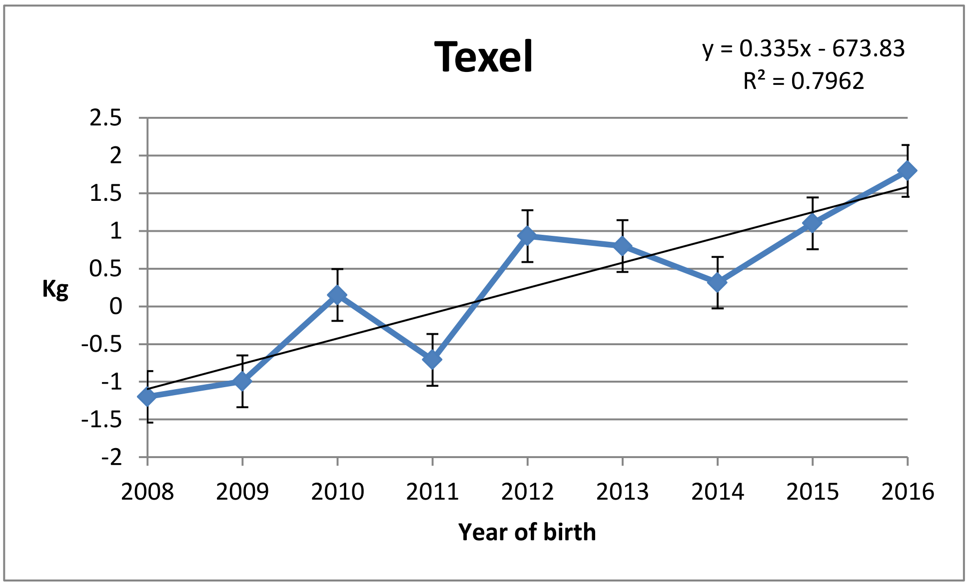
Genetic trends based on EBVs of rams with ≥10 progeny (Figure 1) indicate that positive genetic gain is occurring in all live body weight traits. Significant ($P<0.05$) trends were observed for all live body weight traits in the Texel breed, pre weaning weight in the Suffolk breed and weaning weight in the Charollais breed. Muscle depth had a strong positive significant trend for all breeds, while fat depth had weakly positive significant trends for both the Suffolk and Charollais breeds. There was considerable variation in genetic trends estimated for the same trait among the three studied breeds with higher rates of genetic gain being achieved in the Texel breed for live body weight traits and muscle depth in comparison to the other two breeds.

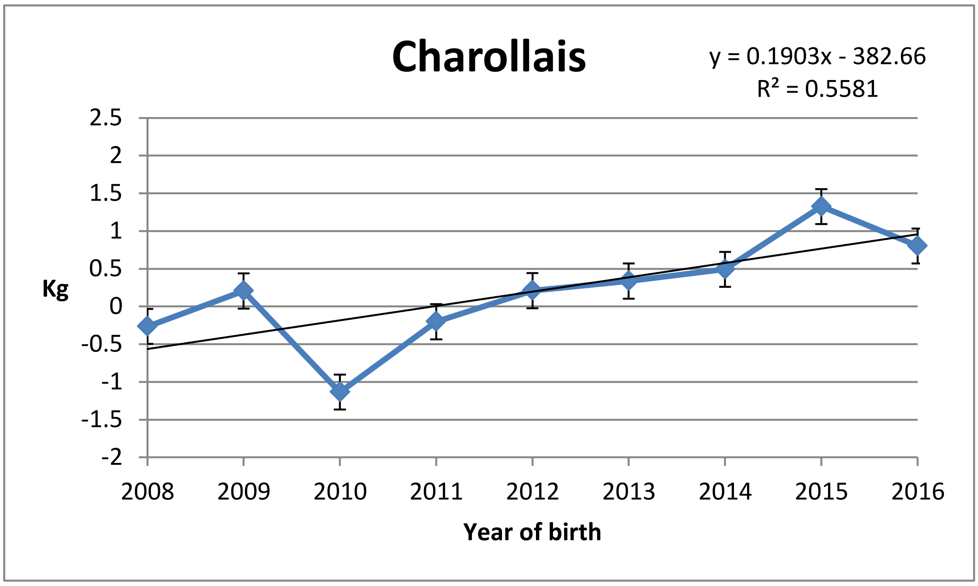
a. Pre weaning weight (kg)



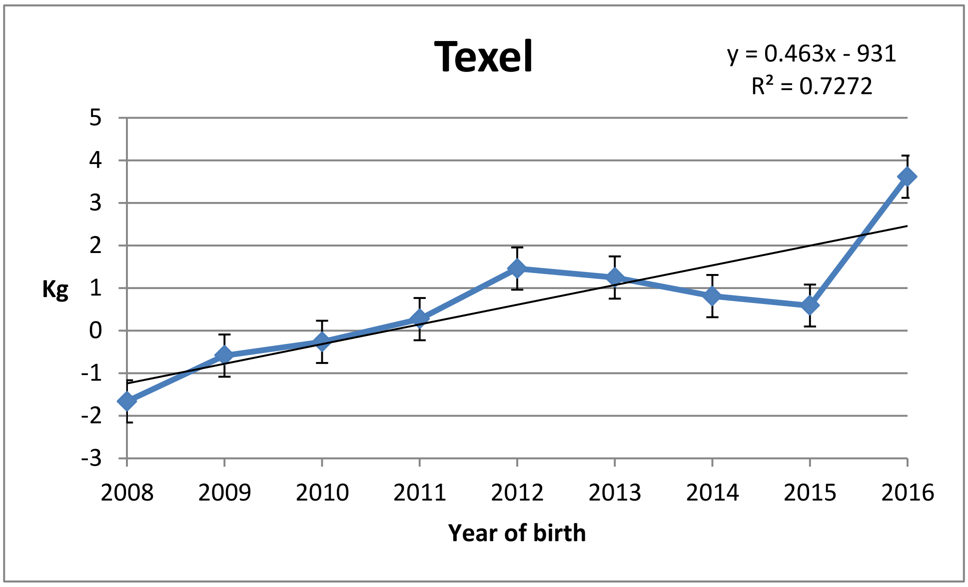


b. Weaning weight (kg)

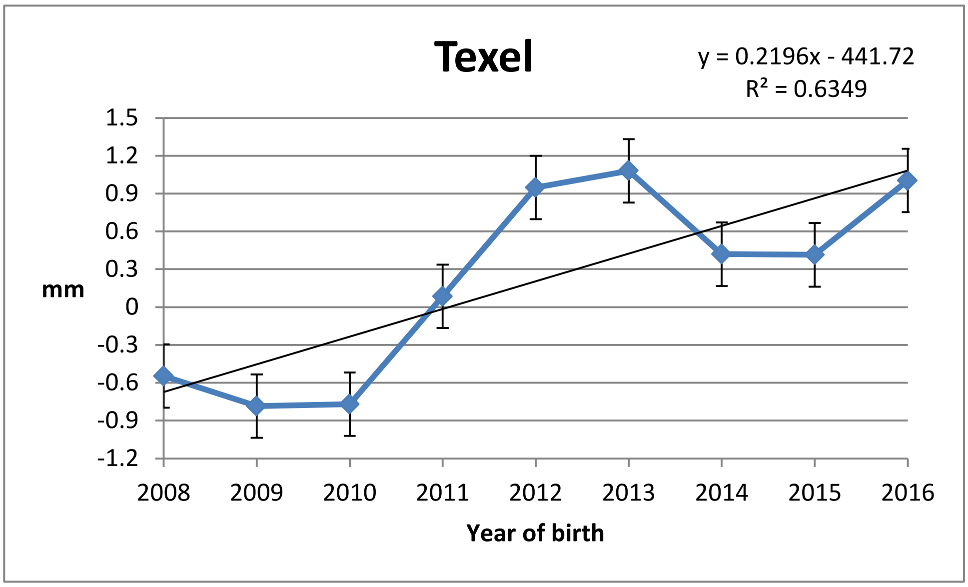


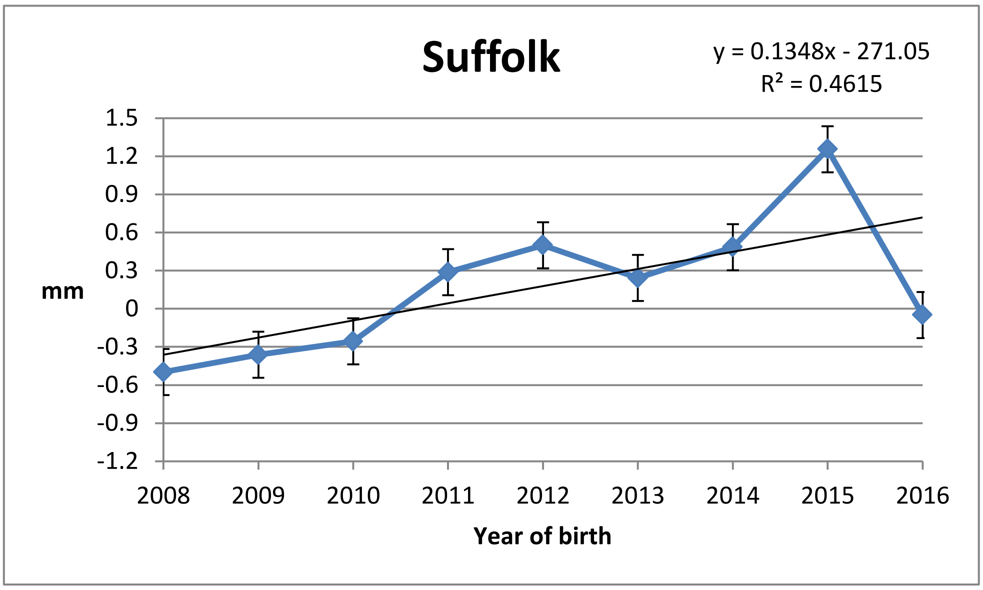


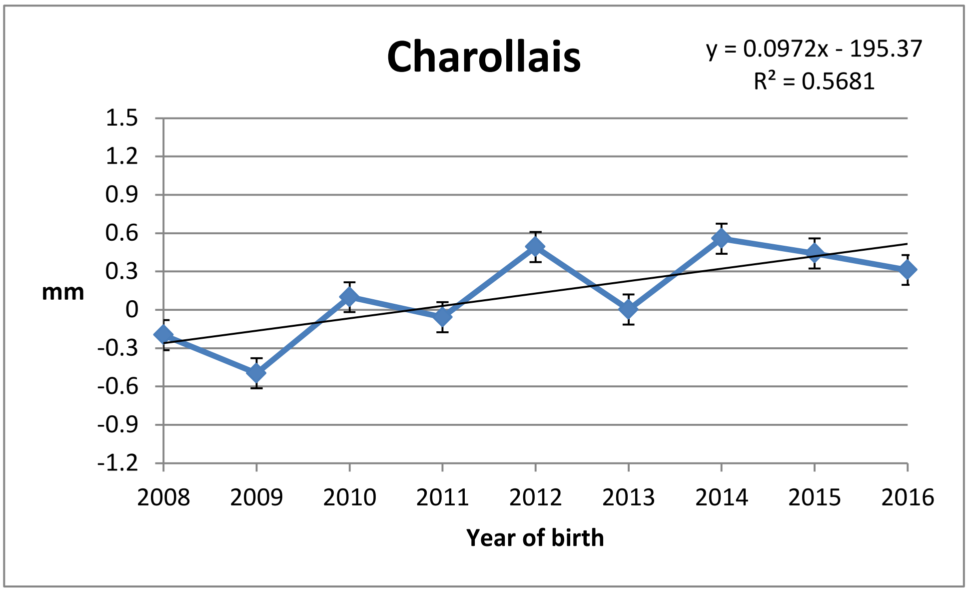
c. Post weaning weight (kg)



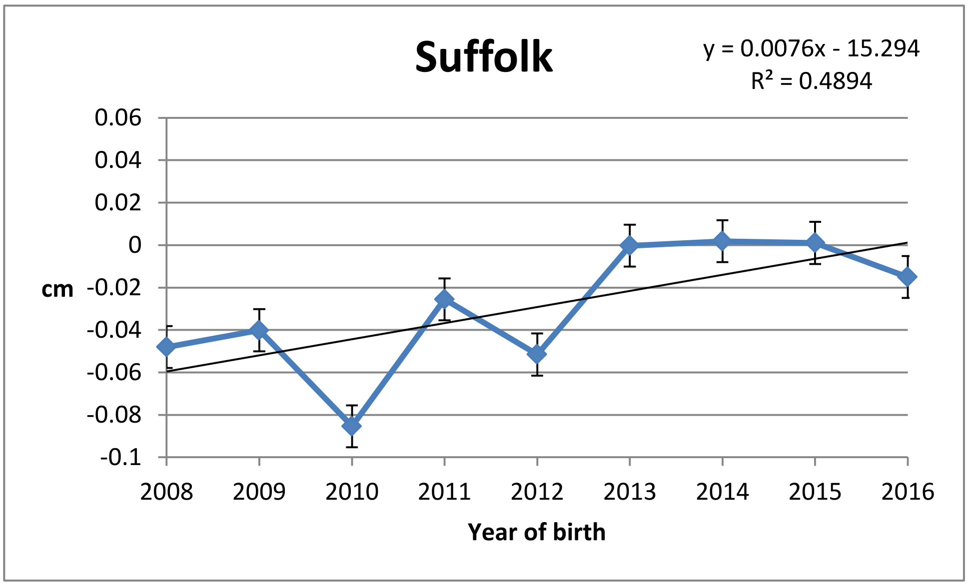
d. Muscle depth (mm)







e. Fat depth (cm)



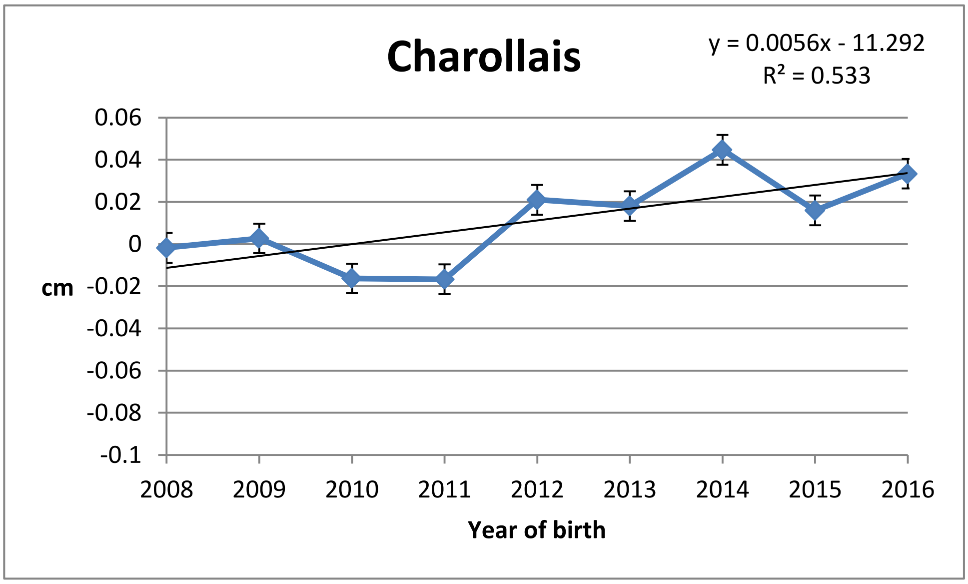


Figure 2.1 Significantly different from zero ($P<0.05$) genetic trends of estimated breeding values of rams (standard errors shown in error bars) for (a) pre weaning weight, (b) weaning weight (c) post weaning weight (d) muscle depth and (e) fat depth.

