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Genome Wide Association Studies for carcass traits measured by video image analysis in crossbred lambs

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Abstract

This is the first UK genome wide association study investigating potential links between Video Image Analysis (VIA) carcass traits and molecular polymorphisms in crossbred sheep. Phenotypic and genotypic data were collected from two crossbred lamb populations: Texel x Scotch Mule (TxSM, n = 2,330) and Texel x Lleyn (TxL, n = 3,816). Traits measured included live weights at birth, eight weeks and weaning (~15 weeks). VIA-predicted traits included total weights and weights of fat, muscle and bone in the whole carcass and primal (hind leg, saddle, shoulder) regions. Within-breed heritabilities estimated for the VIA traits ranged from 0.01 to 0.70, indicating potential for inclusion of some traits in breeding programmes. The two crossbred populations differed in SNPs associated with different traits. Two SNPs on chromosomes two (s74618.1) and eight (s68536.1), respectively, reached genome-wise significance for TxSM, explaining <1% of trait variance, for whole carcass fat and muscle weights, hind leg and saddle fat weights and shoulder bone weights. For TxL, four SNPs reached genome-wise significance, on chromosome two for hind leg muscle weight (OAR2_117959202 and OAR2_11804335), on chromosome 10 for whole carcass bone weight (OAR19_8995957.1), and on chromosome 19 for weaning weight (s40847.1), each explaining <1% of trait genetic variation. Differences in apparent genetic control of carcass traits may be influenced by the lambs' cross-breed, but also by management decisions

affecting environmental variance and trait definitions, which should be understood in order to define protocols for incorporation of carcass traits into (cross)breeding programmes.

Keywords

Genome Wide Association Study (GWAS), carcass traits, crossbred lambs, Video Image Analysis (VIA)

Implications

Combining VIA-measured carcass traits with conventional production traits in a breeding programme could potentially improve the production and product quality of meat sheep. Phenotypes for VIA traits could be collected relatively easily if VIA machines were present at all abattoir sites. The current study and future Genome Wide Association Studies may help to identify potentially informative molecular markers, that explain large proportions of the genetic variance observed in VIA-measured carcass traits. Including this information in the estimation of breeding values could increase the accuracy of prediction, increasing the potential rate of genetic improvement for product quality. This study confirms the polygenic architecture of the investigated carcass traits, with a small number of molecular markers that each explain a small amount of genetic variation. Further studies across breed types are recommended to further test and validate molecular markers for traits related to lamb carcass quality, as measured by video image analysis.

1. Introduction

Genotyping of livestock to identify superior animals for breeding is routinely undertaken in some livestock species and populations, but not currently for most UK sheep populations.

Data from single nucleotide polymorphism (SNP) arrays have the potential to be used for the estimation of genomic breeding values (gEBVs) to contribute to established and structured breeding programmes. Along with their use in routine genetic evaluations to increase the accuracy of prediction of breeding values (VanRaden et al., 2009; Kaseja et al. 2022), genotypes can also be used to perform genome-wide association studies (GWAS) that can reveal potential genomic regions or quantitative trait loci (QTL) affecting traits of interest. Potential QTL for meat production from sheep have already been reported in multiple studies (Cavanagh et al., 2010; Matika et al., 2016 amongst others), some of which affect carcass composition and muscle distribution. However, the optimal strategies to exploit these QTL in sheep breeding programmes are not always clear, especially within cross-breeding schemes. Although many studies have found associations between QTLs, or in some cases causative SNPs, and carcass traits, the results of association studies should be confirmed through independent studies in the target population or breed-type before the information can be used in practice, as the associations between genotype and phenotype can differ (Hocquette et al. 2012).

The UK is one of the largest producers of lamb meat in Europe, slaughtering around 12 million lambs per year (AHDB, 2021). The stratified nature of the UK sheep industry relies on crossbreeding to maximise potential from the variety of environments and breeds within the UK. Around 66% of UK slaughter lambs are born to commercial crossbred mothers, exploiting the advantages of heterosis (Boon & Pollott, 2021), with the Scotch Mule traditionally being one of the most common types of crossbred ewe. However, the Lleyn breed is becoming increasingly popular as a maternal breed in the UK, with an increase in the purebred population and in the use of crossbred Lleyn ewes (Boon and Pollott, 2021). Terminal sire breeds contribute about 40% of the genes of all UK slaughter lambs, with the Texel being the predominant breed (Boon and Pollott, 2021). Genetic selection has

previously been performed only in pure breeds, with crossbred ewes and lambs rarely performance-recorded. However, evidence in pigs suggests that genetic correlations between pure-bred and cross-bred performance can often be low (Dekkers, 2007). Duijvesteijn and Van der Werf (2016) suggested that sheep breeding programmes should combine pure- and cross-bred performance in their genetic evaluations in order to assign the most relevant breeding values. In the UK from 2018 onwards, terminal sire breeding programmes have provided EBVs from a combined breed analysis (Moore et al., 2016), incorporating data from pure- and cross-bred performance-recorded sheep. Increased focus on cross-bred performance, particularly for product quality traits, could make breeding values more relevant for commercial lamb producers.

Meat yield and tissue distribution (muscle, fat, bone) are considered difficult to measure traits and not commonly recorded, for pure- or cross-bred lambs, although they have a major impact on the value of the lamb carcass within the supply chain. Video Image Analysis (VIA) technology that can be used in-line at the abattoir and has been shown to more accurately predict lean meat yield and primal cut weights than the EUROP grades (Rius-Vilarrasa et al., 2009). Recently-calibrated VIA algorithms can accurately predict weights of fat, muscle and bone from the total carcass and from primal (shoulder, saddle, hind-leg) regions (Tolkamp et al., 2020).

The aim of this study was to use genotypes and VIA-derived phenotypes (muscle, fat and bone weights in the whole carcass and in primal regions) from crossbred Texel lambs to: i) estimate variance components and heritabilities for the traits of interest in two populations with differing maternal breeds; ii) perform genome wide association studies in lambs from two different maternal breeds, in order to identify any significant regions of the genome associated with these carcass traits, and iii) assess whether there are similar genomic regions influencing VIA carcass traits across different maternal genotypes of Texel-sired lambs.

