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Genome-wide association study of health and production traits in meat sheep

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Abstract

Genotypes are currently widely used in animal breeding programmes to enhance the speed of genetic progress. With sufficient data, a Genome-Wide Association Study (**GWAS**) can be performed to identify informative markers. The aim of this study was to investigate the genetic background of health (footrot and mastitis) and production (birth weight, weaning weight, scan weight, and fat and muscle depth) traits using the available phenotypic and Single Nucleotide Polymorphism (**SNP**) data collected on the UK Texel sheep population. Initially, 10 193 genotypes were subject to quality control, leaving 9 505 genotypes for further analysis. Selected genotypes, recorded on four different Illumina chip types from low density (15k SNPs) to high density (606 006 SNPs), were imputed to a subset of 45 686 markers from 50k array, distributed on 27 chromosomes. Phenotypes collected on 32 farms across the UK for footrot and mastitis and extracted from the UK National database (iTexel) for the production traits were used along with pre-estimated variance components to obtain de-regressed breeding values and used to perform GWAS. Results showed three SNPs being significant on the genome-wise level ('OAR8_62240378.1' on chromosome 8 for birth weight, 's14444.1' on chromosome 19 for weaning weight and 's65197.1' on chromosome 23 for scan weight). Fourteen subsequent SNPs were found to be significant at the chromosome-wise level. These SNPs are located within or close to previously reported QTLs impacting on animal health (such as faecal egg count or somatic cell count) and production (such as body or carcass weight and fat amount). These results indicate that the studied traits are highly polygenic with complex genetic architecture.

Keywords

Genome-Wide Association Study, footrot, mastitis, live weight, small ruminants

Implications

Combining health traits with conventional production traits into breeding programmes will lead to improvements in flock health and productivity. Production traits can be collected relatively easily, whilst the collection of phenotypes for health traits is more

difficult and may be limited by age and/or sex. Genome-Wide Association Study may identify informative molecular markers that explain measurable amounts of a trait variance. Including this information in estimation of breeding values may increase accuracy and enhance the rate of progress from genetic selection. This study confirms the polygenic architecture of investigated traits with a small number of Single Nucleotide Polymorphisms that explain small amount of variation.

Introduction

To select the best animals for the future generations, often, a national breeding programme is created where all the animals from a particular breed can be assessed together (if genetic connectivity is at a satisfactory level). The use of molecular genetics makes it possible and cheaper than ever to incorporate information coming from genotypes into such a programme, allowing for the production of genomic breeding values (**gEBV**). Genotyped animals not only benefit from the higher reliability of gEBVs compared to conventionally obtained Estimated Breeding Values (**EBVs**) (Kaseja et al., 2023), but can also benefit from parentage verification, screening for congenital defects and disease, and the opportunity to enhance genetic improvement if chromosomal regions containing loci affecting particular traits of interests are discovered (Andersson 2001). For this to be enabled, genotypes along with phenotypes are used to undertake a Genome-Wide Association Study (**GWAS**) to detect potential Quantitative Trait Loci (**QTL**) affecting the performance of an animal by indicating the DNA polymorphism and genes associated with a particular trait. The assumption of GWAS is to detect statistical associations between the trait of interest and any of the markers, which are often single nucleotide polymorphisms (Goddard and Hayes 2009).

Several studies using GWAS have been conducted on many different livestock species/breeds, revealing some QTLs associated for example with meat production in Merino sheep (Al-Mamun et al. 2015; Cavanagh et al. 2014), early age weight traits in Baluchi sheep (Gholizadeh et al., 2015), fatty acid composition (Karamichou et al., 2006), birth weight in Lori-Bakhtiari sheep (Ghasemi et al. 2019), postweaning weight traits in Lori-Bakhtiari sheep (Almasi et al., 2021) and somatic cell count in Valle del Belìce dairy sheep (Sutera et al., 2021). Broadly speaking, body weight in sheep is known to be influenced by many known genes, such as *GF-I*, *Leptin*, *MSTN* or *ADRB3* (Forrest et al., 2007; Gholibeikifard et al., 2013). Comprehensive studies performed on many different sheep breeds focused especially on genome regions known to be advantageous for meat production, such as the OAR2 region containing *myostatin* gene responsible for double muscling (Broad et al., 2000; Johnson et al., 2009; Marshall et al., 1999; Hadjipavlou et al., 2008; Telebi et al., 2022).