Discussion

Live body weight measurements on lambs are amongst the key performance indicators in profitable sheep production systems. To date, most genetic studies undertaken in Ireland have tended to estimate genetic parameters for lamb weight and carcass composition traits simultaneously across a range of breeds rather than investigating on an individual breed basis. Therefore, in the present study we investigated if estimates of genetic parameters and breeding values differed between breeds within the Irish sheep population when the breeds were evaluated on a within breed basis. Results showed significant differences in additive genetic variance and direct heritability of each trait between the Texel, Suffolk and Charollais breeds, warranting within-breed genetic analyses.

Phenotypic values

In comparison to previous studies conducted on an Irish sheep population, lamb live body weight in the present study was greater for all three live body weight traits examined. Previously pre weaning, weaning and post weaning weight in Irish purebred lambs was shown to be 19.64 kg, 33.00 kg and 48.00 kg, respectively (McHugh *et al.*, 2016, McHugh *et al.*, 2017). The increased live body weight observed in the current study may be attributed to the fact that only terminal purebred lambs were examined whereas maternal and crossbred lambs had been also included in the previous studies. The carcass composition traits in the present study showed similar results to those previously reported in the literature for purebred Irish lambs. An earlier study conducted in Ireland (O'Brien *et al.*, 2017) showed a mean of 33.21 mm and 7.55 mm for muscle and fat depth traits, respectively. The first study carried out in the UK on live body weight and carcass composition traits in terminal sire sheep was reported by Simm and Dingwall (1989) from which selection indices for terminal sire breeds was implemented in practice for the UK sheep industry and responses to selection reported. Jones et al. (2004) reported similar findings to the present study for post weaning weight, muscle depth and fat depth traits for the three breeds studied in terms of breed ranking however fat depth proved to be considerably higher in the present study. Other studies have been reported for crossbred and hill lambs (Jones et al., 1999; Merrell *et al.*, 1990; Conington *et al.*, 2004). Again these findings were very similar to the present study for the post weaning weight and muscle depth values however, fat depth proved to be higher for all breeds in the present study although the ranking of the breeds remained the same. Merrell *et al.* (1990), reported weight at slaughter for Suffolk, Texel and Charollais crossbred lambs in the UK, which was recorded at a similar age to post weaning weight in the present study, ranging from 39.50 kg (Texel) to 41.10 kg (Suffolk). Although these lambs were lighter than those in the present study the ranking of breeds was similar with the Suffolk breed having the highest live body weight and the Texel breed having the lowest post weaning live body weight. Throughout the rest of the world many studies have recorded live body weight in lambs at different time points however few of these studies have focused on the breeds investigated in the current study (Safari and Fogarty, 2003) although Shrestha *et al.* (1985) reported similar findings for pre weaning and weaning weights in Canadian Suffolks. Furthermore, a US study of Texel and Suffolk sired crossbred lambs (Leymaster and Jenkins, 1993) showed similar live body weight results to the present study with the Suffolk breed proving to be heaviest at both weaning and post weaning weights in comparison to the Texel breed. One contrast observed in Leymaster and Jenkins' (1993) study compared to the present study was that the Suffolk and Texel breeds were recorded to have the same mean weight for pre weaning weight whereas in the present study the Suffolk is considerably heavier for all live body weights; however, this may be attributed to the multiple-rearing environment having a greater effect on the growth potential of the Suffolk lambs over the Texel lambs.

Many of the studies on carcass composition previously conducted are not comparable to the present study due to different methods used and time points of measurement (Safari and Fogarty, 2003). Many of these studies tended to measure both muscle and fat depth at a later time point with the majority measured when the lamb is between 7 and 16 months of age (Safari and Fogarty, 2003). However one study conducted by Jones *et al.* (2004b) showed very similar results to the present study with the Suffolk breed having the highest muscle and fat depth and the Texel breed having the lowest fat depth out of the three studied breeds.

Genetic Parameters

Direct and maternal heritability estimates reported in the present study for live body weight and carcass composition traits are all within the ranges previously reported in the literature. Within the present study with the exception of pre weaning weight and fat depth, direct heritability differed substantially among breeds for all traits analysed with most variability observed in the post weaning weight trait where direct heritability ranged from 0.16 (Suffolk) to 0.32 (Texel). Genetic parameter estimates have not previously been reported in Ireland on a per breed basis. One previous study reported genetic parameter estimates within a multi breed analysis (McHugh *et al.,* 2017) including a heritability estimate for pre weaning weight in Irish lambs of 0.09, which is lower than all pre weaning weight estimates in the present study. This may be attributed to the differences between the breeds lowering the heritability in the previous study in comparison to the present study, which was conducted on genetically more homogeneous purebred populations. Higher accuracy of EBVs would also be expected in within breed genetic evaluations as a result of increased direct heritability estimates. Maternal heritability estimates were low for all three live body weight traits measured and were not significant for the two carcass composition traits. These results contrast significantly with the study on pre weaning weight by McHugh *et al*. (2017) where a maternal heritability of 0.25 was reported in a multi-breed Irish sheep population. This difference may however be due to different models used in the analysis as much of the variation in the present study was due to the common environmental effect, which was not included in the study of McHugh et al. (2017). In the UK, previous studies have estimated genetic parameters for the Suffolk breed for all traits analysed in the present study (Maniatis and Pollott, 2002a; Maniatis and Pollott, 2002b; Simm *et al.,* 2002) and results were generally similar. Simm *et al. (*2002) suggested that direct heritability estimates would increase with lamb age due to the lessening maternal influence and increased direct influence. This was indeed the case in the present study for Texel and Charollais breeds. For the Suffolk breed, however, the opposite was true as direct heritability decreased from 0.22 (pre weaning) to 0.16 (post weaning) while maternal heritability also decreased.

The strong positive direct genetic correlations among the three live body weight traits were as expected, indicating that lambs that are genetically heavier early in life are also more likely to be genetically heavier later on. Whilst these figures corresponded well with the literature, some of the estimates in the present study were outside the ranges previously reported with weaker correlations observed in the present study compared to those previously reported (Safari and Fogarty, 2003). This, however, may be due to the fact that few studies estimated genetic correlations between live body weight traits at the specific times that were reported in the present study and may also be due to many of the previous studies being based in Australia or Asia where the studied breeds being differ greatly to those in the current study (Safari and Fogarty, 2003). Many of these studies also tended to have a far greater age spread between weight ages than those reported in the present study. No previous studies have investigated at genetic correlations among growth traits for the Texel or Charollais breeds, individually. However, there was one UK study by Simm *et al.* (2002) that showed the direct and maternal genetic correlations between pre weaning and post weaning weight for the Suffolk breed to be 0.69 and 0.86, respectively. These results were broadly in the range of those reported in the present study although stronger maternal genetic correlations between the traits were recorded in the present study. The difference between the previous study and the present study may be attributed to the fact that the previous study (Simm *et al.*, 2002) was based on one flock only whereas the present study includes the entire recorded population.

As with the live body weight traits, strong positive correlations were also seen among the two carcass composition traits and post weaning weight. Very few previous studies have estimated correlations among these traits at the similar time points to the present study; however, the direct correlations estimated here are broadly within the range previously reported (Atkins *et al.*, 1991; Simm *et al.*, 2002; Ingham *et al.*, 2003). These strong positive correlations indicate that by breeding for heavier lambs we are also breeding for more muscular but also fatter lambs. The former is desirable but the latter undesirable. Although these traits are antagonistic we need to aim to select for animals that are more muscular and less fat while still achieving live body weight targets in order to maximise genetic gain and profitability. Appropriate selection indices need to be developed for this matter, optimally combining live body weight and carcass traits.

For pre weaning and weaning weight, a negative correlation was observed between the direct additive and maternal genetic effects. Although this corresponded with the majority of the literature for growth and live body weight traits (Notter, 1998; Safari and Fogarty, 2003; Maxa *et al.*, 2007), previous studies have reported very mixed results with some positive correlations appearing also between live body weight traits (Tosh and Kemp, 1994; Nasholm and Danell, 1996; Snyman *et al.*, 1996; Yazdi *et al.*, 1997; Rao and Notter, 2000). This variation of results previously reported in the literature may be indicative of differences in data structure but may also be due to breed differences (Maniatis and Pollott, 2002a). The antagonistic correlation reported between direct and maternal effects in the present study suggests that by selecting rams to breed heavier lambs their daughters will have lighter lambs. In order to counteract this, optimal combination of antagonistic traits in a properly developed selection index is needed to support selection decisions.

Genetic trends

To our knowledge, this is the first time genetic trends on Irish sheep are reported for the studied traits. Genetic trends varied between the three breeds for all traits in the present study. From the genetic trends, the Texel breed appears to be achieving the most genetic gain as significantly positive trends were recorded for all live body weight traits as well as the muscle depth trait. No significant trend was found for fat depth in the Texels, indicating that this trait is remaining relatively static which is more desirable than the increasing trend observed for the Suffolk and Charollais breeds. The muscle depth trait showed a positive trend for all three breeds. These results are indicative of the on-going genetic selection programme in Ireland based on the emphasis that is being placed on muscle depth for all breeds as well as the increase in genetic gain in live body weight that has been seen in all three breeds.

Conclusion

Variance components and genetic parameters derived in the present study for five live body weight and carcass traits may be used to support the breeding programme of sheep in Ireland. Considerable differences in genetic analysis results were found between the Texel, Suffolk and Charollais breeds for each of the five traits examined in the present study. Differences were observed in both heritability and genetic correlation estimates suggesting that current genetic improvement systems may benefit by considering these breeds separately in future genetic evaluations.

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2.3 Chapter Conclusion

This Chapter reports significant differences between the Irish Texel, Suffolk and Charollais breeds in additive genetic variance and heritability for all live body weight and carcass composition traits analysed, which warrant genetic evaluations to be conducted on a within-breed basis. Strong heritability estimates were produced for all traits and breeds suggesting there is significant room for genetic improvement within these three breeds. The incorporation of the results of this Chapter into the Irish sheep genetic evaluation programme would provide breeders enhanced tools for the genetic selection of purebred breeding stock.

Chapter 3: Towards future genetic evaluations for live body weight and carcass composition traits in UK sheep

3.1 Chapter Introduction

Genetic evaluations have been on-going for over 30 years in the UK, however, much potential still exists for further genetic improvement. This Chapter estimates genetic parameters and breeding values for two live body weight and two carcass composition traits within purebred Texel, Suffolk and Charollais lambs born in the UK and also determines whether between breed differences occur within these traits. This Chapter has been published in the Journal of Small Ruminant Research (DOI: https://doi.org/10.1016/j.smallrumres.2021.106327) and the results address the first objective of this thesis. All work conducted related to this Chapter was completed by the PhD candidate under guidance from supervisors and in collaboration with all listed co-authors of the manuscript.

3.2 Manuscript

Towards future genetic evaluations for live weight and carcass composition traits in UK sheep

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Abstract

The main aim of the current study was to perform a genetic analysis of two live body weight and two carcass composition traits in purebred UK-born Texel, Suffolk and Charollais lambs separately in order to produce future across country evaluations. The two live body weight traits considered were early-life weight (40 to 85 days of age) and scan weight (121 to 180 days of age), and the two carcass composition traits were muscle depth and fat depth. Only records from lambs born between 2010 and 2017 were used in the present study resulting in a total of 132,490 records from 55,155 lambs spread over 374 flocks being included for further analysis. An animal linear mixed model was used to derive (co)variance components for the studied traits, for each breed individually. Fixed effects included in the model were contemporary group, dam age at lamb's birth, dam age at first lambing, a birth type by rearing type of the lamb interaction and a sex by age of the lamb at measurement interaction. Random effects included in the model were the animal additive genetic effect, the dam maternal effect, the litter environment effect and the residual effect. The dam maternal effect applied only to the analysis of early-life weight. Heritability estimates ranged from 0.12 to 0.30 for the two live body weight traits across the three breeds. The two carcass composition traits had heritability estimates ranging from 0.18 to 0.42. Strong positive genetic correlations were observed between all traits analysed. Results from the present study show that genetic variation still exists within breeds for the traits studied indicating that even after over 30 years of genetic selection within the UK they are still amenable to genetic improvement. Furthermore, significant differences in genetic parameters between breeds were observed, especially for carcass composition traits, indicating that genetic evaluations should be calculated separately for each breed.