2. Material and Methods

2.1. Data description

All procedures involving animals were approved by the Scotland's Rural College (SRUC) Animal Ethics Committee (ED AE 33-2014) and were performed under UK Home Office license, following the regulations of the Animals (Scientific Procedures) Act 1986.

Data were available from two studies involving SRUC, the Texel Sheep Society (TSS) and ABP Food group. The data included sire and lamb genotypes, information collected on-farm from birth to slaughter, and data collected at the abattoir at the point of slaughter. The Texel sires (n = 93) used to produce the project lambs for each trial were selected from the performance recorded TSS population and were genetically related to each other. Nine of the 93 sires were used across both projects.

2.1.1. Data set 1 - Texel x Scotch Mule (TxSM) lambs

Crossbred Texel x Scotch Mule (Bluefaced Leicester x Scottish Blackface) lambs (n=2,330) were produced in one year (2018) across four farms and were recorded from birth to slaughter. The farms were all located in Scotland, with three in Dumfriesshire and one in Fife. The lambs were produced from a total of 1,105 mixed-age Scotch Mule ewes, with no associated pedigree records, and 43 performance-recorded Texel sires from 15 pedigree flocks. Lambs were recorded as having been reared to weaning as being either singletons (n=214), twins (n=1,324), triplets (n=742) or quadruplets (n=35), with 15 lambs of unknown rearing rank. Female (n=1,110), castrated male (n=1,206) and entire male (n=14) lambs were used. Lambs were reared to slaughter on low-ground pastures and supplementary feeding was only offered to late- finishing batches, that were unlikely to finish off grass alone. Live

weights were recorded at birth (BWT), at an average age of 8 weeks (8WKWT), and again at an average age of 15 weeks (15WKWT).

Lambs were selected for slaughter in batches, depending on their body condition score (target score 3) and live weight (target 42 kg). Lambs were finished in 14 batches, with each batch including lambs of different sexes and most batches representing more than one farm. Lambs travelled to an abattoir in Dorset for slaughter, where the carcass data collection was undertaken. To avoid excessive daily travel time, lambs were delivered from their home farm to a collection centre in Penrith in the North of England the day before slaughter, where they were rested before travelling onwards to an abattoir (approximately 325 miles) for slaughter the following day. Cold carcass weight (CCWT; predicted as standard by the abattoir, by subtracting 0.5 kg from hot carcass weight measured immediately post-slaughter, to account for estimated evaporative loss) was rounded to the nearest 0.1 kg.

2.1.2. Data set 2 - Texel x Lleyn (TxL) lambs

Crossbred Texel x Lleyn lambs (n=3,816) were produced across two years (2018 and 2019) from six farms and were recorded from birth to slaughter. The farms were located in Scotland, England and Wales. The lambs were produced by a total of 964 mixed-age Lleyn ewes (2-8 years old), with no associated pedigree records and 59 performance-recorded Texel sires from 21 pedigree flocks. Lambs were recorded as either singletons (n=663), twins (n=2,232), triplets (n=617), quadruplets (n=84) or quintuplets (n=8), with 212 lambs of unknown rearing rank. Female (n=1,751) and castrated male (n=2,065) lambs were used. Lambs were reared to slaughter on low-ground pastures and supplementary feeding was only offered to late-finishing batches that were unlikely to finish off grass alone. Live weights were recorded from birth to weaning (BWT, 8WKWT, 15WKWT).

Lambs were selected for slaughter in batches, depending on body condition score (target score 3) and live weight (target 42 kg). Lambs were finished in 54 batches – each batch including lambs of different sexes and most batches representing lambs coming from more than one farm. Lambs travelled to the same abattoir in Dorset for slaughter, where carcass data collection was undertaken. Similarly as for the TxM, cold carcass weight was rounded to the nearest 0.1 kg.

2.1.3. Video Image Analysis (VIA) data

After slaughter, all lambs from datasets 1 and 2 were scanned using a VIA machine (VSS2000, E+V Technology Gmbh, https://www.eplusv.com/en/products/sheep/vss-2000/) that was installed on the slaughter line. The VIA machine had been calibrated by the manufacturer (E+V) against results obtained by CT scanning (Tolkamp et al., 2020), using similar carcasses at this abattoir, to predict 19 VIA traits (WC_TWT - whole carcass total weight, HL_TWT - hind leg primal total weight, SAD_TWT - saddle primal total weight, SH_TWT - shoulder primal total weight, WC_BWT - whole carcass bone weight, WC_BWT_6P – whole carcass bone weight from a maximum of 6 predictors, WC_FWT - whole carcass fat weight, WC_FWT_6P – whole carcass fat weight from a maximum of 6 predictors, WC_MWT - whole carcass muscle weight, WC_MWT_6P – whole carcass muscle weight from a maximum of 6 predictors, HL_BWT - hind leg bone weight, HL_FWT - hind leg fat weight, HL_MWT - hind leg muscle weight, SAD_BWT - saddle bone weight, SAD_FWT - saddle fat weight, SAD_MWT - saddle muscle weight, SH_BWT - shoulder bone weight, SH_FWT - shoulder fat weight, SH_MWT - shoulder muscle weight). Weights of fat, muscle and bone in the whole carcass were predicted by E+V in two ways, i) by using the best combinations of predictors from across all VIA parameters, or ii) limiting the number of predictors to 6 in the prediction equation (denoted as 6P). Both methods had provided

similar accuracies in the original calibration trials in which the predictions were developed, and both were retained in this study to investigate the genetic control of these traits for the first time. Each trait was predicted independently by E+V using VIA parameters (lengths, widths, areas, colour parameters). The prediction equations are commercially sensitive, so are not available for publication.