SNPs detected as a result of GWAS studies that are within or close to the genes of interest can affect the trait, hence these SNPs are important for animal breeding because including them in the genetic model for prediction of breeding values increases the accuracy of prediction.

The aim of the present study was to investigate the genetic background of health (footrot and mastitis) and production (birth weight, weaning weight, scan weight, and fat and muscle depth) traits in UK Texel meat sheep utilising detailed phenotypic and Single Nucleotide Polymorphism data collected over five years on 32 farms across the

UK. We estimated genomic breeding values and identified genomic regions that can potentially impact on the traits of interest. To the authors' knowledge, this was the first such study incorporating nationwide commercially collected production and health phenotypes for meat sheep.

Material and methods

Genotypic data

Initially, 10 193 genotypes of Texel sheep reared in 1 578 farms in the UK, collected between January 2015 and March 2019 were available for this research. Animals had been genotyped with four different DNA arrays, including 1 180 genotypes on the Illumina OvineHD BeadChip based on 606 006 SNPs (**HD**), 2 894 genotypes on Illumina OvineSNP50 based on 54 241 SNPs (**50k**), 2 463 genotypes on Illumina OvineLD BeadChip based on 15 000 SNPs (**LDv1**) and 3 656 genotypes on Illumina OvineLD BeadChip based on 16 560 SNPs (**LDv2**). Selection of animals for genotyping was random and included both adult and young stock. Genotypes were subject to standard quality control as described in (Kaseja et al. 2022), leaving 9 505 genotypes for further analysis.

Since the genotypes were collected on four arrays with different SNPs, all genotypes were imputed to a sub-set of SNPs from the 50k array, resulting in 45 686 markers distributed on 27 chromosome pairs (26 autosomes and one sex chromosome X), after removing SNPs that were not in Hardy-Weinberg equilibrium, had minor allele frequency of <0.05, or had a call rate below 0.98. For the purpose of GWAS, the position of markers was determined using a map provided for Illumina OvineSNP50, reduced to the subset of SNPs selected for analysis. FindHap V3 software was used for imputation (VanRaden et al. 2011).

Phenotypic data

Two datasets were analysed in this study: health traits scores (footrot, **FRT** and California Mastitis Test, **CMT**) and production traits (birth weight, **BWT**, weaning weight, **WW**, scan weight, **SWT**, muscle depth, **MD** and fat depth, **FD**). Health trait data were collected between 2015 and 2019 on 32 farms across the UK on 3 434 genotyped milking females (CMT) and 4 506 genotyped animals (FRT) by the Texel Sheep Society. Production phenotypes were extracted from the UK national database iTexel (https://www.itexel.uk). Live weights were collected at birth (BWT), around eight week of age (WW) and during ultrasound scanning (around 21 weeks of age; SWT, MD and FD). Health traits were scored on a five-point scale, ranging from zero indicating no infection to four for the most severe level of infection, as described in Kaseja et al. (2023). CMT was used as the proxy trait to mastitis, because of its high correlation with milk somatic cells count (McLaren et al. 2018), which is a widely accepted mastitis indicator. All records underwent quality control to eliminate potential errors, by looking at the range (minimum and maximum values) of recorded traits as

well as the variance and standard deviation within the flock to identify potential errors from data entry or flocks with no variance for particular traits.

Although the production traits were recorded as a single measurement per trait per animal, health traits were recorded multiple times, specifically between one and four times for CMT (4 787 measurements) and one and six times for FRT (9 123 measurements). Thus, health traits were analysed using all the available records with a repeatability model. As the health traits were not normally distributed, they were subject to transformation using the natural logarithm transformation of the sum of scores (+1) for either all hooves (FRT) or both sides of udder halves (CMT), collected during one measuring event, as described by McLaren et al. (2018) and Kaseja et al. (2023).

Pedigree

Pedigree records were extracted from the iTexel database. For the production traits, all animals having records on at least one of the traits were extracted together with an eight-generation pedigree, totalling 821 693 animal records. For the health traits, all the animals recorded for at least one health trait were extracted with eight-generation pedigree, totalling 208 505 animals. Where possible, the pedigree was checked for correctness using the opposing homozygote method (Hayes, 2011) and in case of an error – the parent was corrected or changed to being unknown, as described in detail by Kaseja et al. (2022).