Keywords

Lamb growth, genetic parameters, muscle depth, fat depth, ultrasound scanning

Introduction

Genetic evaluation and improvement schemes have increasingly been used in the UK sheep industry, particularly in recent years. These schemes have proved to be extremely beneficial with an estimated return of over £15.5 million per year being achieved from genetic improvement within the beef and sheep industries, with much of this economic return attributed to improved growth and carcase traits (Signet, 2019). Much potential exists for further improvement within the UK sheep industry; for example, genetic progress achieved from just 10 years of using a terminal sire breeding programme has led to an economic benefit of £11.5 million to the sheep industry alone (Amer et al., 2007). The opportunity for across-breed evaluations and also that for international collaboration, as is currently the case for dairy (Interbull) and beef (Interbeef) could be a realistic option for the UK sheep industry. For this to happen, firstly trait definition and genetic parameters in respective breeds and countries need to be estimated. Genetic variability has been shown to exist according to the definition of traits and also for the same trait between breeds. This variability tends to be heightened when comparing terminal and maternal traits or terminal and maternal breeds (Safari et al., 2003). High levels of variability across live body weight and carcass composition traits at both a phenotypic and genetic level have been reported, not only in the UK (Simm et al., 2002; Jones et al., 2004; Rius-Vilarrasa et al., 2008), but also in Ireland (McHugh et al., 2017; O'Brien et al., 2017; Fitzmaurice et al., 2020) and elsewhere (Mousa et al., 1999; Safari et al., 2005; Thiruvenkadan et al., 2011). Previous genetic studies were mostly based on research flocks or other special data subsets that, although useful for the purposes of the specific studies, were not representative of the national flock and sheep population. Furthermore, in the UK, genetic evaluations for sheep are currently conducted on the entire sheep population including multiple breeds and crossbreds.

The aim of the present study was to quantify the genetic variation present in two key live body weight traits and two carcass composition traits within the three most commonly recorded terminal sire breeds in the UK, namely Texel, Suffolk and Charollais. Results from this study will determine if separate within-breed analysis should be considered in future genetic evaluation systems within the UK.

Material and methods

Data

All available data were extracted from the UK National Sheepbreeder Database (AHDB) and subsequently edits were performed to provide a more informative data set. Three breeds were considered for analysis, namely Texel, Suffolk and Charollais and only purebred animals from these three breeds were retained.

Lamb live body weights were recorded at the early-life and scanning stages using weigh-scales. Carcass composition traits were recorded at the same time point as scan weight, post weaning, using ultrasound scanning. Early-life weight was defined as live weight measured between 40 and 85 days of age and weighing between 12 and 45 kg. Scan weight was defined as live weight taken between 121 and 180 days; only lambs weighing between 25 and 75 kg were retained for further analysis. Muscle depth had to measure between 10 and 44 mm to be retained for further analysis. Only fat depth records measuring between 0.5 and 8.0 mm were included in further analyses. For both live body weight traits, average daily gain (ADG) was calculated for all lambs; only lambs with ADG between 100 and 650 g/day were retained.

Additional lamb records were discarded if they had an unknown sire, dam, maternal grandsire or flock of birth. In order for a lamb record to be retained both their sire and maternal grandsire were required to have at least five progeny each. Dams with no known age or aged >9 years had their lamb records discarded; dam age number was then categorised as 1,2,3,4, or ≥5 years. Age at first lambing was defined as the age of the dam at her first lambing and this ranged from 1 to 3 years. Birth type was defined as the number of lambs born per lambing event per ewe. Only lambs with a birth type between 1 (single) and 4 (quadruplets) were included in subsequent analysis. Rearing type was defined as the number of lambs reared per litter per ewe; only lambs with a rearing type of between 1 and 3 were retained. Lambs that were born as a result of embryo transfer, lambs that were artificially reared or not reared by their biological dam were not used as part of the present study. After all previously mentioned edits were performed, lambs were allocated to a contemporary group of breed-by-flock-by-week of weighing. Only contemporary groups with at least five records were retained for further analysis.

After all data edits were completed a total of 132,490 live weight and carcass composition records from 55,155 animals across 374 flocks between the years 2010 and 2017 remained. Trait specific numbers have been included as part of Table 3.1.

Genetic Analysis

A linear animal mixed model was built for the genetic analysis; each studied trait was analysed separately within breed. The model fitted was:

$$Y_{inhdkljzm} = CG_i + AFL_n + Dam\ age_h + Sex_d * Age + Birth\ type_k * Rearing\ type_l + Animal_j + Dam_z + Litter_m + e_{inhdkljzm}$$

Where $Y_{inhdkljzm}$ = lamb record, CG_i=fixed effect of the i^{th} contemporary group (i=1 to 871), AFL_n = fixed effect of n^{th} age of the dam class at first lambing (1 to 3), Dam age_h = fixed effect of the h^{th} age of the dam at lambing class (1 to 5), Sex_d*Age = the interaction between the d^{th} (1 to 2) sex of the lamb and age of the lamb at record, Birth $type_k$*Rearing $type_l$ = the interaction between the birth type k (1 to 4) and rearing type *l* of the lamb (1 to 3), $Animal_j$ = random additive genetic effect of j^{th} animal (lamb) including all pedigree available, Dam_z = random maternal effect of z^{th} dam of animal *j*, $Litter_m$ = random common environmental effect among lambs in the m^{th} litter, and $e_{inhdkljzm}$ = random residual effect.

The above model was built up for each trait and breed separately. Significance of random effects was examined using the log-likelihood ratio test (Ferreira *et al.*, 1999). The random dam maternal effect was an overall collective maternal effect including both a genetic and permanent environment effect of the dam using an identity matrix to link the data to the dams. Early-life weight was the only trait to include all random effects included in the model above. All other traits only included additive genetic and common environmental random effects as no significant dam effect was observed for these traits.

Heritability of each trait was calculated as the proportion of the total phenotypic variance accounted for by the additive genetic effect. The ratios of the maternal and common environmental variances to the total phenotypic variance were also derived in a similar manner. Genetic correlations between traits were estimated using the same model in a series of bivariate analyses of all traits studied.

To ensure accurate estimation of (co)variance components, an informative subset of well-connected flocks was formed, where sires were required to have progeny in at least 2 flocks. Sires were used in a maximum of 56 flocks with 48-60% of sires being used in only 2 flocks. Subsequently, estimated breeding values (EBV) were calculated for each animal and trait on the entire edited dataset using these (co)variance component estimates. Genetic trends for each trait were then derived for sires with at least 10 progeny by regressing the average sire EBV on sire year of birth.

All above-mentioned analyses were performed using the ASReml software (Gilmour *et al.,* 2009). Data was analysed in a similar manner as Fitzmaurice et al. (2020).

Results

Descriptive Statistics

Data after edits used for further genetic analysis is shown in Table 3.1. The Texel breed had the highest number of records by far across all traits studied. They also had the highest number of sires, dams, maternal grandsires, flocks and contemporary groups. The coefficient of variation suggested that substantial phenotypic variation was present in the studied traits and breeds.

Table 3.1 Number of lambs (n), trait mean (μ) and standard deviation (SD), corresponding mean lamb age, and number of sires, dams, maternal grandsires (MGS), flocks and contemporary groups (CGs) by trait and breed.

Trait (unit of measurement)	Breed	n	μ (SD)	Age (d)	Sires	Dams	MGS	Flocks	CGs
Early life weight (kg)	Texel	21,480	27.16 (6.48)	65.53	300	10,399	1,475	199	871
	Suffolk	12,302	28.86 (6.95)	66.85	132	5,206	606	73	408
	Charollais	16,452	27.45 (6.20)	66.43	186	6,233	651	81	513
Scan weight (kg)	Texel	13,219	49.00 (9.24)	146.7	192	6,986	1,171	179	627
	Suffolk	7,736	50.14 (11.27)	144.8	95	3,827	498	62	265
	Charollais	7,778	52.01 (9.52)	146.6	120	3,797	463	71	312
Muscle depth (mm)	Texel	12,619	28.69 (4.05)	146.8	180	6,680	1,134	174	594
	Suffolk	7,519	29.62 (5.17)	144.2	88	3,701	486	58	249
	Charollais	6,971	29.43 (3.53)	146.6	105	3,493	445	69	287
Fat depth (mm)	Texel	12,527	2.45 (1.26)	146.8	180	6,650	1,130	174	593
	Suffolk	7,383	3.31 (1.66)	144.2	87	3,649	480	58	244
	Charollais	6,504	4.15 (1.73)	146.6	101	3,317	426	66	274

Genetic Parameters

Statistically greater than zero ($P<0.05$) heritability estimates were found for all breeds and traits in Table 3.2. Heritability estimates for the live body weight traits increased as lambs got older for all breeds. The maternal effect was significant ($P<0.05$) for all breeds for the early-life weight trait. The litter environmental effect accounted for a high proportion of total phenotypic variance for all traits particularly within the Texel breed, where it accounted for up to 22% of total variance. Heritability estimates differed between breeds for the carcass composition traits. The Suffolk breed had a higher heritability estimate ($P<0.05$) for muscle depth compared to all other breeds and Charollais had a significantly higher heritability estimate than the Texel breed for fat depth ($P<0.05$).

Positive genetic correlations were calculated between the additive genetic effects for all traits in all breeds (Table 3.3). All pairwise correlations were significantly ($P<0.05$) different from zero, except between muscle depth and fat depth for the Charollais breed. Genetic correlations were strongest between the two live body weight traits reaching a maximum of 0.92 (± 0.02) between early-life weight and scan weight in the Texel breed. These strongly positive correlations between the live body weight traits indicate that lambs that grow well early in life will also perform better during subsequent growth phases.

Genetic trends were estimated for all traits and breeds from sire EBVs. In order to increase reliability only sires with ≥10 progeny were included in the trends shown in Figure 3.1. Significantly positive ($P<0.05$) trends were found for all breeds and traits, with the exception of fat depth in the Charollais breed where no significant trend appeared ($P>0.05$). Substantial variation was observed between breeds for all traits, with the Suffolk breed showing the highest rate of genetic gain for scan weight and muscle depth compared to the other two breeds in the present study.

Table 3.2 Lamb heritability (h^2), and proportion of the phenotypic variance due to the maternal (m^2) and common environmental (C^2) effect; model of analyses of scan weight, muscle and fat depth did not include a maternal effect; SE=standard error of estimate.

	Breed	h^2 (SE)	m^2 (SE)	C^2 (SE)
Early life weight	Texel	0.18 (0.03)	0.09 (0.01)	0.20 (0.02)
	Suffolk	0.14 (0.03)	0.08 (0.02)	0.17 (0.02)
	Charollais	0.12 (0.02)	0.08 (0.01)	0.19 (0.01)
Scan weight	Texel	0.22 (0.03)		0.22 (0.02)
	Suffolk	0.30 (0.04)		0.14 (0.02)
	Charollais	0.21 (0.03)		0.10 (0.02)
Muscle depth	Texel	0.19 (0.03)		0.17 (0.02)
	Suffolk	0.42 (0.04)		0.08 (0.02)
	Charollais	0.28 (0.04)		0.07 (0.02)
Fat depth	Texel	0.18 (0.03)		0.18 (0.02)
	Suffolk	0.29 (0.04)		0.16 (0.02)
	Charollais	0.32 (0.04)		0.09 (0.02)

Table 3.3 Correlations (standard error in parentheses) between the additive genetic effects for the studied traits by breed.

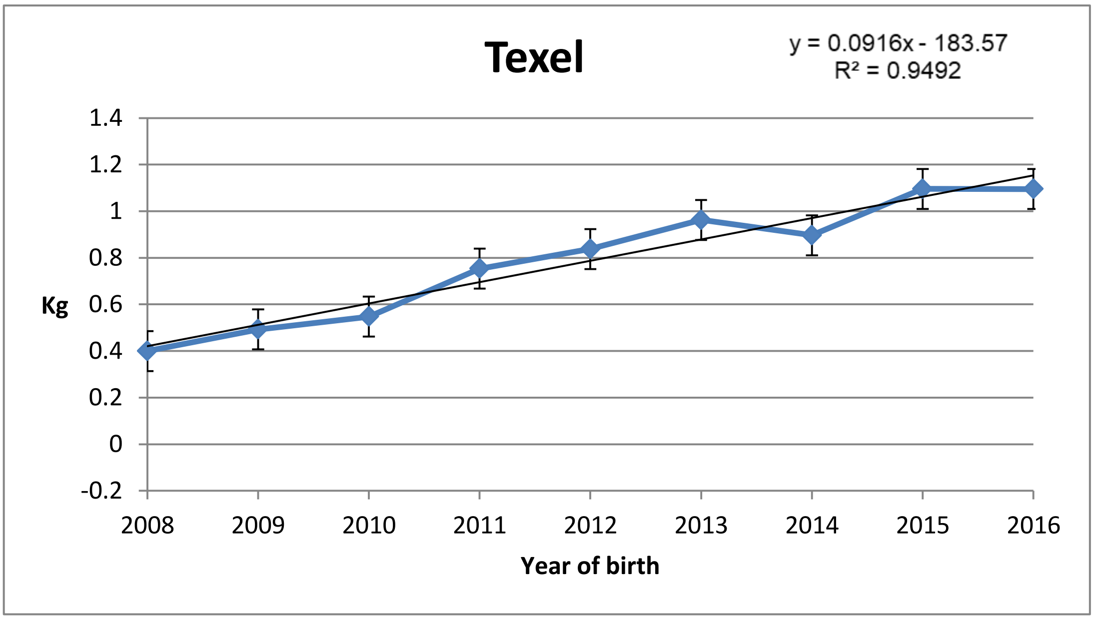
Breed	Trait	Early life weight	Scan weight	Muscle depth
Texel	Early life weight			
	Scan weight	0.92 (0.02)		
	Muscle depth	0.45 (0.06)	0.50 (0.05)	
	Fat depth	0.49 (0.06)	0.50 (0.06)	0.35 (0.07)
Suffolk	Early life weight			
	Scan weight	0.90 (0.03)		
	Muscle depth	0.56 (0.06)	0.65 (0.05)	
	Fat depth	0.46 (0.08)	0.39 (0.07)	0.43 (0.06)
Charollais	Early life weight			
	Scan weight	0.81 (0.04)		
	Muscle depth	0.40 (0.08)	0.43 (0.08)	
	Fat depth	0.34 (0.09)	0.38 (0.08)	0.03 (0.10)