2.2. Genotypes

Genotypes were available for a subset of each of the two independent sets of animals that had VIA data. In data set one, 834 TxSM lambs were genotyped on the Illumina low density LDv2 which consists of 16,560 Single Nucleotide Polymorphisms (SNPs). Therefore, only a sub-set of the animals from data set one had genotypes, as well as VIA data, but these lambs represented all four farms across slaughter batches. In data set two, 2,852 TxL lambs were genotyped on two chip types - Illumina LDv2 (n=1,423 animals) and Illumina 50k with 45,205 SNPs (n=1,429 animals). As the TxL lambs were genotyped on two different chip arrays and there were not enough data to perform the imputation with satisfactory accuracy, a subset of common SNPs on both chip arrays was selected (n=15,747 SNPs overlap) and used for this study. All genotypes were subject to standard quality control, removing animals with low genotype call rates (<81%). Only genotypes from autosomal chromosomes were used in this study.

2.3. Heritability estimation

Both datasets were cleaned for the purpose of genetic parameter estimation. Lambs without measurements, with lack of information on sex or dam were excluded from the analysis, leaving n=1,429 lambs for TxSM and 2,789 lambs for TxL.

The pedigree file used contained all relevant information from the full Texel Sheep Society pedigree records, including 3,164 animals for TxSM and 5,096 animals for TxL. No pedigree information was available on the Scotch Mule or Lleyn dams of the study lambs.

Variance components for crossbred carcass VIA traits were estimated within breed type in ASReml (Gilmour et at., 2015) using single-trait sire models. Multiple models were tested, and the significant terms retained in the models for these two populations included fixed effects of farm, year, slaughter batch, sex and carcass weight as a covariate (except for WC_TWT), with an additional random effect of dam (permanent environment). Including carcass weight as a covariate meant that the weights of the different tissues and regions were predicted relative to total weight of the carcass.

2.4. Population structure

Genotypes available for project lambs that passed the quality control (n=825 for TxSM and n=2,768 for TxL) along with genotypes for pure-bred Texel sheep, collected by TSS between 2015 and 2018 (n=9,485), were used to assess the population structure using Principal Component Analysis (PCA; Macciotta et al. 2010; Mucha et al. 2015) in R software (R Development Core Team, 2021). This analysis was undertaken to identify potential outliers which might not be connected strongly enough to the core (pure-bred Texel) population, indicating population stratification. Pure-bred Texel sheep genotypes were included to check if the (cross-bred) lambs clustered within, or close to, the pure-breed population. As the genotypes used in the population structure analysis were collected on five different chip types (genotypes for the pure-breed Texel; from high density to low densities, where low density includes also genotypes for the TxSM and TxL lambs), a subset of 8,474 common SNPs was extracted as described in Kaseja et al. (2022) and used in this part of the study only.

2.5. Genome wide association study

GWAS was performed using a multi-locus mixed model algorithm (Segura et al. 2012) implemented in the R (R Development Core Team, 2011) package 'statgenGWAS' (van Rossum et al., 2022). An additive genetic model was used, where the major homozygous genotype was coded as zero, heterozygous as one, and minor homozygous as two. Datasets used in this part of the research included lambs that had a valid genotype (i.e. passed the QA checks) and valid phenotypic records. This further reduced the available datasets to 718 TxSM lambs and 2,636 TxL lambs.

Missing SNPs were imputed randomly (i.e. missing values were replaced by a random value calculated using allele frequencies per SNP). Kinship was calculated using the method described in VanRaden (2008). For the selection of candidate loci, Bonferroni correction was used with a LOD-threshold of $-log_{10}(^{0.05}/_{m})$, where m is the number of SNPs. Genome wide association study was carried out for all available traits with adjustment for both the fixed effects (as described above for the heritability estimation) and for the first two principal components (from the analysis described in the previous section) to account for the population stratification (Zhang et al, 2018).

To test the presence of inflated values, the inflation factor (λ) was calculated as being the observed median value of the chi square test for the null markers divided by the expected median value (Hinrichs et al., 2009). The proportion of phenotypic variance explained by each SNP was computed as $\beta^2_{SNP} * var_{(SNP)}/var_{(pheno)}$, where β is the solution vector of coefficients of the SNP fixed effect (van Rossum, 2022).

SNPs that were significantly associated with a particular trait were checked against previously reported QTL in https://www.animalgenome.org/. Candidate genes located near the SNPs that reached genome-wise significance SNPs were identified using the Ensembl database, and gene annotation information was obtained from the ovine genome assembly

version Oar_v3.1 (www.ensembl.org/biomart/). Candidate regions for gene detection were defined within 400Kb windows (200Kb downstream and 200Kb upstream) from the genome-wise significant SNPs position.

The Database for Annotation, Visualisation and Integrated Discovery (DAVID) v6.8 tool (Huang et al., 2009) was used to classify genes in accordance with their biological function. Candidate genes were further analysed using the GeneCards (Stelzer et al., 2016), the Ensembl Genome Browser (Yates et al., 2019) and the NCBI database resources (Sayers et al., 2020).

3. Results and discussion

3.1. Phenotypic data

Live weights and predicted VIA traits are summarised in Table 1 for TxSM lambs and Table 2 for TxL lambs. Slaughter age (SLAGE) of TxSM lambs ranged from 85 days to 322 days (average 195 days) and for TxL lambs ranged from 95 days to 360 days (average 213 days).

3.2. Population structure

In the PCA analysis of the genotypes, over 55% of the variation was explained by the first ten principal components, with 38.5% and 6.01% explained by first and second component, respectively. Figure 1 illustrates the clustering of the studied populations by plotting the first and second principal components of the genomic relationship matrix, indicating that TxL and TxSM lambs cluster together, disconnected from the cluster of pure-breed Texel animals. This result indicates that there is a genomic difference between pure-breed and cross-breed animals included in this study, supporting the hypothesis that crossbred animals cluster together.