Calculation of estimated breeding values and de-regressed estimated breeding values

Estimated breeding values (**EBVs**) of all animals for the traits described above were de-regressed to develop phenotypes for the ensuing GWAS. This was to remove the potential bias associated with animals having different number and type of relatives influencing the breeding value estimate.

The following mixed model was used:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{Wp} + \mathbf{e}$$

where **y** is vector of observations; **b** is the vector of fixed effects; **a** is a vector of random additive genetic effects, solutions of which constituted animal EBV for each trait; **p** is vector for random permanent environment effect; and **e** is a vector of random residual effects. Matrices **X**, **Z** and **W** are incidence matrices relating records to their respective effects. Random effects were assumed to be normally distributed with the mean of zero. Exact fixed and random effects for each separate trait analysis and respective variance components used for the estimation of EBVs were reported in Kaseja et. al (2023).

Subsequently, de-regressed proofs based on Jairath et al. (1998) and Schaeffer (2001) were derived for each individual and trait, with an EBV reliability of at least 0.30.

De-regressed EBVs were then used as input variables to the ensuing GWAS to (a) maximise information from more than one source (i.e. multiple measurements on the health traits and/or information from relatives) and (b) to include as many phenotypes of genotyped animals as possible. Both EBV calculation and de-regression were performed in the software package MiX99 (MiX99 Development Team, 2022).

Genome-Wide Association Analysis

The GWAS was performed using multi-locus mixed model algorithm (Segura et al. 2012) implemented in the R (R Development Core Team, 2022) package 'statgenGWAS' (Bart-Jan 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. The input (de-regressed EBVs) was calculated based on the model described above, by adjusting for fixed effects using **BLUP** (Best Linear Unbiased Predictor) which already accounted for fixed and random effects (hence no covariate matrix in GWAS was used).

Bonferroni correction was applied to obtain significance thresholds for each analysed trait. Markers were considered as being significant at the genome-wise level if the $-\log_{10}(\text{p-value}) > -\log_{10}(0.05/n)$, where n=45 686 (number of markers), giving the threshold of 5.96. Chromosome-wise significance of the marker was assessed by having $-\log_{10}(\text{p-value}) > -\log_{10}(0.05/n)$, where n is the number of markers on each chromosome. The proportion of the variance explained by the SNP was computed as $\boldsymbol{\beta}^2_{SNP} * var(\text{SNP})/var(\text{pheno})$, where $\boldsymbol{\beta}$ is solution vector of coefficients of the SNP fixed effect (van Rossum, 2022). Presence of inflation was examined by calculating the Inflation factor, lambda, as the observed median value of the chi square test for the null markers divided by the expected median value (Hinrichs, Larkin, and Suarez 2009).

Significant SNPs were checked for the reported QTLs in https://www.animalgenome.org/. Candidate genes located near the genome-wise significant SNPs were identified using the Ensembl database and gene annotation information on the sheep genome version Oar_v3.1 (www.ensembl.org/biomart/). Candidate regions for gene detection were defined within 400Kb windows, 200Kb downstream and 200Kb upstream of the genome-wise significant SNPs position.

Classification of genes in accordance with biological function was performed using the Database for Annotation, Visualisation and Integrated Discovery (DAVID) v6.8 tool (Huang et al., 2009). 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).

Results

Descriptive statistics for the collected phenotypes of health and production traits, as well as the de-regressed EBVs, are summarized in **Table 1** and **Table 2**, respectively. In total, between 5 855 (for CMT) and 9 173 (for SWT) 'pseudo' phenotypes (de-

regressed EBVs) for genotyped animals were used to perform GWAS. This is significantly more than the available number of raw individual phenotypic records. For example, for health traits there were only 4 506 and 3 434 genotyped animals with phenotype, compared to 7 113 and 5 855 with pseudo-phenotypes for FRT and CMT, respectively. The increase in the number of genotyped-phenotyped animals is also seen for the production traits, where the number increased from 2 194 to 8 620 for BWT, from 5 164 to 8 987 for WW, from 5 685 to 9 173 for SWT, from 5 990 to 9 145 for MD and from 5 990 to 9 153 for FD. This is especially important for the health traits where phenotypes are available only for adult females, and after using pseudo-phenotypes, some sires were also included in the dataset. Estimated Breeding Values were calculated and were normally distributed. **Figure 1** shows the distribution of de-regressed EBVs used as the input for GWAS and only for animals with reliability of >0.30.