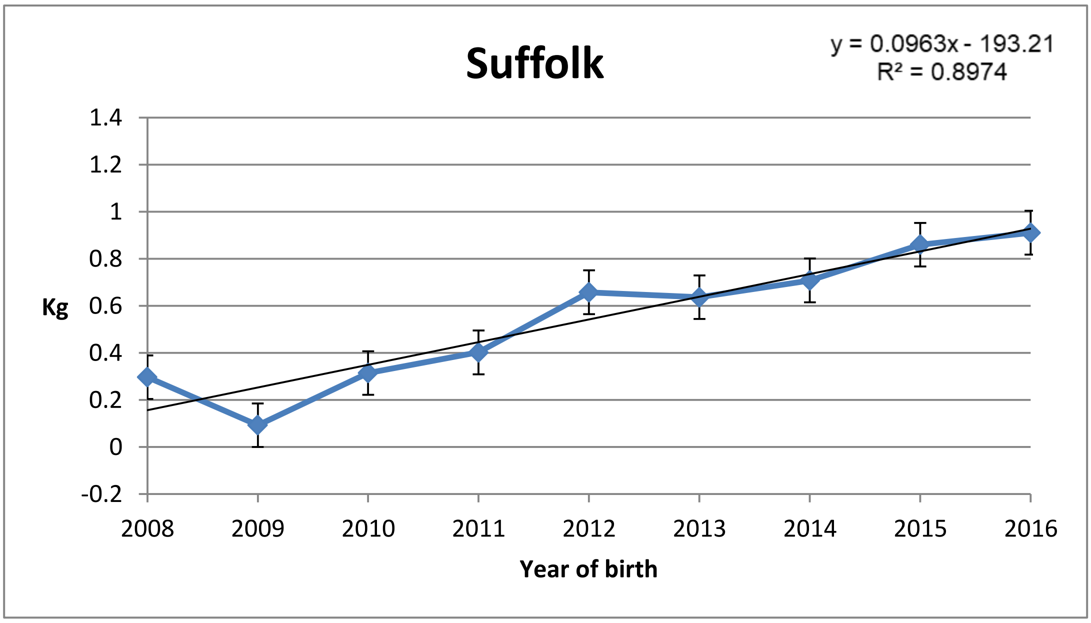
Discussion

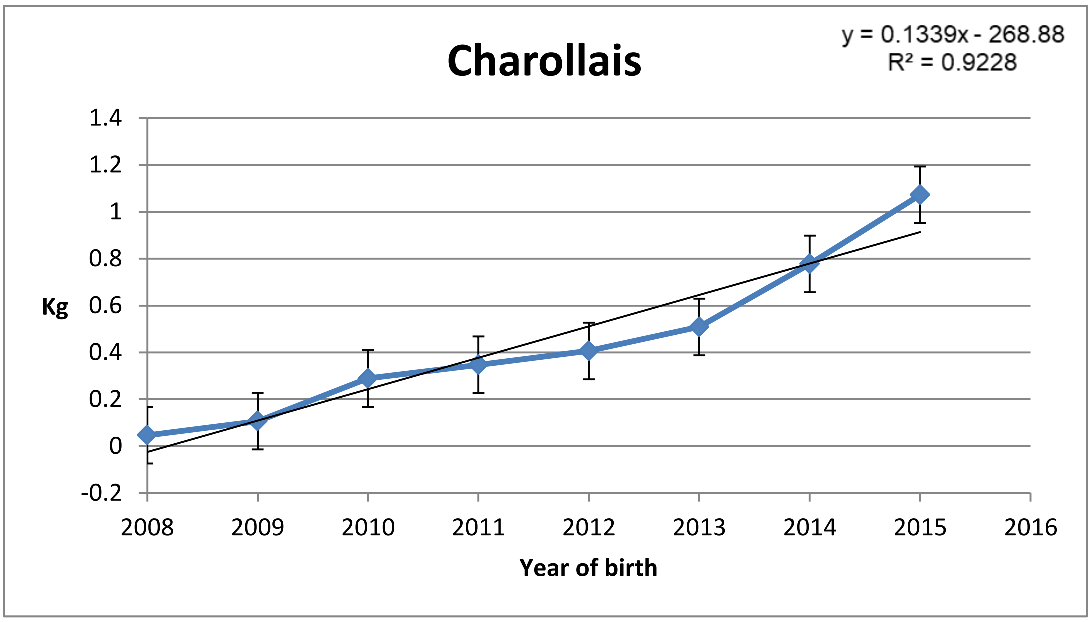
Improved growth and carcass traits due to genetic evaluation and selection schemes in the UK have been shown to be of significant economic benefit to the UK sheep industry (Signet, 2019). In the present study we set out to use national data to estimate within-breed genetic parameters in the UK sheep population after over 30 years of genetic selection had taken place. Results showed that there is still substantial genetic variation present meaning further genetic improvement is attainable and future selection will continue to be successful for live body weight and carcass composition traits.

Heritability estimates calculated in the present study correspond well with the literature for all traits analysed, although the heritability in the Suffolk breed for muscle depth exceeded previous ranges reported for the trait (Safari and Fogarty, 2003). Heritability estimates differed significantly between breeds for both carcass composition traits; however, no significant differences were observed between breeds for the live body weight traits. Genetic variability was highest in the muscle depth trait where the Suffolk breed showed significantly higher heritability compared to the Texel and Charollais breeds. Between breed differences in heritability estimates were also observed for the fat depth trait, where the estimate for the Charollais breed was significantly higher than for the Texel breed, but in all cases this trait can be selected for to effect genetic progress in the future. Differences between breeds also reflect the selection decisions that have been made relating to the different selection indices

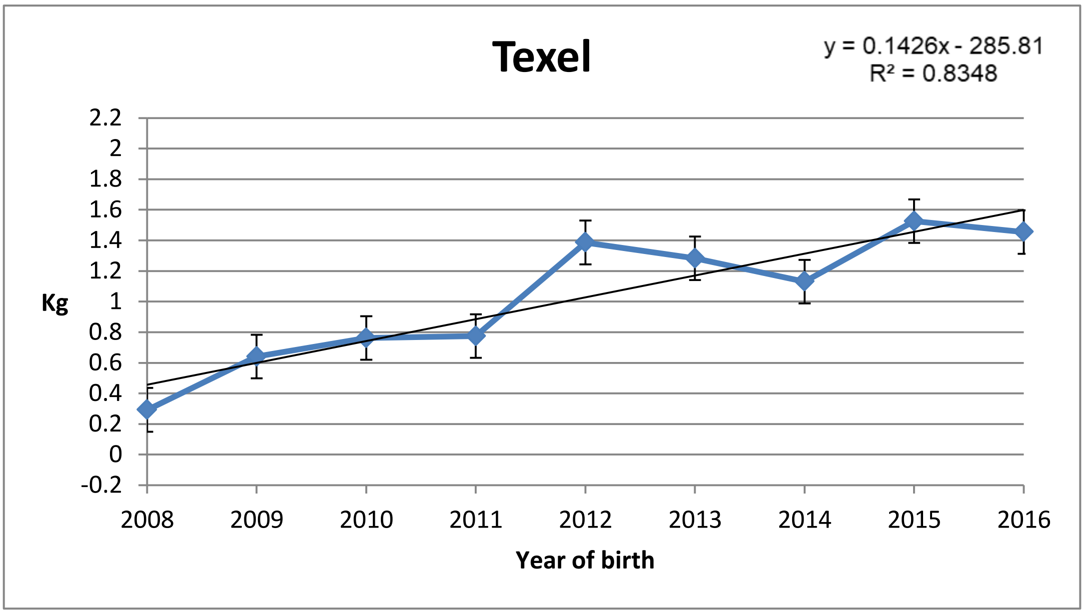
a. Early life live body weight (kg)

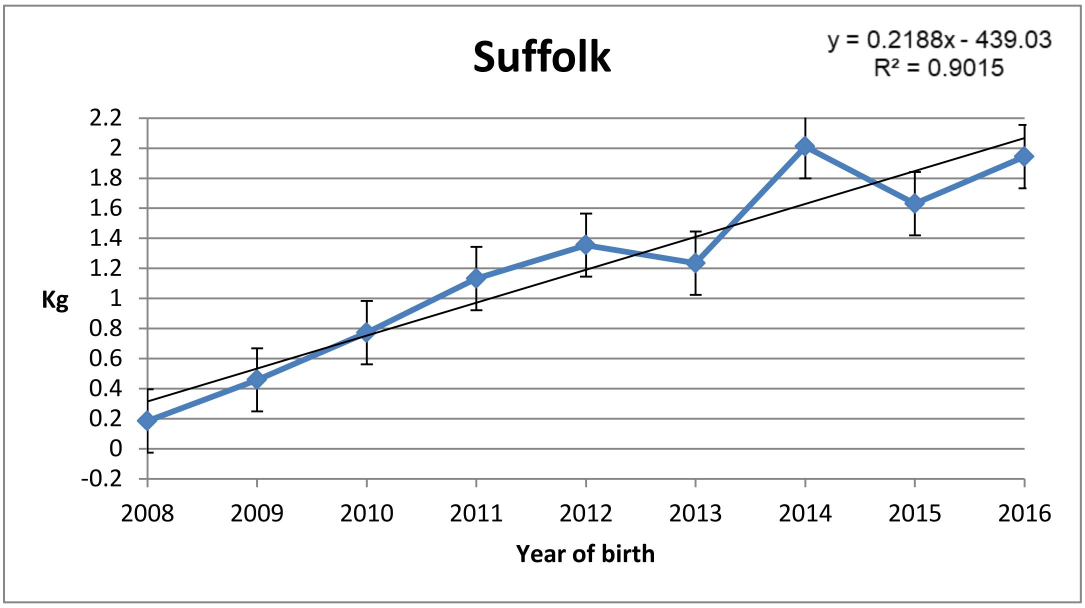


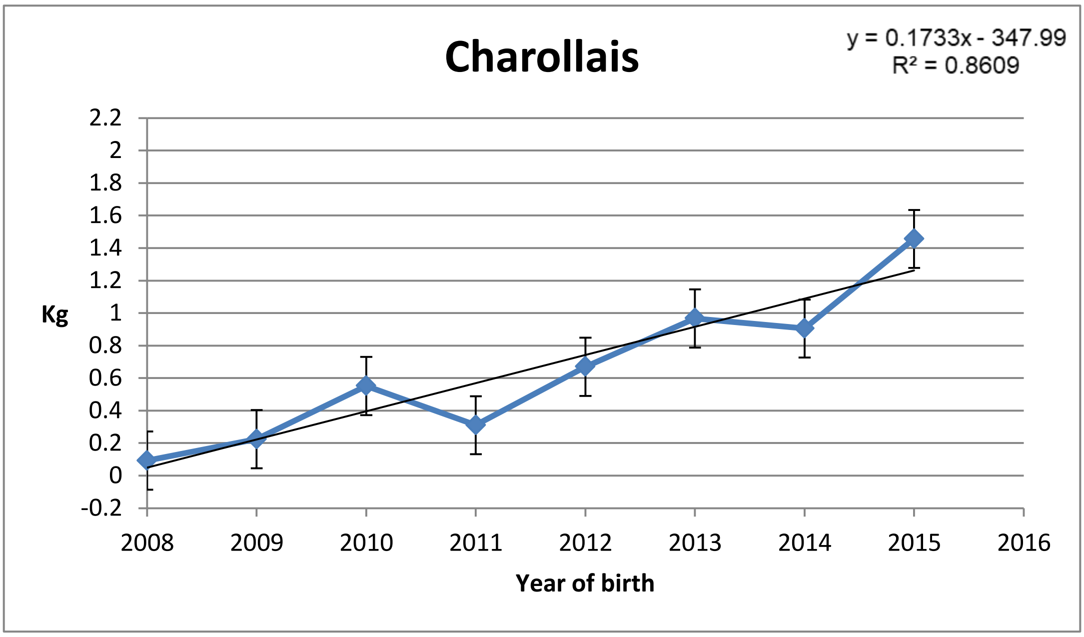




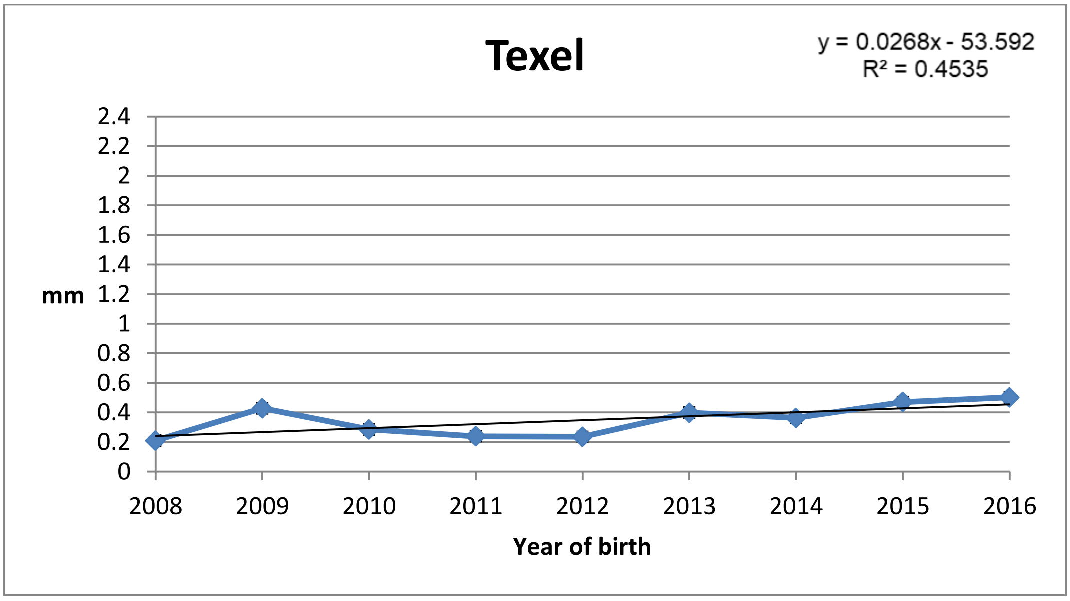
b. Scan live body weight (kg)