3.3. Heritability estimation

Variance component estimation identified the majority of traits as heritable, with heritability estimates ranging from low to high (Table 3). Since all the VIA traits except WC-TWT were adjusted for carcass weight, they were not considered as absolute weight traits, but were predicting weights of the different tissues and regions relative to total weight of the carcass (i.e. as proportions). The heritability estimates indicate that there is a difference in the inheritance of individual traits between TxL and TxSM crossbred populations. Overall, heritabilities for each trait were higher in the TxSM population than the TxL population. Within the TxSM lambs, some of the highest heritabilities were estimated for fat weights in the whole carcass (WC_FWT; WC_FWT_6P) and the primal regions (HL_FWT; SAD_FWT; SH_FWT), ranging from 0.38 to 0.70. Muscle and bone weight traits were moderately heritable in TxSM (0.19-0.48), except for WC_MWT_6P and SH_BWT, where the heritabilities were not significantly different from zero. Since the predictor parameters included in the VIA trait prediction equations are not available (owned by e+v), it is difficult to speculate on the reason why WC_MWT is substantially more heritable in this population than WC_MWT_6P, which is predicting the same trait with fewer predictors. However, this result suggests that WC_MWT may be a better predictor of whole carcass muscle weight to consider including in a breeding programme. Heritability estimates for total weights of the primal regions ranged from 0.16 to 0.30 in the TxSM lambs. Heritabilities estimates for WC_BWT_6P were much higher for the TxSM (0.42) than for TxL (0.04), however as the σ_p are similar (29724 and 26693, respectively) the greatly reduced heritability for TxL must be due to significantly reduced genetic variance. The reason for this is unclear. It may be that the component VIA dimensions or parameters included in the prediction equation for this trait are under greater genetic control in the TxSM cross lambs. Within the TxL lambs, heritabilities estimated for all VIA traits were <0.2, except for bone weights in the whole

carcass, hind leg and saddle regions, where they ranged from 0.20 to 0.37. Heritabilities previously reported for VIA traits on crossbred lambs tend to be low to moderate, depending on the trait (Rius-Vilarrasa et al., 2009; Einarrson et al., 2015) and are generally in line with the findings from this research. Payne et al. (2009) examined 6,565 progeny of New Zealand terminal sire rams and also found the heritabilities for VIA measured traits to be low to moderate. The difference in heritability estimates between breeds observed in the current study may be partly as a result of the differences between the two projects in terms of the ability of individual farms to deliver lambs for slaughter at the correct specifications. Although the target weight and condition score of selection for slaughter were set at 42kg and score 3 across the two trials, in reality there was wide variation in these parameters, especially within the TxL lambs, partly due to the practicalities of transporting batches of lambs to the ABP Yetminster abattoir at the optimum time from the various UK farms involved in the trial. The increased variation in TxL lambs can be observed by the higher standard deviations for most carcass traits measured (Tables 1, 2 and 3). Although carcass weight was adjusted for in the model, a range of >45kg in live weights at selection for slaughter would mean that some of the lambs would be at a different point of the growth curve when slaughtered than others, affecting carcass composition. A linear adjustment for weight may not, therefore, be fully accounting for this variation.

3.4. Genome wide association studies

The association analysis using 'statgenGWAS' identified SNPs that reached the genome-wise significance threshold ($p < 0.05$; Table 4) on chromosomes two and eight for the following traits for the TxSM lambs: WC_FWT_6P, WC_MWT_6P, HL_FWT, SAD_FWT and SH_BWT. No significant SNPs were discovered for the live weight traits; however, this may be caused by the limited dataset available at the time of this research (Table 1), with only

around 300 phenotypes available for BWT and 15WKWT. The dataset for 8WKWT included only 669 phenotypes, which may still be insufficient to identify candidate SNPs. Figure 2 shows the Manhattan plots for TxSM lambs.

For the TxL lamb dataset, three SNPs reached the genome-wise significance threshold ($p < 0.05$; Table 4) for the VIA traits: one on chromosome 19 for WC_BWT_6P and two on chromosome two for HL_MWT. One SNP on chromosome 19 reached the significance threshold for weaning weight. Figure 3 shows the Manhattan plots for the TxL dataset.

Results confirmed 15 genes neighbouring the genome-wise significant SNPs. The majority of these genes are protein coding genes located on chromosomes two and 19, but one is located on chromosome eight and is a gene of miscellaneous RNA (Yates et al., 2019, Sayers et al., 2020). Two genome-wide significant SNPs for TxL on chromosome two (for trait HL_MWT, located at SNP positions 117959202 and 118043352) were close to the Myostatin (MSTN) gene which has known effects on skeletal muscle cells and close to the previously reported mutation of rs408469734 at the position 118150665 in many sheep breeds (Talebi et al., 2020), providing that a polymorphism of the MSTN gene on chromosome two, reported to segregate in various breeds or strains of sheep (Clop et al., 2006), results in increased muscle growth (Broad et al., 2000) and can also affect fat traits (Johnson et al., 2005). This mutation is known to be almost fixed in the UK Texel breed and segregating in a number of other UK breeds (Hadjipavlou et al., 2008). For muscle growth traits, the mode of inheritance of this MSTN polymorphism is usually reported as being partially recessive (Masri et al., 2011; Hadjipavlou et al., 2008), implying that the heterozygous animals differ only moderately from homozygous wildtype animals.

Other major genes or quantitative trait loci (QTL) have been reported to affect carcass traits in different sheep populations, many of which have been found on chromosome 18. These

include a mutation in the Callipyge gene on chromosome 18 resulting in a major increase in hindquarter muscling caused by muscle hypertrophy (Cockett et al., 1999), expressed in heterozygous animals with maternal imprinting, meaning that the mutation is only expressed when a single copy is inherited from the sire (Cockett et al., 1996; Shackelford et al., 1998; Freking et al., 1998). The Carwell (or LoinMax®; Dodds, 2007) mutation, also identified on chromosome 18 and thought to be maternally imprinted, shows a smaller phenotypic effect than Callipyge on muscling, increasing the weight and area of the *longissimus* (Nicoll et al. 1998; Hopkins and Fogarty, 1998; Masri et al. 2010). Another QTL identified on chromosome 18 in Texel sheep (Texel Muscling (or TM-) QTL, Walling et al. 2004), has been found to increase loin muscle dimensions and weights (by ~4 to 14%) in purebred and crossbred carrier lambs (Walling et al. 2004; Macfarlane et al. 2009; 2014). The TM-QTL has also been shown to exhibit the same polar over-dominant mode of inheritance as Callipyge (Macfarlane et al. 2010; Macfarlane et al. 2014; Lambe et al. 2011). However, in the current study, no SNPs on chromosome 18 were found to significantly affect the carcass traits measured by VIA, including those relating to muscle weights in the carcass or primal regions, in either crossbred lamb population.