Stratification of this particular population that could affect the results of the GWAS have already been reported using principal component analyses (Kaseja et. al 2023). The results from that analysis of the population stratification did not reveal any outliers included in this particular dataset, hence all genotyped animals with available phenotypes were used in the current GWAS.

The Quantile-Quantile (**Q-Q**) plots of expected vs observed $-\log_{10}$(p-values) obtained as part of the GWAS analysis are shown in **Figure 2**. The Q-Q plots indicate that there are significant marker effects only for BWT, WW and SWT. Inflation factor lambda for analysed traits were 1.01 for CMT and FD, 1.02 for FRT, BWT, WW and MD, and 1.03 for SWT thus implying the absence of any significant inflation (Hinrichs et al., 2009).

Manhattan plots for the traits are shown in **Figure 3**. Only three genome-wise significant (Bonferroni-adjusted p-values < 0.05) markers were identified and are detailed in **Table 3**. SNP 'OAR8_62240378.1' on chromosome eight explains 0.21% of variance for BWT, SNP 's14444.1' on chromosome 19 was significant for WW, explaining 0.11% of variance and SNP 's65197.1' was found significant on the genome-wise level on chromosome 23 for SWT, explaining 0.12% of variance.

Fourteen more SNP markers found to be significant at the chromosome level are summarised in **Table 4**. Interestingly, some of these SNPs were remarkably close to reaching the genome-wise threshold (5.96); for example, SNP ('OAR3_192372203.1') located on chromosome three was significant for FD and had a $-\log_{10}$(p-value) equal to 5.67; similarly SNPs on chromosomes 21 ('OAR21_28724590.1') and 23 ('s36409.1') that were significant for SWT and FRT respectively, had $-\log_{10}$(p-value) equal to 5.50. the number of chromosome-wise significant SNPs discovered for all the examined traits varied between one (for BWT, FD and MD) and three (for FRT, WW and SWT). Many of the identified SNPs are located in regions already reported for health and production traits, as summarized in **Table 4**.

Results confirmed four genes neighbouring genome-wise significant SNPs. Three genes: interferon gamma receptor 1 (*IFNGR1*, Ensembl gene ID: ENSOARG00000000510), interleukin 22 receptor subunit alpha 2 (*IL22RA2*, Ensembl gene ID: ENSOARG00000000475) and oligodendrocyte transcription factor 3 (*W5NX34_SHEEP*) were located 119Kb downstream, 145Kb downstream and 174Kb upstream of the significant SNP for BWT on chromosome eight, respectively. One gene, MAM domain-containing protein (*W5PCX1_SHEEP*), was located 65Kb

upstream of the significant SNP for WW on chromosome 19. No previously reported annotated genes were found close to the significant SNP for SWT on chromosome 23.

Discussion

The aim of the present study was to investigate molecular markers (SNPs) that were significantly associated with health and welfare (FRT and CMT) and production (BWT, WW, SWT, MD and FD) traits in the UK Texel sheep population. De-regressed EBVs of individual animals for each trait, which were used in this study, are widely considered in GWAS as they may constitute informative aggregate animal phenotypes of multiple records per animal, adjusted for fixed effects and may also be available for genotyped animals without their own phenotypic records (Mucha et al. 2018; Ekine et al. 2014). The increase seen in the number of records used to perform GWAS for traits such as BWT (+6 426) or CMT (+2 421) is undoubtedly desirable, thereby making the breeding programme more cost-effective. At the same time, caution needs to be exercised in the de-regression process of using EBVs with low accuracy, as this may inflate the resulting de-regressed EBVs, and increase the probability of false positives in the ensuing GWAS (Ekine et al. 2014). In the present study, a minimum EBV reliability of 0.30 was used to address the issue above, therefore we are confident that our approach has led to genuine results. For production traits, population data including 821 693 animals collected within the UK national sheep evaluation programme were used, resulting in generally high EBV reliability values. However, the number of records for footrot and mastitis was limited to females included in the present study. The low estimated heritability of health traits (0.07 and 0.12 for CRT and CMT, respectively, Kaseja et al., 2023) has likely limited the number of highly reliable EBVs. The consequence of this has led to a reduction in the number of genotyped animals that could potentially have been used for the GWAS studies. Regardless, there are still many more animals following the steps taken here, compared to the actual number of animals having both genotype and phenotype available on either of these two traits. Furthermore, by using the de-regressed EBVs the health trait data are not only limited to adult females thereby enabling males to be included.