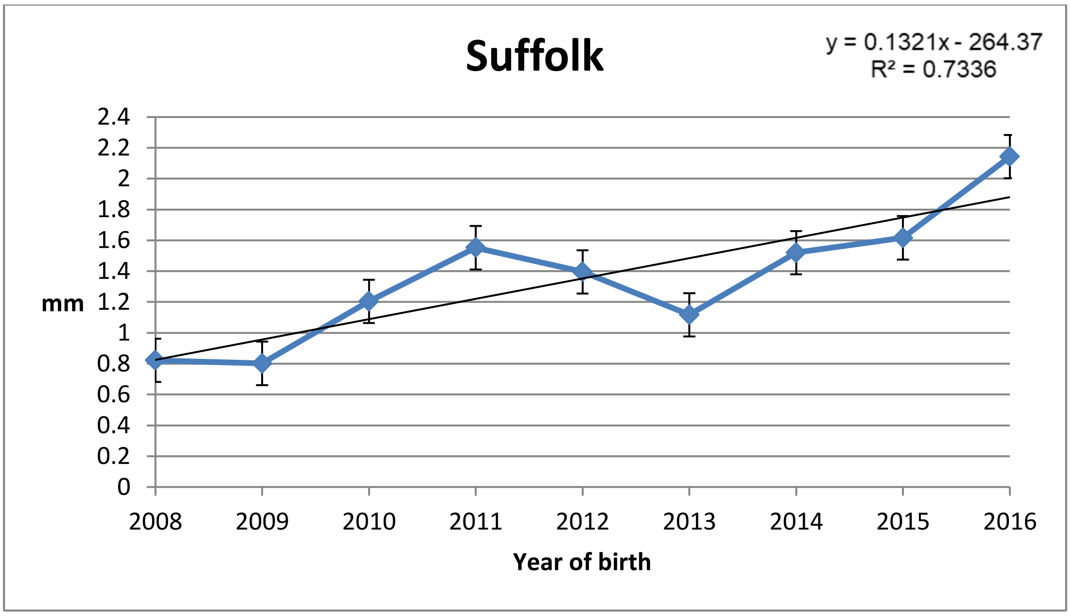


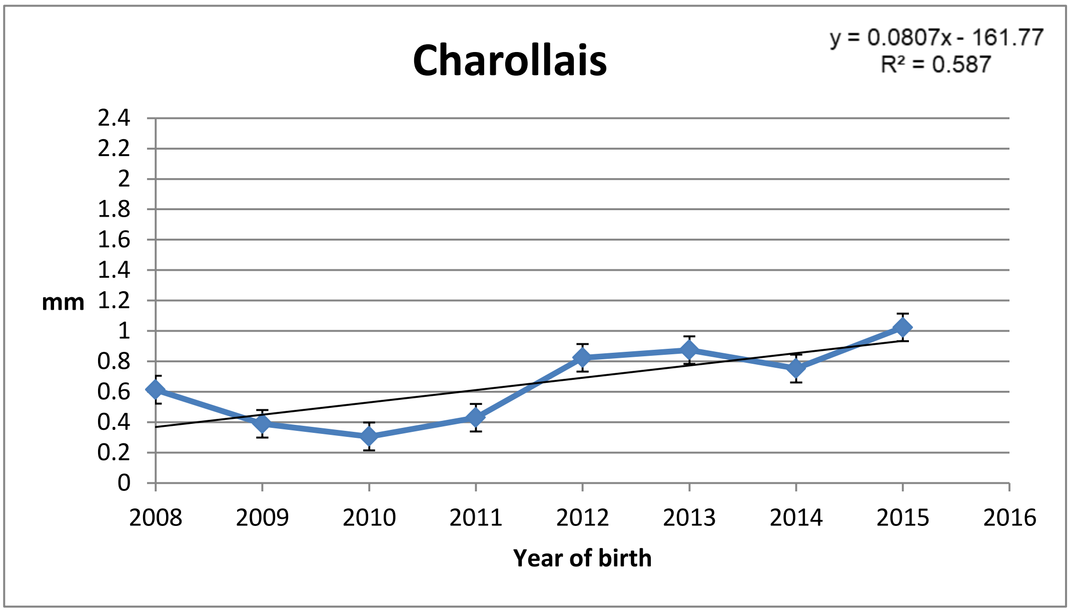

Suffolk
y = 0.2188x - 439.03
R² = 0.9015
Kg
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
2008
2009
2010
2011
2012
2013
2014
2015
2016
Year of birth


Charollais
y = 0.1733x - 347.99
R² = 0.8609
Kg
2.2
2
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.2
2008
2009
2010
2011
2012
2013
2014
2015
2016
Year of birth

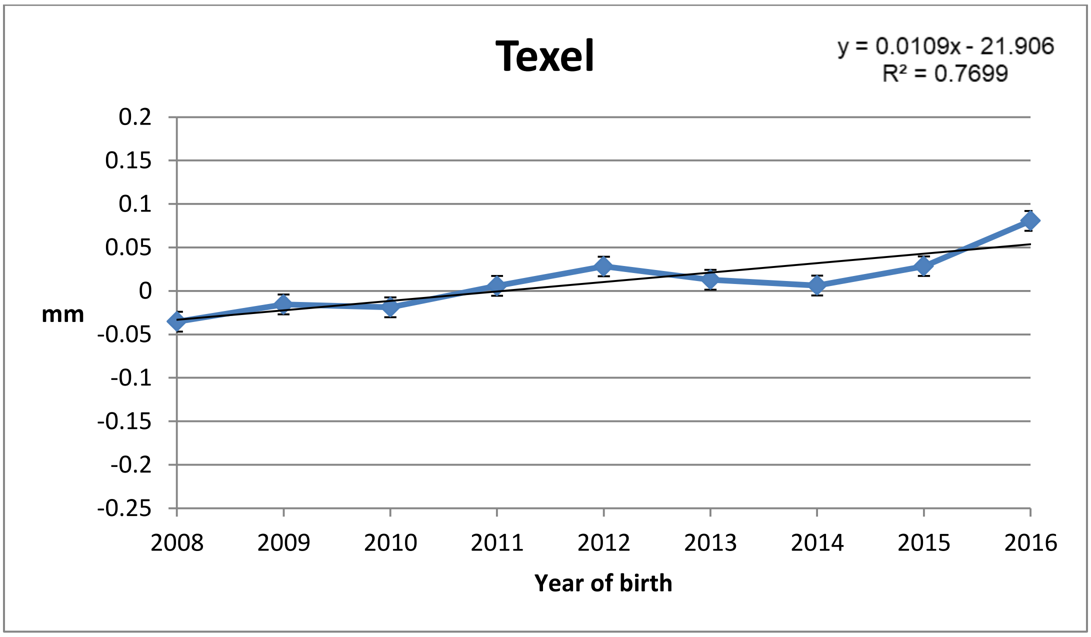
c. Muscle depth (mm)

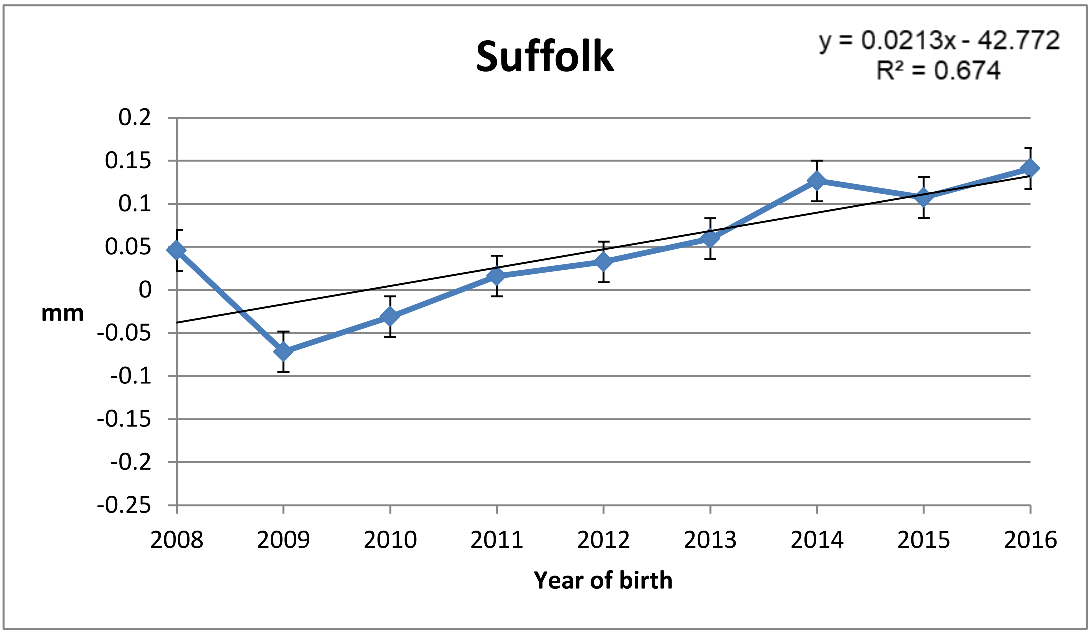






d. Fat depth (mm)





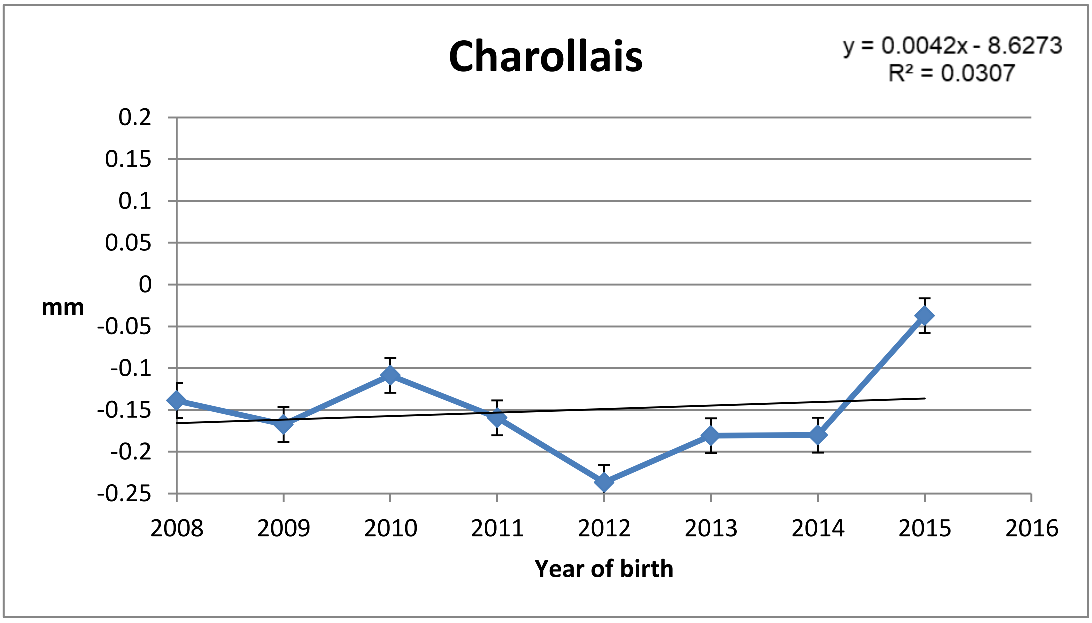


Figure 3.1 Genetic trends of estimated breeding values of rams (standard errors in bars) for (a) early-life live body weight, (b) scan live body weight, (c) muscle depth and (d) fat depth for the Texel, Suffolk and Charollais breeds.

placing different emphasis on each breed. In the UK, within breed genetic parameters have previously been reported by Jones *et al.* (2004b) for the same breeds as the present study. The study of Jones *et al.* (2004b) was based on data from research flocks and sire referencing schemes resulting in higher heritability estimates for scan weight, muscle depth and fat depth, particularly for the Texel breed, whereas relatively similar results were obtained for the Suffolk and Charollais breeds. For the Texel breed, substantial differences were observed particularly between the scan weight and fat depth traits; for example, in the present study heritability for fat depth was estimated to be 0.18 whereas Jones *et al.* (2004b) reported a heritability of 0.38 for fat depth. Whilst it is difficult to pinpoint the exact reason for the differences between the studies, we speculate that the discrepancy may be due to differences between the genetic model used or may also be due to changes in genetic variation due to selection over time. In fact, Jones *et al.* (2004b) did not include a common environmental litter effect which may have led to an inflation of the genetic variance (and hence heritability) compared to the present study, where the common environmental effect accounted for a high proportion of the variance. In addition, the data used by Jones *et al.* (2004b) originated from both a research flock and a sire referencing scheme, which would likely have had stronger across-flock genetic linkages leading to higher heritability estimates. Furthermore, previous studies in the UK have reported genetic parameter estimates for the Suffolk breed for all live body weight and carcass composition traits examined in the present study (Maniatis and Pollott, 2002a; Maniatis and Pollott, 2002b; Simm *et al.*, 2002) and observed very similar results to the heritability estimates within the Suffolk breed reported in the present study. Simm *et al.* (2002) also reported heritability estimates to increase with age, which was found to be the case for the Suffolk and Charollais breed in the present study.