The SheepQTLdb (http://www.animalgenome.org/cgi-bin/QTLdb/OA/index) contains all curated sheep QTL, amounting to 4729, to August 25th, 2023, based on 248 publications, with associations to 272 traits. This includes 563 QTL associated with meat and carcass traits. However, very small numbers of QTL appear to have been identified that relate to tissue weights and distribution within lamb carcasses, similar to those assessed by VIA.

The results indicate that there are no common SNPs that were significantly associated with traits in both crossbred populations studied. Those that did reach genome-wise significance

for individual traits within a population explained only a low percentage of the genetic variation, indicating that these are likely to be highly polygenic traits. This result can perhaps be partially explained by the relatively low number of available phenotypes and genotypes, and also because of the relatively low-density of the array types used in this study.

Inflation factors λ for analysed traits were between 0.95 and 1.01 for all the traits in both datasets, implying the absence of any significant artificial inflation (Hinrichs et al., 2009). Results obtained in this study indicate that all the traits have complex genetic architecture and are polygenic, although future work might build on this research to investigate regions (SNP windows) or various lengths that potentially could explain measurable proportions of the phenotypic variance of the traits (Fragomeni et al., 2014). The current study did not identify molecular markers that explain large proportions of the genetic variance observed in VIA-measured carcass traits in these first-cross Texel lamb populations, implying limited value of including this information in the estimation of breeding values for these new traits across similar crossbred populations. However, it is known that the Texel breed is almost fixed for at least one SNP affecting carcass traits (the mutation on the MSTN gene documented by Clop et al., 2006, which is partially recessive, Hadjipavlou et al., 2008), therefore similar investigations in other breed crosses may identify QTL with greater effects. More larger studies across breed types are recommended to further test and validate molecular markers for traits related to lamb carcass quality, as measured by video image analysis.

4. Conclusions

Results of this research will contribute to future studies on similar traits. If sheep carcass grading progresses to use VIA more widely, to better reflect carcass quality and value, breeding for traits that reflect carcass composition and tissue distribution will become more valuable along the supply chain. The results presented here indicate that there is potential for

genetic selection and for further exploration of the sheep genotype in order to improve meat yield and quality. However, genetic control of these traits may be influenced by the genetic background (breed or cross-breed) of the sheep or may be masked by management decisions influencing time of slaughter. These considerations should be understood in order to define protocols for incorporation of these carcass traits into breeding programmes for crossbred lambs. Optimal breeding and management strategies can then be developed for the production of high-quality slaughter lambs.

Ethics approval

All procedures involving animals were approved by the Scotland's Rural College (SRUC) Animal Ethics Committee and were performed under UK Home Office license, following the regulations of the Animals (Scientific Procedures) Act 1986.

Data and model availability statement

The data that support the study findings are private and confidential.

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All authors have read and approved the final manuscript.

Declaration of Generative AI and AI-assisted technologies in the writing process

The authors did not use any artificial intelligence assisted technologies in the writing process.

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Declaration of interest

None.

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Table 1: Data summary for live weights and Video Image Analysis traits for 718 Texel cross Scotch Mule (TxSM) lambs

Trait	**Definition**	**Min.**	**Mean**	**SD**	**Max.**	**Records available**
BWT	Birth weight (kg)	1	4.09	1.18	8	307
8WKWT	Eight week weight (kg)	8	23.32	4.95	41	669
15WKWT	Weaning weight (kg)	15	32.82	6.67	52	285
WC_TWT	Whole carcass total weight (kg)	11.90	18.38	1.70	25.33	711
HL_TWT	Hind leg primal total weight (kg)	4.78	6.72	0.57	8.84	707
SAD_TWT	Saddle primal total weight (kg)	3.28	5.10	0.58	7.47	700
SH_TWT	Shoulder primal total weight (kg)	4.73	6.50	0.61	9.22	707
WC_BWT	Whole carcass bone weight (g)	1920	3506	260	4568	700
WC_BWT_6P	Whole carcass bone weight (6 predictors; g)	2277	3492	283	4670	700
WC_FWT	Whole carcass fat weight (g)	138	1989	649	5040	711
WC_FWT_6P	Whole carcass fat weight (6 predictors; g)	271	1921	671	4938	699
WC_MWT	Whole carcass muscle weight (g)	8841	12737	1081	16271	711
WC_MWT_6P	Whole carcass muscle weight (6 predictors; g)	9049	13584	5396	57446	711
HL_BWT	Hind leg bone weight (g)	870	1137	83	1423	700

HL_FWT	Hind leg fat weight (g)	125	537	143	1112	700
HL_MWT	Hind leg muscle weight (g)	3611	5066	403	6363	700
SAD_BWT	Saddle bone weight (g)	682	931	93	1448	711
SAD_FWT	Saddle fat weight (g)	26	746	345	2261	691
SAD_MWT	Saddle muscle weight (g)	2363	3309	285	4455	707
SH_BWT	Shoulder bone weight (g)	948	1566	1265	11782	711
SH_FWT	Shoulder fat weight (g)	268	763	156	1484	699
SH_MWT	Shoulder muscle weight (g)	3027	4622	414	6012	700

Table 2: Data summary for live weights and Video Image Analysis traits for 2636 Texel cross Lleyn (TxL) lambs:

Trait	**Definition**	**Min.**	**Mean**	**SD**	**Max.**	**Records available**
BWT	Birth weight (kg)	1	4.45	1.10	9	2565
8WKWT	Eight week weight (kg)	3	20.71	5.73	44	2550
15WKWT	Weaning weight (kg)	14	33.48	6.55	69	2243
WC_TWT	Whole carcass total weight (kg)	11.16	17.58	2.08	27.55	2598
HL_TWT	Hind leg primal total weight (kg)	4.37	6.54	0.70	9.81	2612
SAD_TWT	Saddle primal total weight (kg)	2.09	4.77	0.69	8.18	2579
SH_TWT	Shoulder primal total weight (kg)	4.04	6.26	0.73	9.74	2612
WC_BWT	Whole carcass bone weight (g)	2379	3392	281	4567	2579
WC_BWT_6P	Whole carcass bone weight (6 predictors; g)	2223	3358	314	4459	2579
WC_FWT	Whole carcass fat weight (g)	9	1735	713	4914	2587
WC_FWT_6P	Whole carcass fat weight (6 predictors; g)	34	1611	732	4863	2495
WC_MWT	Whole carcass muscle weight (g)	7957	12337	1365	18394	2598
WC_MWT_6P	Whole carcass muscle weight (6 predictors; g)	8049	12759	3885	57707	2598
HL_BWT	Hind leg bone weight (g)	285	1089	105	1506	2579
HL_FWT	Hind leg fat weight (g)	0.5	470	164	1221	2534

HL_MWT	Hind leg muscle weight (g)	3042	4939	505	7091	2579
SAD_BWT	Saddle bone weight (g)	646	891	89	1251	2598
SAD_FWT	Saddle fat weight (g)	0.4	606	349	2355	2370
SAD_MWT	Saddle muscle weight (g)	1958	3211	358	4695	2612
SH_BWT	Shoulder bone weight (g)	869	1457	878	11961	2618
SH_FWT	Shoulder fat weight (g)	2	654	174	1420	2578
SH_MWT	Shoulder muscle weight (g)	2560	4218	506	6670	2579

Table 3: VIA-predicted trait means (and sd), phenotypic variances (σ_p) and direct heritabilities (h^2 and se) estimated for TxSM and TxL.

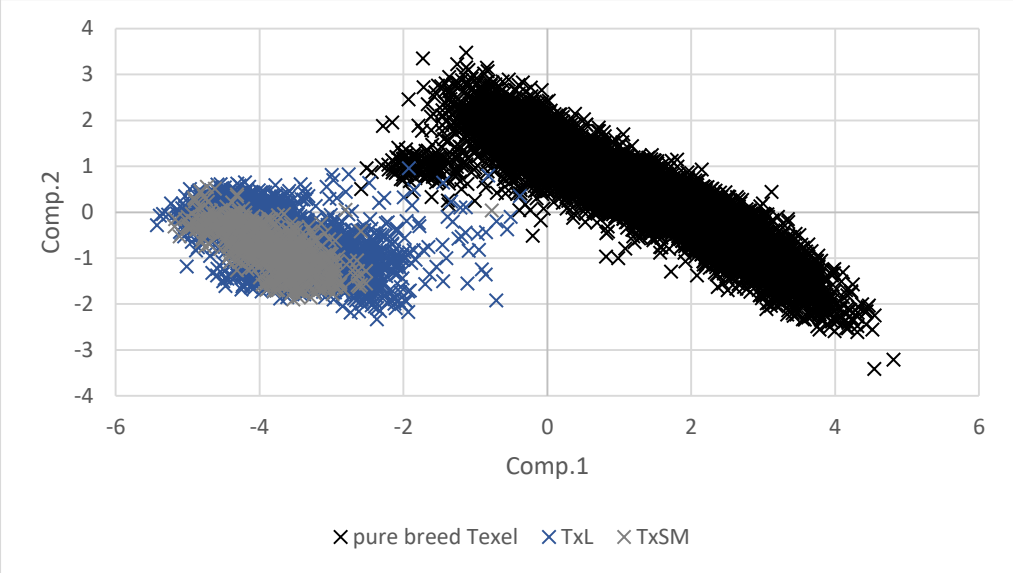
	TxSM			**TxL**		
Trait	**mean**	σ_p	**h^2 (se)**	**mean**	σ_p	**h^2 (se)**
WC_TWT	18.44	2.41	0.07 (0.05)	17.58	2.89	0.04 (0.03)
HL_TWT	6.74	0.03	0.26 (0.09)	6.54	0.04	0.03 (0.02)
SAD_TWT	5.11	0.03	0.16 (0.07)	4.77	0.04	0.003 (0.02)
SH_TWT	6.53	0.03	0.30 (0.10)	6.26	0.05	0.01 (0.02)
WC_BWT	3523	24245	0.36 (0.11)	3393	23903	0.27 (0.08)
WC_BWT_6P	3509	29724	0.42 (0.12)	3282	26693	0.04 (0.03)
WC_FWT	1997	17774	0.56 (0.15)	1746	15391	0.18 (0.06)
WC_FWT_6P	1930	18258	0.47 (0.14)	1969	16578	0.14 (0.05)
WC_MWT	12760	154880	0.43 (0.12)	12330	223250	0.08 (0.03)
WC_MWT_6P	13340	147270	0.04 (0.04)	12750	134500	N/A
HL_BWT	1142	2676.1	0.22 (0.08)	1089	3996.6	0.20 (0.06)
HL_FWT	537.8	9318.5	0.43 (0.13)	472.4	8989.7	0.09 (0.04)
HL_MWT	5080	34687	0.19 (0.08)	4937	50074	0.06 (0.03)
SAD_BWT	935.1	4123.7	0.48 (0.13)	890.4	3550.8	0.37 (0.08)
SAD_FWT	753	58422	0.38 (0.12)	613.3	47792	0.13 (0.05)
SAD_MWT	3314	14198	0.29 (0.09)	3212	17110	0.01 (0.02)
SH_BWT	1511	836025	0.05 (0.04)	1435	786280	N/A
SH_FWT	761.9	11014	0.70 (0.17)	655	10152	0.19 (0.06)
SH_MWT	4382	37728	0.23 (0.09)	4216	49937	0.18 (0.05)

N/A means the parameters could not be estimated

Table 4: Significant SNPs identified in the association analysis using 'statgenGWAS' R package:

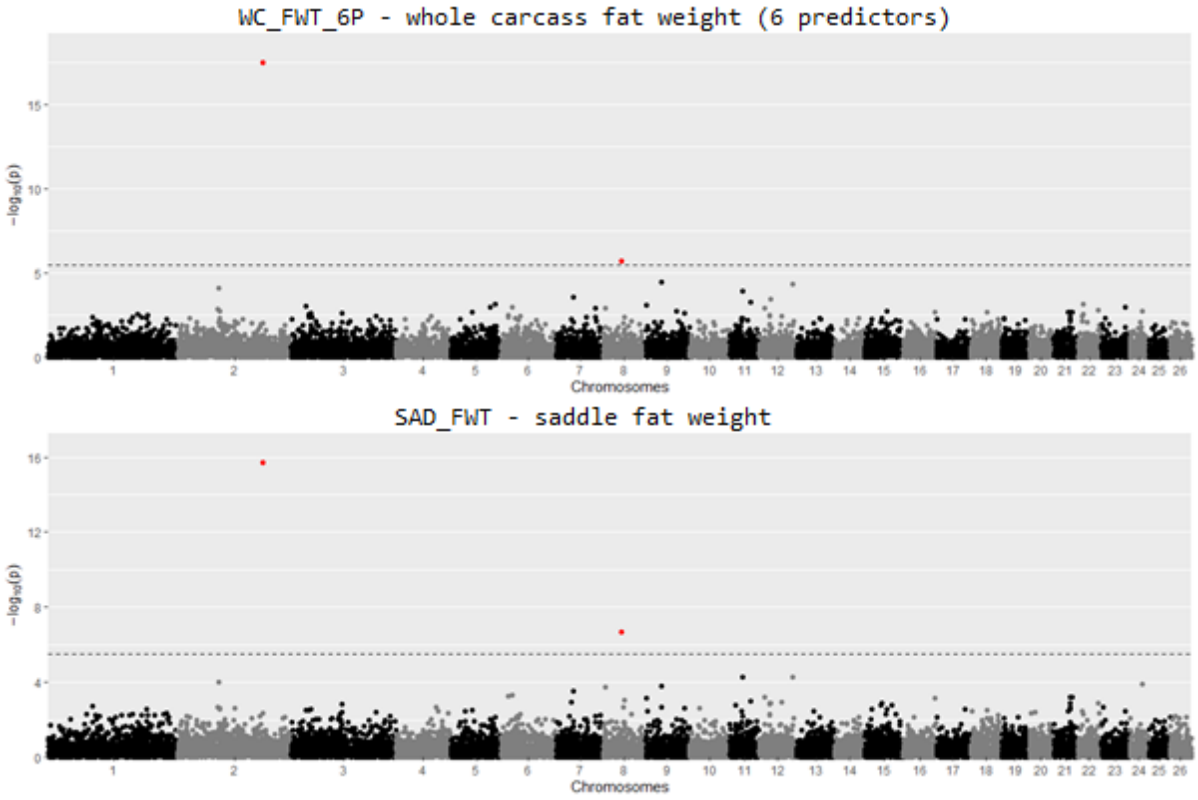
		Chromosome	SNP position	P Value	Proportion of SNP variance
TxSM	**WC FWT 6P**				
	s74618.1	2	196253756	1.0465e-16	0.094
	s68536.1	8	42239578	2.7387e-07	0.037
	WC MWT 6P				
	s74618.1	2	196253756	3.2030e-18	0.103
	s68536.1	8	42239578	1.7068e-06	0.033
	HL FWT				
	s74618.1	2	196253756	1.0378e-16	0.094
	s68536.1	8	42239578	3.5579e-07	0.036
	SAD FWT				
	s74618.1	2	196253756	2.0484e-16	0.092
	s68536.1	8	42239578	2.5187e-07	0.037
	SH BWT				
	s74618.1	2	196253756	3.5629e-17	0.098
	s68536.1	8	42239578	1.5159e-06	0.033
TxL	**WC BWT 6P**				
	OAR19_8995957.1	19	8995957	2.5034e-06	0.011
	HL MWT				
	OAR2_117959202	2	117959202	6.6189e-07	0.020
	OAR2_118043352	2	118043352	3.0750e-06	0.018
	WEANING WEIGHT				
	s40847.1	19	11706755	2.9193e-08	0.108

Figure 1: Plot of first (Comp.1) and second (Comp.2) principal components of the genomic relationship matrix



TxL – Texel x Lleyn dataset
TxSM – Texel x Scotch Mule dataset

Figure 2: Manhattan plots of the GWAS genome-wise significant results ($-\log_{10}(p)$ of the corresponding p values corrected for the Bonferroni correction). Genome wise ($p < 0.05$) threshold is represented as a dotted line for traits with significant SNPs discovered on the TxSM lambs dataset:



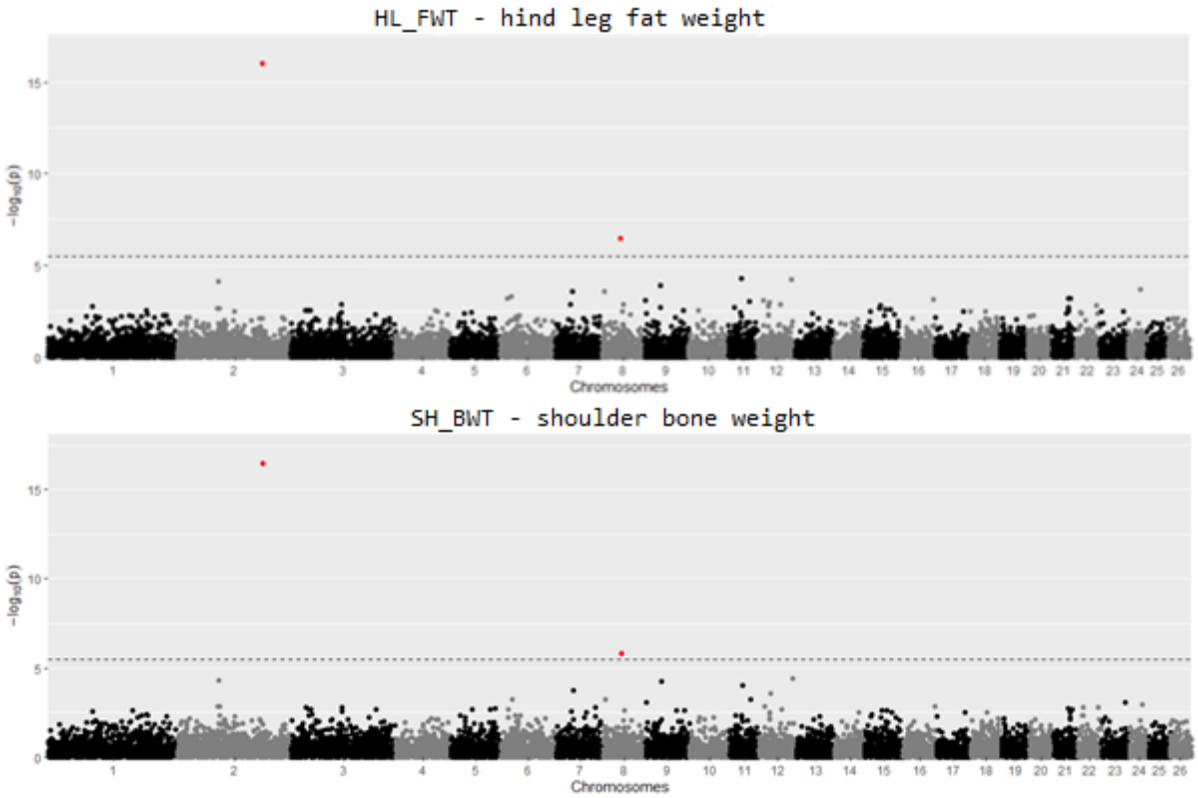
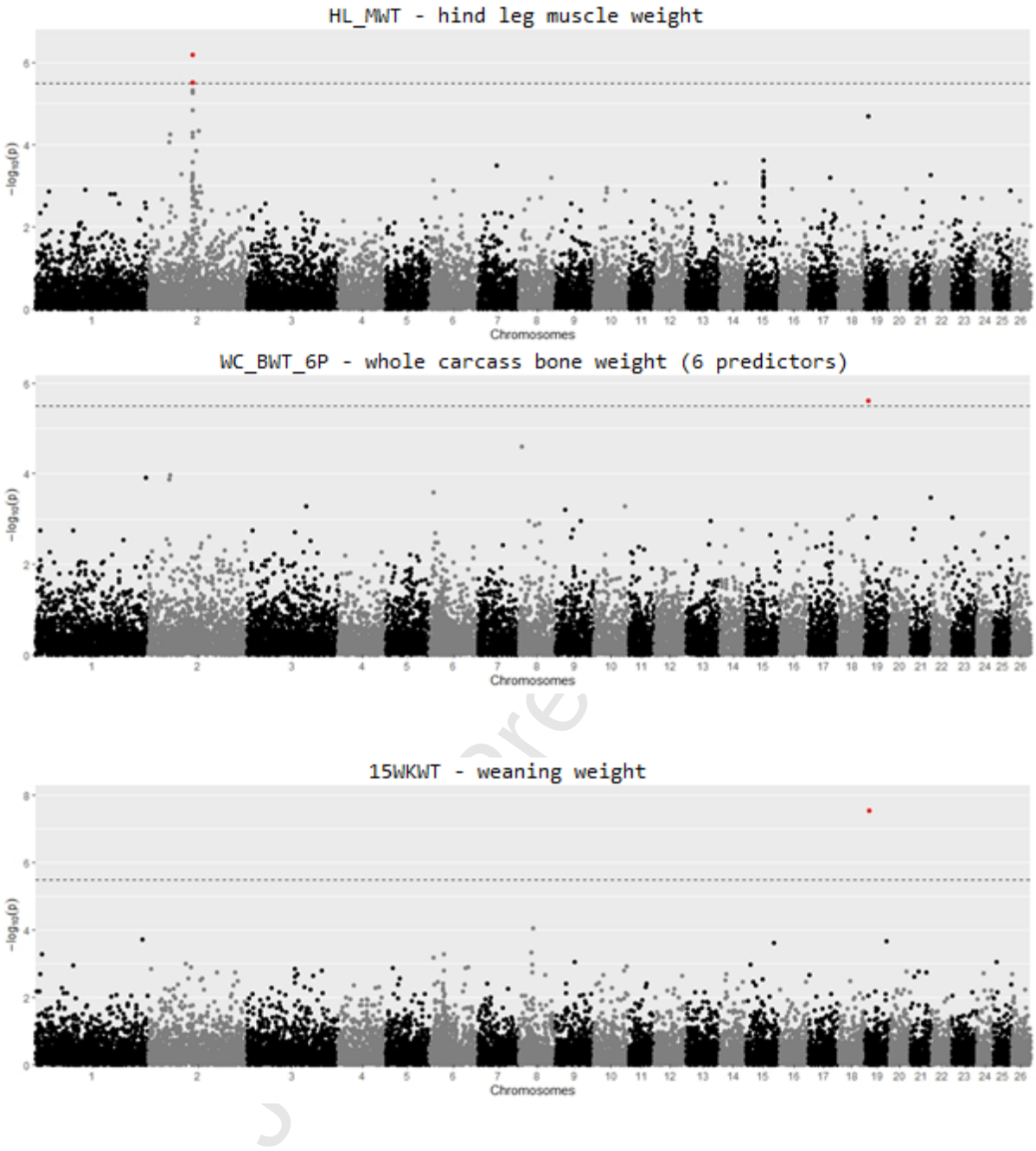


Figure 3: Manhattan plot of the GWAS genome-wise significant results ($-\log_{10}(p)$ of the corresponding p values corrected for the Bonferroni correction). Genome wise ($p < 0.05$) threshold is represented as a dotted line for traits with significant SNPs discovered on the TxL lamb dataset:



Author' contributions

Karolina Kaseja: Formal analysis, Investigation, Writing - Original Draft, Writing - Review & Editing. Joanne Conington and Nicola Lambe: Conceptualization, Resources, Writing - Review & Editing, Supervision. John Yates and Ed Smith: Resources, Writing - Review & Editing.

All authors have read and approved the final manuscript.

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