Our results indicate that the traits in this analysis were highly polygenic and mainly controlled by multiple genes, each having a modest effect. Nevertheless, three genome-wise and 14 chromosome-wise significant SNPs were detected; with some of the latter very close to the genome-wise threshold. Some of the detected genome-wise significant SNPs are situated within or close to previously reported QTLs. SNP 'OAR8_62240378.1' on chromosome eight, significant for BWT, is within the QTL for 'Internal fat amount' reported for (Awassi×Merino)×Merino sheep (Cavanagh et al. 2014); SNP 's14444.1' on chromosome 19, significant for WW, is situated around 30Mbp away from any previously identified region. The closest reported QTLs are for 'leg length', associated with Myostatin gene, reported for Soay sheep by (Hernández-Sánchez et al. 2010) and a QTL for 'internal fat amount' reported by (Cavanagh et al. 2014). Unfortunately, SNP 's65197.1' on chromosome 23, that is significantly associated with SWT, is not within or near any known QTL for health or production traits in sheep. Regrettably none of the significant SNPs identified in the current study were within, or close to, a significant region or previously reported genes (Golden Helix

GenomeBrowse® visualization tool (Version 2.x) [Software]. Bozeman, MT: Golden Helix, Inc. Available from http://www.goldenhelix.com).

Interestingly, previous research for footrot on part of the dataset used in the present study, including 3 573 records obtained from 2 229 animals that were genotyped with the 50k array, also did not reveal any genome-wise significant SNPs (Mucha et al., 2015). Other research conducted on lameness (caused by bovine footrot) in different species, such as Holstein–Friesian dairy cattle, acknowledge that the genomic architecture of this particular trait is very complex with the impact of several genes all having a role in disease presentation (Sánchez-Molano et al. 2019).

Similarly, several studies of mastitis involving both dairy and meat sheep breeds, as well as cattle indicate different QTL regions associated with somatic cell count, confirming that the genetic architecture of this trait is indeed complex (Oget, et al. 2019; Banos et al. 2017; Conington et al. 2008; Mucha et al. 2022). A study by Sutera et al. (2021) used de-regressed breeding values to identify genomic regions associated with somatic cells count in Valle del Belice dairy sheep and reported eight significant SNPs, of which one at the genome-wise significance level. None of these SNPs were located within known QTLs related to mastitis, however several candidate genes associated with immunity or udder conformation were found close to the SNPs.

Similar results can be seen in multiple studies in sheep investigating body weight or meat quality traits (Matika et al. 2016; Ghasemi et al. 2019; Duijvesteijn et al., 2018), however traits such as body weight tend to be influenced by fewer QTLs that explain a substantial part of the additive genetic variance, which can be seen across many mammal species (Al-Mamun et al. 2015). A study by Garza Hernandez et al. (2018) performed on 384 UK Texel rams revealed no genome-wise significant SNPs associated with growth, carcass composition nor examined health and welfare traits. However, Hernandez's research disclosed some significant chromosome-wise SNPs, that explained a small proportion of the variance, thus confirming the complexity of these traits (Hayes and Goddard, 2010).

Of the three genes neighbouring genome-wise significant SNPs located on chromosome eight, two (*IFNGR1* and *IL22RA2*) are reported as novel genes for protein coding in Ensembl database (Jiang et al., 2014), not having previously been connected to animal body weight. Future genomic association analyses based on denser DNA arrays may allow new variants to be discovered.

This research used a subset of the SNPs available on the 50k matrix after the quality analysis (n = 45 686 SNPs), however, according to the research conducted on the Lacaune dairy sheep population by (Oget et al. 2019), using the 50k SNP array can increase the accuracy of EBVs by 18.02% when comparing conventional BLUP and weighted single-step method, when the emphasis of SNPs in regions with strong effect on traits is included in the model. This is in line with research performed on dairy cattle by (Mouresan et al. 2019), which has led to an increase in accuracy especially for traits related with fat content in milk.