Genetic parameters were reported for the same three breeds of the present study for scan weight, muscle depth and fat depth in the Irish sheep population (Fitzmaurice *et al.*, 2020). These parameters were estimated using similar genetic models as the present study in order to build towards future international evaluations; however, the resulting heritability estimates still differed. In the Irish study (Fitzmaurice *et al.*, 2020), the highest heritability estimates were derived for the Texel breed for all traits, whereas in the present study highest trait heritability was estimated mostly for the Suffolk breed. Similarly high levels of the common environmental effect were found in both studies with the Irish estimates ranging between 0.15-0.35 for live body weight and carcass composition traits (Fitzmaurice *et al.*, 2020). Other studies in Ireland also estimated heritability estimates for some of the same traits as the present study with O’Brien *et al.* (2017) reporting estimates to range from 0.22 to 0.28 for lamb live weight, muscle depth and fat depth, although that study included both purebred and crossbred lambs. Throughout the rest of the world there have been numerous similar studies undertaken particularly in Australia (Brown *et* al., 2016) and New Zealand (Brito *et al*., 2017). Both of these studies focused on terminal breeds including the Texel and Suffolk breeds and reported substantial genetic variation for all traits analysed, consistently with the results of the present study.

In the present study, the highest genetic correlations were observed between the two live body weight traits, namely early-life and scan weight. This indicates that the two traits are mostly under similar genetic control meaning lambs that are heavier in early-life will also be heavier at a later stage in the growth cycle. Muscle depth was highly correlated with both live body weights in all three breeds indicating that increases in the latter will also lead to an increase in muscle depth in the carcass. Genetic correlation estimates in the present study corresponded relatively well with the literature and results are within the ranges previously reported. Jones *et al.* (2004) reported similar genetic correlations between scan weight, muscle depth and fat depth for the Texel, Suffolk and Charollais breeds in the UK, although highest estimates were derived for the Texel breed compared to the Suffolk breed in the present study. Simm *et al.* (2002) reported relatively weaker correlations between the same traits for the Suffolk breed in the UK. Fitzmaurice *et al.* (2020) estimated genetic correlations for the same three breeds in Ireland and reported similar results for genetic correlations between live body weight and carcass composition traits as in the present study. In general, previous studies throughout the world have reported genetic correlations among similar lamb traits ranging from 0.14 to nearly unity (Safari and Fogarty, 2003). This high level of variation is probably due to the substantially different animal populations, breeds, models of analysis and trait definitions included in the Safari and Fogarty (2003) review. While, for the most part, the positive genetic correlations observed between traits would facilitate genetic improvement, care must be taken when producing selection indices to encourage early live body weight gain and muscle development without detrimentally increasing the fat levels in the carcass or compromising aspects of maternal performance.

Finally, the genetic trends calculated in the present study indicate satisfactory levels of genetic gain achieved from genetic selection on most traits in the three breeds. Desirable positive trends were observed over a nearly 10-year period for live body weights and muscle depth. Stable genetic levels for fat depth were observed in the Charollais breed, which is also desirable, as we do not want to breed animals that are genetically predisposed to being too lean or too fat. Positive genetic trends for fat depth in the other two breeds, however, may raise the issue of revising the respective breeding strategies to ensure future lamb generations do not develop carcasses that are too fat. In order to keep fat depth at an optimal level within a breeding programme, economic weights on relative traits must be adjusted constantly in line with genetic and market trends. Ideally genetic trends for fat depth should remain relatively static rather than increase as is the desire for the other traits analysed. Genetic trends have previously been reported in the UK for hill sheep for similar traits (Conington *et al.,* 2006) and also for the Suffolk breed for live body weight, muscle depth and fat depth (Simm *et al.,* 2002), showing similar positive trends for the first two traits but less so for fat depth, where a greater negative trend was reported. This negative trend may be due to the deliberate relaxing of the original selection index (Simm and Dingwall, 1989) in order to ensure that lambs finish for slaughter at the desired level of fatness. Similar trends have also been observed in Ireland where steady levels of genetic gain in all traits are being achieved (Fitzmaurice *et al.,* 2020). The main disparity that occurs between genetic trends within the two countries is for the fat depth trait. Fitzmaurice *et al.* (2020) observed an increasing trend for fat depth in both the Suffolk and Charollais breeds while the Texel breed remained stable. The present study however shows increasing fat depth for all breeds apart from the Charollais which is remaining stable. However, this difference may be attributed to contrasting breeder preferences within the two countries. The trends observed in the present study are suggestive of the current genetic selection system in the UK where increased intensity of selection is occurring for higher growth rates in lambs with increased carcass value.

As mentioned previously, Fitzmaurice *et al.* (2020) have performed similar analysis on Irish data for the same three breeds as the present study. Existing data and high levels of linkage between the two countries as well as similar live weight and carcass composition traits can facilitate across-country genetic evaluations. Implications of the latter would underpin trade of stock and improve accuracy of genetic evaluations between countries.

Conclusion

The four growth and carcass composition traits studied are highly heritable and positively correlated to each other. Results from the present study could be used within the UK sheep industry to support breeding programmes into the future and underpin international cooperation for cross-country genetic evaluations. Significant differences in the estimated genetic parameters for the carcass composition traits were observed between breeds, suggesting that within-breed analysis in future genetic evaluation systems would be recommended in order to achieve high rates of genetic gain. These analyses have also laid the foundation for an across-country genetic evaluation of these breeds in the UK and Ireland. The technical aspects of such an analysis are currently being addressed. Overall benefit of across-country genetic evaluations to the respective industries is yet to be determined but it is expected that significant gains at both a genetic and economic level could be achieved.

Acknowledgements

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3.3 Chapter Conclusion

This chapter produces strong heritability estimates for all traits and breeds indicating that there is further room for genetic improvement after over 30 years of genetic selection within the UK sheep population. In addition to this, between breed differences were observed for carcass composition traits indicating that future genetic evaluation systems could benefit from evaluating these breeds separately. This Chapter paves the way for future across-country genetic evaluations in sheep between Ireland and the UK with the hope of further increasing the rate of genetic gain.

Chapter 4: Across-country genetic evaluations of meat sheep from Ireland and the UK

4.1 Introduction

Pedigree sheep breeding is an international activity with high levels of trade of breeding stock occurring between countries. Growth and carcass composition traits are of high economic importance worldwide (Cocks *et al.*, 2002; Byrne *et al.*, 2010) and genetic selection of these traits has led to substantial economic gain in the global sheep industry (Jones *et al.*, 2004; Conington *et al.*, 2004; Amer *et al.*, 2007). International genetic evaluations will allow for across-country genetic selection of breeding stock. This will increase the rate of genetic gain achieved in comparison to within-country selection alone due to a higher selection intensity attained from the increased number of selection candidates (Banos and Smith, 1991; Smith and Banos, 1991; Lohuis and Dekkers, 1998). To date, no across-country genetic evaluations have been produced for sheep. However, across-country genetic evaluations have successfully been established for both beef and dairy cattle through the development of Interbeef (Interbeef, 2020) and Interbull (Interbull, 2020), respectively. Outcomes from these initiatives already inform selective breeding programmes in multiple countries worldwide.

In sheep, large amounts of performance recording have been undertaken particularly in pedigree flocks across Ireland (Sheep Ireland) and the UK (AHDB) resulting in a high volume of data being available particularly for live body weight and carcass composition traits measured on certain common breeds. Therefore, it could be of significant advantage to pool all this data together into an across-country evaluation system to allow breeders to accurately compare animals across-country as well as giving them a greater choice of selection candidates.

The objective of the present study was to assess the feasibility of combining live body weight animal phenotypic and pedigree data from Ireland and the UK in order to develop an international (across-country) genetic evaluation system for pedigree Texel sheep. An additional objective was to quantify the potential benefit of selection based on across-country genetic evaluations in comparison to within-country genetic evaluations.

4.2 Materials and Methods

4.2.1 Data

All data used to conduct international genetic evaluations in the present study were obtained from Sheep Ireland, the Irish national database (http://www.sheep.ie) and AHDB, the UK national Sheepbreeder database (https://ahdb.org.uk/beef-lamb). Live body weight and carcass composition data used in the present study were as described in Chapters 2 and 3 of the thesis for the within-country analyses; however the present study focused solely on the Texel breed. Both carcass composition traits, namely muscle depth and fat depth by ultra-sound scanning, corresponded directly across the two countries although they are measured at different depths in both countries. The same was true for scan weight, which in the analysis of Irish data was referred to as post weaning weight (Chapter 2) although both were measured at the same time point (121-180 days). However, whilst the early life body weight traits were similar in age range, they were not directly comparable between the two countries. This meant that early-life weight as defined in the UK (Chapter 3) had to be combined with either pre weaning or weaning weight from Ireland (Chapter 2).

Live body weight and carcass trait data records were available on 177,307 Irish and 521,244 UK lambs born between 2010 and 2017. Breeding animals that had progeny with records in both countries were first identified. A total of 8,392 common ancestors were found, including 1,188 common sires. For the creation of the international dataset, a full dataset from Ireland and the UK for live body weight and carcass composition trait data were combined. Following all previous data edits described in Chapters 2 and 3, 30,776 early-life/pre weaning weight records, 30,913 early-life/weaning weight records, 23,975 scan weight records, 20,328 muscle depth records and 17,331 fat depth records remained across both countries. An international pedigree file was then produced for all animals in the original unedited dataset to allow all across-country links to be considered in the evaluations.

4.2.2 Genetic Analysis

Combined data from Ireland and the UK were considered in a series of bivariate analyses with the following model:

$$\begin{gathered} Y = CG + AFL + Parity + Dam\ age + Sex * Age + Birth\ type * Rearing\ type \\ + Country + Animal + Dam + Litter + e \end{gathered}$$

Where Y = lamb live body weight or carcass composition record, CG=contemporary group in which the lamb is raised, as defined in Chapters 2 and 3, AFL = age of the lamb’s dam at first lambing as defined in Chapters 2 and 3, Parity = parity of the lamb’s dam at lambing as defined in Chapter 2 (Irish data only), Dam age = age of the lamb's dam at lambing as defined in Chapter 3 (UK data only), Sex*Age = the interaction between the sex of the lamb and age of the lamb at recording, Birth type*Rearing type = the interaction between the birth type and rearing type of the lamb (as defined in Chapters 2 and 3), Country = country of birth of the lamb, Animal = random additive genetic effect of the animal (lamb) including all pedigree available, Dam = random maternal effect of the lamb's dam, Litter = random common environmental effect among lambs in the same litter, and e= random residual effect.

The model was first applied to each country, separately, after removing the country effect, to derive within-country estimates of variance components and breeding values of individual animals. Subsequently, bivariate analyses were conducted on joint across-country data. In the latter analyses, all variance component estimates across-country were fixed to the previous calculated within-country variance component estimates to allow for a direct comparison of EBVs from within-country and across-country evaluations. Residual covariance estimates due to dam and litter effects as well as between countries were fixed to zero as no animal had phenotypic records in both countries. Estimated breeding values (EBVs) and accuracies of EBVs were derived for all animals in the bivariate analysis and were expressed on the scale of each country.

All these analyses were conducted with the ASReml software (Gilmour *et al.*, 2009).

4.2.3 Response to Selection

Predicted response to selection was calculated using the following equation (Rendel and Robertson, 1950):

$$\Delta G = i * r * \sigma_a$$

Where ΔG = rate of genetic gain achieved per generation and trait; i = selection intensity; r = accuracy of genetic evaluation; and σ_a= additive genetic standard deviation for the trait in question.

This formula was used to derive the predicted response to selection of sires based on both across-country and within-country genetic evaluations for all traits in the study. Only sires with a minimum EBV accuracy of 0.65 were considered in this step.

4.3 Results

Phenotypic description of the studied traits is given in Table 4.1. This Table summarises the traits as included pairwise in the bivariate analyses. Overall, trait phenotypic results were relatively similar between the two countries; however, muscle depth and particularly fat depth are lower in the UK. This may be attributed to different techniques used in the two countries when measuring fat depth using the ultrasound scanning machine.

Genetic parameters from the univariate and bivariate analyses are also summarised in Table 4.1. For reasons that could not be determined, the bivariate analysis of muscle depth in the two countries failed to converge. Therefore, an approximate genetic correlation was derived in this case based on the correlation between EBVs of common sires calculated within-country and adjusted for EBV accuracy according to Calo *et al.* (1973).

Genetic correlation estimates between the two countries were stronger than 0.80 in all cases except when weaning weight from Ireland was combined with early life weight from the UK. In this case, the weak genetic correlation (0.38) suggests that the across-country evaluation for these traits would not be beneficial. Therefore, no further analyses were conducted for this trait combination. However, the other trait measured in Ireland at an early growth phase, pre-weaning weight, was highly correlated with UK early life weight. In the latter case as well as for all carcass traits the strong genetic correlation estimated between the two countries warrants possible benefits from a joint genetic evaluation. Strong genetic correlations between traits also indicate that limited re-ranking of sires would be expected between the two countries.

Table 4.1 Number of records (N), trait mean (μ) and standard deviation (SD), corresponding mean age of lambs, and estimates of heritability (h^2) with their standard error (SE) and genetic correlation of traits between countries.

Trait	Country	n	μ (SD)	Age	h^2 (SE)	Genetic correlation
Pre weaning weight (kg)	Ireland	11,891	20.86 (4.70)	46.59	0.19 (0.03)	0.82
Early-life weight (kg)	UK	21,480	27.16 (6.48)	65.53	0.18 (0.03)	
Weaning weight (kg)	Ireland	12,388	36.69 (7.63)	96.92	0.30 (0.03)	0.38
Early-life weight (kg)	UK	21,480	27.16 (6.48)	65.53	0.18 (0.03)	
Scan weight (kg)	Ireland	12,074	48.70 (9.47)	144.76	0.32 (0.03)	0.88
	UK	13,219	49.00 (9.24)	146.70	0.22 (0.03)	
Muscle depth (mm)	Ireland	8,810	32.59 (4.09)	146.57	0.31 (0.03)	0.85
	UK	12,619	28.69 (4.05)	146.80	0.19 (0.03)	
Fat depth (mm)	Ireland	8,782	6.10 (2.70)	146.63	0.20 (0.03)	0.85
	UK	12,527	2.45 (1.26)	146.80	0.18 (0.03)	

4.3.1 Response to selection

In order to further examine and quantify the benefit of across-country genetic evaluation, predicted response to sire selection within and across-country was estimated for each trait separately (Table 4.2, Table 4.3, Table 4.4, Table 4.5). Two different selection scenarios were considered for illustration assuming selection of the top 10 and top 20 sires in each case. These numbers are generally reflective of the current practice in the two countries.

Difference between response to selection based on across- versus within-country evaluation would be expected to be mainly due to difference in EBV accuracy and selection intensity. In the present study, the accuracy of sire EBVs differed very little between the two types of analyses with average accuracy values for all traits ranging from 0.53 to 0.62 for within-country evaluations in Ireland, 0.65 to 0.70 for within-country analysis in the UK and 0.54 to 0.65 for all across-country analysis. However, expectedly, selection intensity was always higher when sires were selected based on the across-country evaluations in comparison to selecting from the within-country evaluations.

After the minimum accuracy threshold of 0.65 was imposed there were between 119 to 369 sires remaining in the within-country analysis and 182 to 473 sires remaining for the across-country analysis, depending on the trait. Across-country evaluations were of benefit to both Ireland and the UK for all traits studied with a potential increase in predicted genetic gain between 2.59 and 19.63% in comparison to using within-country evaluations alone. The lowest predicted response to selection was for early-life weight in the UK and the highest was for scan weight in the UK. Overall, predicted response to selection using across-country evaluations was of more benefit to the UK than Ireland for carcass traits although the opposite was true for live body weight in the early growth stage.

Table 4.2 Expected response (*ΔG*) to top sire selection within and across-country for early-life body weight; r=average accuracy of selection candidate EBVs, i=intensity of selection, σ=genetic standard deviation of trait; % ΔG achievable within- compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*I*	*r*	*σ*	*ΔG*	*%*
Within-country - Ireland							
Top 10 Sires	192	5.21	2.063	0.74	1.39	2.12	95.19
Top 20 Sires	192	10.42	1.755	0.74	1.39	1.81	93.51
Within-country - UK							
Top 10 Sires	194	5.15	2.063	0.76	1.78	2.79	97.41
Top 20 Sires	194	10.31	1.755	0.76	1.78	2.37	95.52
Across-country - Ireland							
Top 10 Sires	276	3.62	2.197	0.73	1.39	2.23	100
Top 20 Sires	276	7.25	1.9025	0.73	1.39	1.93	100
Across-country - UK							
Top 10 Sires	260	3.85	2.175	0.74	1.78	2.87	100
Top 20 Sires	260	7.69	1.887	0.74	1.78	2.49	100

Table 4.3 Expected response (ΔG) to top sire selection within and across-country for scan weight; r=average accuracy of selection candidate EBVs, i=intensity of selection, σ=genetic standard deviation of trait; % ΔG achievable within- compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*i*	*r*	*σ*	*ΔG*	%
Within-country - Ireland							
Top 10 Sires	369	2.71	2.309	0.76	3.46	6.06	97.35
Top 20 Sires	369	5.42	2.023	0.76	3.46	5.31	96.02
Within-country - UK							
Top 10 Sires	137	7.3	1.887	0.77	2.82	4.1	85.89
Top 20 Sires	137	14.59	1.554	0.77	2.82	3.38	80.37
Across country - Ireland							
Top 10 Sires	473	2.11	2.4035	0.75	3.46	6.23	100
Top 20 Sires	473	4.23	2.135	0.75	3.46	5.53	100
Across-country - UK							
Top 10 Sires	325	3.08	2.2555	0.75	2.82	4.77	100
Top 20 Sires	325	6.15	1.985	0.75	2.82	4.2	100

Table 4.4 Expected response (ΔG) to top sire selection within and across-country for muscle depth; r=average accuracy of selection candidate EBVs, i=intensity of selection, σ=genetic standard deviation of trait; % ΔG achievable within- compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*i*	*r*	*σ*	*ΔG*	%
Within-country - Ireland							
Top 10 Sires	279	3.58	2.197	0.76	1.66	2.77	97.00
Top 20 Sires	279	7.17	1.918	0.76	1.66	2.42	96.07
Within-country - UK							
Top 10 Sires	125	8	1.858	0.75	1.3	1.81	87.42
Top 20 Sires	125	16	1.521	0.75	1.3	1.49	82.97
Across-country - Ireland							
Top 10 Sires	348	2.87	2.295	0.75	1.66	2.86	100
Top 20 Sires	348	5.75	2.023	0.75	1.66	2.52	100
Across-country - UK							
Top 10 Sires	246	4.07	2.154	0.74	1.3	2.08	100
Top 20 Sires	246	8.13	1.858	0.74	1.3	1.79	100

Table 4.5 Expected response (ΔG) to top sire selection within and across-country for fat depth; r=average accuracy of selection candidate EBVs, i=intensity of selection, σ=genetic standard deviation of trait; % ΔG achievable within- compared to across-country selection.

Selection Scenario	No. of Sires	Proportion Selected	*i*	*r*	*σ*	*ΔG*	%
Within-country - Ireland							
Top 10 Sires	165	6.06	1.985	0.74	0.1	0.15	93.80
Top 20 Sires	165	12.12	1.667	0.74	0.1	0.13	93.67
Within-country - UK							
Top 10 Sires	119	8.4	1.831	0.75	0.42	0.57	92.99
Top 20 Sires	119	16.81	1.489	0.75	0.42	0.47	89.51
Across-country - Ireland							
Top 10 Sires	228	4.39	2.116	0.73	0.1	0.16	100
Top 20 Sires	228	8.77	1.804	0.73	0.1	0.14	100
Across-country - UK							
Top 10 Sires	182	5.49	2.023	0.73	0.42	0.62	100
Top 20 Sires	182	10.99	1.709	0.73	0.42	0.52	100

4.4 Discussion

International genetic evaluations have already proven their worth in both the beef and dairy cattle industries with the development of Interbeef and Interbull; however, to date no international genetic evaluations have been conducted for sheep. Interbull provides genetic evaluations for a multitude of traits for dairy cattle including production, fertility, health and conformation traits (Mark, 2004; Mark, 2005). Interbeef provides international evaluations for weaning weight and calving ease in beef (Pabiou *et al.*, 2014b; ICBF, 2020); additionally, further research has been conducted on the international evaluations for carcass traits demonstrating the benefits from across-country genetic selection in beef cattle (Englishby, 2018). The development of international genetic evaluations for sheep will be an important factor not only in improving the rate of genetic gain for growth and carcass traits but also in facilitating across-country trade of breeding stock. Therefore, in the present study we addressed this issue by first determining the connectedness between countries and developing an international pedigree file. International EBVs were then produced for all animals and response to selection was estimated comparing the rate of genetic gain from the use of within-country evaluations only in comparison to international (across-country) evaluations. Results from the present study show that international evaluations would be of significant benefit to both Irish and UK sheep industries.

4.4.1 Connectedness

Connectedness among sheep populations in different countries is a key component in the feasibility of conducting international genetic evaluations. This is because bias in

EBV estimation is reduced as connections between flocks and separate management units are increased (Hanocq *et al.*, 1996; Kuehn *et al.*, 2007; Kuehn *et al.*, 2008). Connectedness was found to be relatively high between the Irish and UK Texel populations with 1,188 sires having progeny with records in both countries. Although the number of common sires is relatively high, the number of progeny per sire is relatively low when compared to dairy cattle, where AI is the norm in breeding programmes, and also these progeny appear in relatively few flocks. However, the level of connectedness observed in the present study is only reflective of the true connectedness levels amongst flocks currently participating in performance recording schemes. In order to increase overall connectedness levels amongst populations, an increase in systematic performance recording of the entire population is required in addition to a higher uptake within pedigree flocks. As well as this an increase in the use of AI in both pedigree and commercial breeding settings could create higher levels of connectedness amongst flocks both within and across country. Further advances could also be made through the use of genomics due to the lack of depth in current pedigrees and missing relationship information associated with incorrect parentage (Berry *et al.*, 19).

4.4.2 Genetic Parameters

In general heritability estimates derived here were higher in Ireland than in the UK. There were substantial differences between heritability estimates for scan weight and muscle depth between countries with Irish heritability estimates 10 to 12% higher than the UK for these traits, respectively. These parameters have already been discussed in depth in Chapters 2 and 3, and they are generally consistent with the scientific literature (Safari and Fogarty, 2003). However, for the purpose of the international genetic evaluations the same model was used for pre weaning and weaning weight in Ireland as was used for early-life weight in the UK in order to avoid bias resulting in slightly higher heritability estimates for pre weaning and weaning weight than those discussed in Chapter 2.

The benefit of conducting international evaluations is dependent on the magnitude of the genetic correlation between countries for a trait (Mulder *et al.*, 2005). Selection using across-country genetic evaluations will result in a higher rate of genetic gain than national genetic evaluations when the genetic correlation between traits across country is 0.70 or greater (Mulder *et al.*, 2005). Genetic correlations between Ireland and the UK were strongly positive for all corresponding traits analysed with the highest correlation seen for the scan weight trait at 0.88. This is indicative of the similarity between the traits in both countries. Slightly stronger genetic correlation ranges were previously estimated in international beef evaluations between Ireland and the UK, with across-country carcass trait correlations ranging from between 0.95 to 0.99 (Englishby, 2018). The stronger correlations for beef cattle however may be due to the traits that were chosen for the analysis. Beef carcass grading is standardised using the EUROP grading system in Europe so this trait definition may have led to the strong correlations seen here (Jakobsen *et al.*, 2009; Craigie *et al.*, 2012). This may also be why in the present study scan weight showed the strongest genetic correlation as this trait is almost identically defined in both countries. Although previous across-country carcass trait correlations reported by Englishby (2018) were stronger than those in the present study, other studies on across-country evaluations for weaning weight in Limousin cattle were weaker at

0.76 (Venot et al., 2007), although later studies estimated across-country genetic evaluations for the same trait in Limousin cattle to be 0.88 (Pabiou *et al.*, 2014b), which is similar to the present study. While no direct across-country genetic comparison has previously been completed for sheep, a previous study has produced across-country genetic correlations for selection indices between Ireland and New Zealand where correlations ranged from between 0.66 to 0.86 for terminal and maternal indices between countries, respectively (Santos *et al.*, 2015).

4.4.3 Response to selection

When genetic correlations between countries are sufficiently strong, combined selection of animals across-country as is the case here, should always be on a par if not superior to within-country selection (Smith and Banos, 1991). This was also proven to be true for sheep in the present study, with selection using international evaluations proving to be superior to within-country selection alone for all traits in both Ireland and the UK. Expected benefit in carcass related traits (scan weight, muscle and fat depth) from international evaluations in the present study tended to be higher for the UK than in Ireland with up to a 19.63% and 6.49% predicted increase in genetic gain achieved in the UK and Ireland, respectively. This result was also seen in previous international beef evaluations between the same countries although the extent of the benefit was greater for the latter, with predicted rates of genetic gain increasing by up to 34% (Englishby, 2018). Previous studies for dairy cattle have also reported similar predicted responses to selection from international evaluations with predicted benefits of up to 17% reported by Lohuis and Dekkers (1998).

Pooling data from different countries and combining in an international dataset gives rise to a greater number of selection candidates, thus increasing selection intensity. As accuracy levels remained relatively stable in within- and across-country genetic evaluations, selection intensity was deemed to be one of the most influential factors in increasing the rate of genetic gain achieved per year.

Predicted response to selection derived in the present study demonstrates the benefits for individual traits separately. At a practical level, sires are selected based on across-country overall selection indices rather than individual trait EBV estimates. As the gain differs according to the different traits, when all growth and carcass trait EBVs are combined it is unlikely that the expected increase in genetic gain predicted on a single trait basis would be realised, whether this is operated either within- or across-country selection. This is an area that should be explored in future work.

4.5 Conclusion

Strong links and strong genetic correlations between Ireland and the UK were found which would facilitate a joint genetic evaluation for sheep across the two countries. Through the combination of data and pedigree records across-country this study has demonstrated that a considerable improvement can be achieved in the rate of genetic gain through the informed selection of breeding stock regardless of the country of origin.

Chapter 5: General Discussion

5.1Introduction

Performance recording and genetic evaluation programmes have been at the forefront of improving the rate of genetic gain for multiple traits in numerous sheep breeds across both Ireland and the UK. With over 30 years of genetic selection occurring in the UK and over 20 years of genetic selection in Ireland, significant improvements have been made in both countries; however, this is not to say that rates of genetic gain cannot be improved even further. At the same time the trade of animals and genetic material between the two countries has intensified warranting the need to compare stock across-country. Therefore, the overall aim of this thesis was to develop new models and methods of producing genetic evaluations at both a within-country level and an across-country level in order to inform selection decisions that would improve the rate of genetic gain achieved.