The current study suggests that health and welfare as well as production traits in Texel sheep have a polygenic background. This supports the choice of single-step method for genomic evaluation of this breed which is currently under consideration for exploitation commercially. Further research including more genotyped and

phenotyped animals and, perhaps denser DNA arrays or whole-genome sequence data may lead to discovery of new potentially important SNPs in linkage disequilibrium with QTLs of interest (Calus, 2010). These important SNPs could then receive increased emphasis (weight) in the genomic evaluation process to improve the accuracy of genomic selection in Texel sheep (Liu et al. 2020; Kabanov et al. 2022; Zhang et al. 2016). The present research focussed on the association between individual SNPs and meat sheep production and health. Future work may build on this research to investigate genomic regions (SNPs windows) of varying lengths that may explain measurable proportions of the genetic variance (Fragomeni et al., 2014).

Ethics approval

Not applicable.

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.

Declaration of interest

None.

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Table 1: Number of records (N) and descriptive statistics for genotyped Texel animals' phenotypes

Trait	N	Mean	SD	Minimum	Maximum
*Footrot (FRT)	9 123	0.35	0.63	0.00	2.83
*California Mastitis Test (CMT)	4 787	0.70	0.74	0.00	2.20
Birth weight (BWT, kg)	2 194	5.16	1.23	1.64	8.70
Weaning weight (WW, kg)	5 164	26.57	5.06	9.60	44.40
Scan weight (SWT, kg)	5 685	51.28	10.12	19.80	84.20
Muscle depth (MD, mm)	5 590	29.49	3.69	14.20	43.00
Fat depth (FD, mm)	5 590	2.82	1.36	0.25	9.97

*Log transformed

Table 2: Heritability (h^2), repeatability (Rep), number of Texel sheep with records (N) and descriptive statistics for de-regressed Estimated Breeding Values

Trait	h^2*	Rep	N	Mean	SD	Minimum	Maximum
Footrot (FRT)	0.12	0.34	7 113	0.02	0.02	-0.16	0.18
California Mastitis Test (CMT)	0.07	0.22	5 855	0.01	0.03	-0.13	0.18
Birth weight (BWT, kg)	0.10		8 620	0.22	0.06	-0.15	0.62

Weaning weight (WW, kg)	0.09	8 987	1.51	0.43	-1.06	3.97
Scan weight (SWT, kg)	0.33	9 173	6.14	2.26	-3.49	14.19
Muscle depth (MD, mm)	0.30	9 145	1.48	1.07	-1.54	6.64
Fat depth (FD, mm)	0.31	9 153	-0.11	0.32	-1.45	1.14

*Heritability reported in Kaseja et al. (2023)

Table 3: Summary of genome-wise significant Single Nucleotide Polymorphisms (SNPs)

Trait	SNP name	Chromosome	–log10(p-value)	Variance explained (%)	Nearest QTL/gene
BWT	OAR8_62240378.1	8	6.59	0.21	Within the internal fat amount QTL (Cavanagh et al. 2014)
WW	s14444.1	19	6.82	0.11	Leg length and internal fat amount QTLs on the same chromosome, but distanced (>30Mbp) (Hernández-Sánchez et al. 2010)
SWT	s65197.1	23	7.43	0.12	N/A

BWT = birth weight; WW = weaning weight; SWT = scan weight; N/A = no QTLs/genes reported; QTL = Quantitative Trait Loci

Table 4: Summary of chromosome-wise significant Single Nucleotide Polymorphisms (SNPs)