5.2 Change in methodology for the improvement of within-country genetic evaluations

It has been firmly established that selection using genetic evaluations compared to phenotypic information alone has significant benefits at both a genetic and an economic level. However, the most effective method or model of generating genetic evaluations worldwide has not yet been established although it is highly unlikely that a one size fits all approach would be effective. Genetic evaluations produced as part of Chapter 2 of the present thesis show that genetic variation exists both within breed as well as between traits in three purebred Irish sheep populations. Previous genetic parameters produced in Ireland for live body weight and carcass composition traits were estimated across a multi-breed population (McHugh *et al.*, 2016). This, however, does not account for genetic heterogeneity between breeds, resulting in less accurate genetic evaluations particularly for purebred sheep. Heritability estimates produced from this study indicate that all live body weight and carcass composition traits studied have the potential to benefit from genetic selection allowing farmers to increase efficiency, productivity and profitability on farm.

Genetic evaluations have been on going in Ireland since the 1990's (Murphy *et al.*, 1999) although poor uptake and little incentive for farmers to join resulted in a relatively ineffective genetic evaluation system until the development of Sheep Ireland in 2009. However, since 2009 significant response has been achieved and enormous benefit realised at farm level. For example, response to selection achieved from the use of the terminal index in Ireland has resulted in substantial economic benefit with an increase of €0.25 per year being achieved for the days to slaughter trait (Santos *et al.*, 2015). Through the incorporation of within breed genetic parameters into the national genetic evaluation scheme in Ireland, the rate of genetic gain achieved for selected traits could potentially increase, coupled with increased levels of accuracy which would lead to an overall superior genetic evaluation system.

The UK has been conducting genetic evaluations for sheep for over 30 years. Chapter 3 discusses the substantial levels of genetic variation still present in two live body weight and two carcass composition traits in UK populations of purebred Texel, Suffolk and Charollais sheep. Similar to Ireland, much genetic variation still exists within trait and also within breed in the UK indicating that significant benefit can still be achieved from selection using genetic evaluations particularly when the latter indices are estimated on a within breed basis.

Genetic selection is one of the most economically beneficial methods of improving output at farm level with its main advantages being that it is permanent, cumulative, sustainable and cost effective (Simm and Dingwall, 1989; Pullar, 2003). However, genetic selection must be tailored to market requirements and specifications. Market specifications for lowland lamb production are quite similar in both Ireland and the UK and require a carcass of between 16 and 22 kg with optimal levels of fat and muscle (Jones *et al.*, 2003; Diskin and McHugh, 2012). As carcass value is determined by its weight, conformation and fat levels (Jones *et al.*, 2004a), farmers require lambs to reach the target slaughter weight as quickly as possible while also maintaining good conformation and stable fat levels, meaning neither too fat nor too lean. While the former is the predominant market type there are also separate markets for lighter lambs such as hill lambs. These hill lambs are generally of poorer conformation although they have been shown to be of higher eating quality than lowland breeds (Navajas *et al.*, 2008). These differences in market specifications demonstrate the value of conducting within breed analysis at a genetic level as trait goals differ highly between breeds.

Although genetics have an important role in the profitability of a sheep flock, there are numerous other factors affecting this also. As mentioned earlier, genetic improvement is permanent and cumulative; however, it can be a relatively slow process in terms of seeing significant gains at farm level. Environmental and management factors can have a more immediate effect on overall flock output in a given year and can be misleading at a practical farm level as it takes some time for genetic improvement to be visible. However, a combination of good management practices as well as utilising genetic selection on farm will ultimately provide the most benefit, ensuring high productivity and efficiency in the short term as well as long term genetic gains which will provide a more permanent improvement to the flock.

5.2.1 Direct applications and further research

Through the direct application of these newly generated within-breed genetic parameters, national genetic evaluations could be of increased accuracy and benefit to both Irish and UK sheep industries in terms of improving live body weight and carcass composition traits. Farmers and in particular pedigree sheep breeders will have enhanced tools to allow them to genetically select breeding stock based on how these animals rank within their own breed for these terminal traits allowing significant breed improvements to be made. This means that essentially farmers will be able to select the fastest growing animals with the greatest amounts of muscle and appropriate levels of fat within their particular breed as breeding stock. This will enhance the rate of genetic improvement that could be achieved at farm level.

The results from this thesis indicate that there is much potential for further research in this area including the development of new within breed genetic parameters and evaluations for maternal traits as well as further terminal traits in both Ireland and the UK. This would be of particular benefit to the three breeds studied in this thesis as all three are considered to be terminal breeds. Further research in this area would allow for the development of the maternal traits in these breeds whilst also maintaining strong terminal characteristics supporting the primary purpose of the Texel, Suffolk and Charollais breeds. In addition to this some traits included in genetic evaluations are unique to each country such as CT scanning traits in the UK and so further investigation would be required for these traits. There are numerous other commercially-important breeds in both Ireland and the UK; however, many of these are not performance recorded to the same extent as the three aforementioned breeds. The potential for genetic improvement that can be provided by conducting within breed genetic evaluations for these traits is enormous. Further research conducted in this area for other popular breeds could lead to improved rates of genetic gain which could potentially encourage a higher uptake of performance recording from other breeders.

While this thesis has shown the benefit of using within-breed genetic parameters and evaluations for purebred animals it is not clear whether this method would be of benefit to all breeds or for crossbred animals. High numbers of Texel, Suffolk and Charollais animals have been recorded for years in both Ireland and the UK allowing for the accurate estimation of within breed genetic parameters. However, it is unclear whether this would be the case for some less well recorded breeds, or whether these would benefit more from an across breed evaluation system instead. The same question applies for crossbred animals although it is highly likely that these animals would benefit more from an across breed genetic evaluation system in comparison to the within breed genetic evaluation method discussed in this thesis. Further research is required to determine the method of producing genetic evaluations for other less well recorded breeds and crossbred animals that will produce the greatest level of genetic gain for desirable traits along with acceptable levels of EBV accuracy.

5.3 Benefits of across-country genetic evaluations in sheep

The development of international genetic evaluations in sheep has been long awaited with much success previously achieved from international genetic evaluations in both the beef and dairy cattle industries. Chapter 4 demonstrates the feasibility of an across-country genetic evaluation of Irish and UK Texel sheep and discusses the potential benefit that pooling data from different countries can have on increasing the rate of genetic gain for live body weight and carcass composition traits. The rate of genetic gain achieved from the use of international evaluations can improve due to an increase in EBV accuracy and an increase in selection intensity in comparison to within-country genetic evaluations. Although there was little change in accuracy from conducting across-country genetic evaluations in the present study, selection intensity increased significantly leading to substantial genetic gain being achieved. This increase in selection intensity offers farmers in both Ireland and the UK a wider selection of breeding stock to choose from as they are now able to accurately compare Irish and UK animals at a genetic level and make informed selection decisions based on these across-country evaluations.

Although beneficial, across-country genetic selection needs to be carefully managed to ensure sustainable long-term benefits can be achieved. The challenge is to do this while safeguarding diversity and controlling inbreeding. This can be managed through optimised mating schemes and also by using the optimum contribution theory (Granleese *et al.*, 2015).

The high use of AI in both the dairy and beef industry has significantly benefited both national and international genetic evaluations for both industries as well as considerably improving the rate of genetic gain achieved through the spread of the best genetics to the wider population. The increased use of AI in sheep could, as has been seen in the beef and dairy industry, reap major rewards in terms of improving the rate of genetic gain particularly when incorporated with across-country selection. In addition to this, higher utilisation of AI in the sheep industry could also lead to greater connectedness between flocks and higher accuracy levels for EBVs being achieved. A high level of accuracy is extremely important when producing or using genetic evaluations and this is an area that has significant potential for improvement going forward. Through increased trade of breeding stock and germplasm, genetic links between countries can be increased which in turn will lead to higher accuracy estimates being obtained for live body weight and carcass composition trait EBVs.

The present thesis focused on investigating the links between Ireland and the UK and producing international genetic evaluations for animals in these two countries. However, there are numerous other countries that also have common links within the Texel breed as well as many other breeds such as the Suffolk and Charollais. The inclusion of further countries into an international genetic evaluation system is very much a possibility. Countries such as France, Spain and the Netherlands participate in regular trade of breeding stock with Ireland and the UK and strong genetic links are likely to be present among these countries. The inclusion of more countries and the pooling of additional data from performance recorded breeding stock into the international genetic evaluation system could lead to the production of superior across-country genetic evaluations on a more global basis.

Both Ireland and the UK have almost identical climates and farming environments particularly in the areas where lowland breeds are reared, resulting in limited re-ranking of breeding stock in the two countries due to genotype by environment interactions where strong genetic correlations exist between traits across country. This was manifested by the very strong genetic correlations derived between data from the two countries in the present study. Genotype-by-environment interactions occur due to genetic differences observed in phenotypic plasticity among individuals, breeds and populations (Steinheim *et al.*, 2008). This means that the top performing animals in the international genetic evaluation system including Ireland and the UK may not perform as well in different environments such as a Mediterranean climate for example. For the inclusion of further countries into international genetic evaluations, genotype-by-environment interactions are a major consideration and it will be imperative that future international breeding programs take this factor into consideration.

5.3.1 Direct and further applications of international genetic evaluations

The positive results presented in Chapter 4 demonstrate how the pooling of resources from two different countries can lead to an across-country genetic evaluation that may have a substantial effect on the rate of genetic gain achieved for live body weight and carcass composition traits in purebred Texel sheep. The direct application of international genetic evaluations mainly benefited from the increased selection intensity due to the greater number of selection candidates available. In addition to the improved rate of genetic gain, international genetic evaluations can also improve profitability on both Irish and UK sheep farms.

There is potential for further scientific research to be conducted on the development of international genetic evaluations in sheep. The inclusion of multiple additional countries into these across-country evaluations would be likely to increase selection intensity even further resulting in greater rates of genetic gain being achieved for these traits, although there are some limitations to this. In order for this to happen it is vital that animal traits are recorded at similar time points and using similar methods particularly for less well-connected populations. Otherwise, genetic correlations for traits between countries may be low and result in less accurate genetic comparisons across-country. The introduction of multiple countries into both dairy and beef international genetic evaluation systems has been very successful with 35 countries now participating in Interbull and 12 countries participating in Interbeef, respectively. This global genetic evaluation system developed for dairy and beef cattle is a realistic possibility for sheep and through further research and development in this area, could lead to significant economic gain in the global sheep industry.

In addition to producing international genetic evaluations as demonstrated in the present thesis, further research into the use of genomics within an international evaluation scheme could be extremely beneficial. Not only would it allow for more accurate international evaluations particularly in younger breeding stock, it would also allow the incorporation of more difficult to measure traits into an international analysis. For example, increasingly important traits such as feed efficiency could be included into an international evaluation system through the use of genomics, especially since large-scale phenotyping is highly unlikely to be feasible for such a trait. Genomic information is widely available for the Texel breed in both Ireland and the UK and the incorporation of this data into an international evaluation system could have profound economic and production benefits for this breed and pave the way for future developments on a multi breed basis.

Overall, the introduction of across-country genetic evaluations in conjunction with current national genetic evaluations will have notable benefits in the advancement of both the Irish and UK sheep industries. Through the introduction of more breeds and additional terminal and maternal traits into these international genetic evaluations there is huge scope for improvement within the sheep industry and so this must be explored further in future studies.

5.4 Knowledge transfer to farmers

Farmers are the critical component in both the development and implementation of genetic evaluations in sheep. Although there is a significant economic benefit to farmers from implementing genetic selection, there has been a reluctance to implement data recording and genetic selection at farm level. This could be due to lack of knowledge or lack of acknowledgment of the research findings that have been published. In addition, there are management and/or logistic factors that can hinder the involvement of farmers in data recording and genetic selection including location, breed type, handling facilities and time. Although it may not be feasible for all farmers to record data on their flocks, it is possible for the majority of farmers to select some proportion of stock rams based on both phenotypic and genetic merit rather than selecting based on phenotype alone. There is currently substantial work being conducted in the area of knowledge transfer in both Ireland and the UK through the work of public or levy bodies as well as through some breed societies. For example, in Ireland the use of genetic selection is being promoted through its use on Teagasc research farms as well as commercial farms that are participating as central progeny test flocks for Sheep Ireland. Results obtained from the use of genetic selection on these farms have been highlighted at numerous events as well as being published in popular press and this has generated an interest in the wider farming community into genetic selection. However, in order for wider benefits to materialise, more farmers are needed to performance record animals not only for pedigree animals but on a commercial basis as well if we are to really make significant advancements in genetic gain within the Irish and UK national sheep flocks.

5.5 Benefits of improving efficiency on sheep farms

Through the use of national genetic evaluations discussed in Chapters 2 and 3 as well as international genetic evaluations discussed in Chapter 4 there is considerable potential to increase on-farm efficiency through the use of genetic selection on Irish and UK sheep farms. Now more than ever there is a direct focus on improving efficiency particularly in terms of reducing greenhouse gas (GHG) emissions at farm level. Agriculture is a significant contributor to GHG emissions accounting for between 7 and 18% of total anthropogenic GHG emissions globally (Tapio *et al.*, 2017) with ruminant livestock production estimated to account for approximately 14% of anthropogenic methane released into the atmosphere annually (Huws *et al.*, 2018). Through genetic selection for live body weight traits as discussed in this thesis it is possible to indirectly reduce GHG emissions from the sheep industry as faster growing animals that reach slaughter weight quicker will produce less methane over their lifetime than slower growing animals (Hegarty and McEwan, 2010). In addition, there is also potential for traits such as feed efficiency or direct methane yield traits to be included in future genetic and genomic evaluations at both a national and international level.

5.6 Conclusion

Results from this thesis demonstrate how performance recording and genetic evaluation programmes can be improved at a national and international level in Ireland and the UK. The use of these genetic selection tools could prove to be particularly beneficial for pedigree sheep breeders in the two countries with the potential for increased rates of genetic gain within breed along with an increase in accuracy levels. In addition, the feasibility of international genetic evaluations has been explored and results show that significant improvements in genetic gain can be made for live body weight and carcass composition traits. The results produced in this thesis have been very positive particularly in terms of the development of international genetic evaluations for sheep; however, there is scope for the inclusion of further countries as well as breeds and traits into these evaluations and this is an area that should be explored in future studies.

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