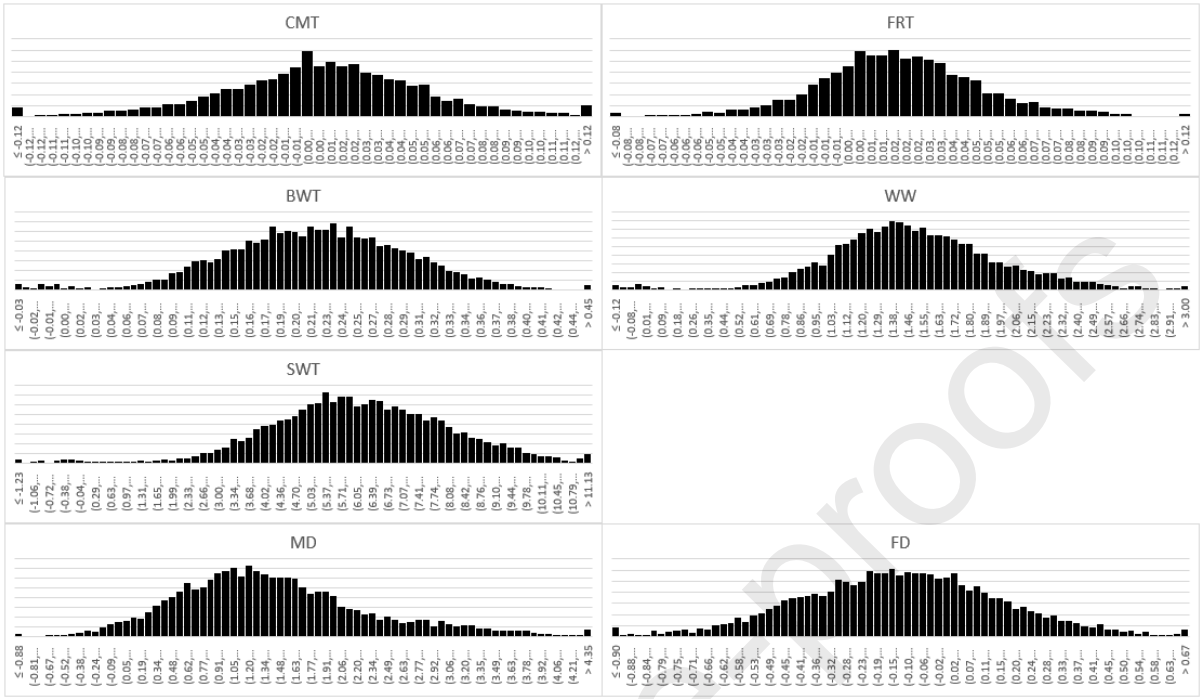
Chromosome	Chromosome-wise significance threshold	Trait	SNP name	–log10(p-value)	Nearest QTL for health/meat production trait
3	4.92	FD	OAR3_192372203.1	5.67	'Body weight (56 weeks)' (Raadsma et al. 2009)
10	4.50	SWT	OAR10_9706403.1	4.65	Distanced (+5Mbp): Meat traits QTLs: 'carcass bone percentage', 'carcass fat percentage', 'fat weight in carcass', 'lean meat yield percentage' (Cavanagh et al. 2010)

11	4.30	MD	OAR11_32227171.1	4.89	‘Internal fat amount’, ‘hot carcass weight’, ‘slaughter body weight’ (Cavanagh et al. 2010)
		BW	OAR11_5688066.1	4.53	‘Internal fat amount’, ‘hot carcass weight’ (Cavanagh et al. 2010)
14	4.29	SWT	s22731.1	4.87	Within QTL ‘bone weight in carcass’ and ‘total bone’ (Cavanagh et al. 2010)
		CMT	s08817.1	5.16	Within meat traits QTL as above, and health traits: ‘Nematodirus FEC1’ (Davies et al. 2006) and ‘Fecal egg count’ (Silva et al. 2012)
15	4.45	WW	s60057.1	4.65	Within QTL for ‘Fecal egg count’ (Silva et al. 2012)
16	4.43	WW	OAR16_52790463.1	4.48	Within meat traits QTL: ‘lean meat yield percentage’, ‘dressing percentage’, ‘subcutaneous fat area and fat thickness’ and ‘body weight at slaughter’ (Cavanagh et al. 2010)
17	4.39	CMT	OAR17_32936496.1	4.51	Within QTLs for ‘Fecal egg count’ (Silva et al. 2012) and ‘aseasonal reproduction’ (Mateescu and Thonney 2010), 14Mbp from ‘somatic cell score’ QTL (Gutiérrez-Gil et al. 2018)
19	4.31	FRT	OAR19_22759405.1	4.43	No meat production or health traits QTLs reported on this chromosome
21	4.19	SWT	OAR21_28724590.1	5.50	Within QTLs for ‘average daily gain (birth-43, 43-56, 56-83 weeks)’

			OAR21_31718415.1	4.21	and ‘body weight (at 43, 56 and 83 weeks)’ (Raadsma et al. 2009)
22	4.26	WW	OAR22_13469217.1	4.38	Within the QTL for ‘somatic cell score’ (Raadsma et al. 2009)
23	4.28	FRT	s36409.1	5.50	No QTLs are reported on chromosome 23 for sheep
26	4.21	FRT	s37597.1	5.23	QTLs for health traits ‘eggs per worm’, ‘worm count’ or ‘Haemonchus Contortus FEC2’ (Marshall et al. 2009) reported within +7Mbp

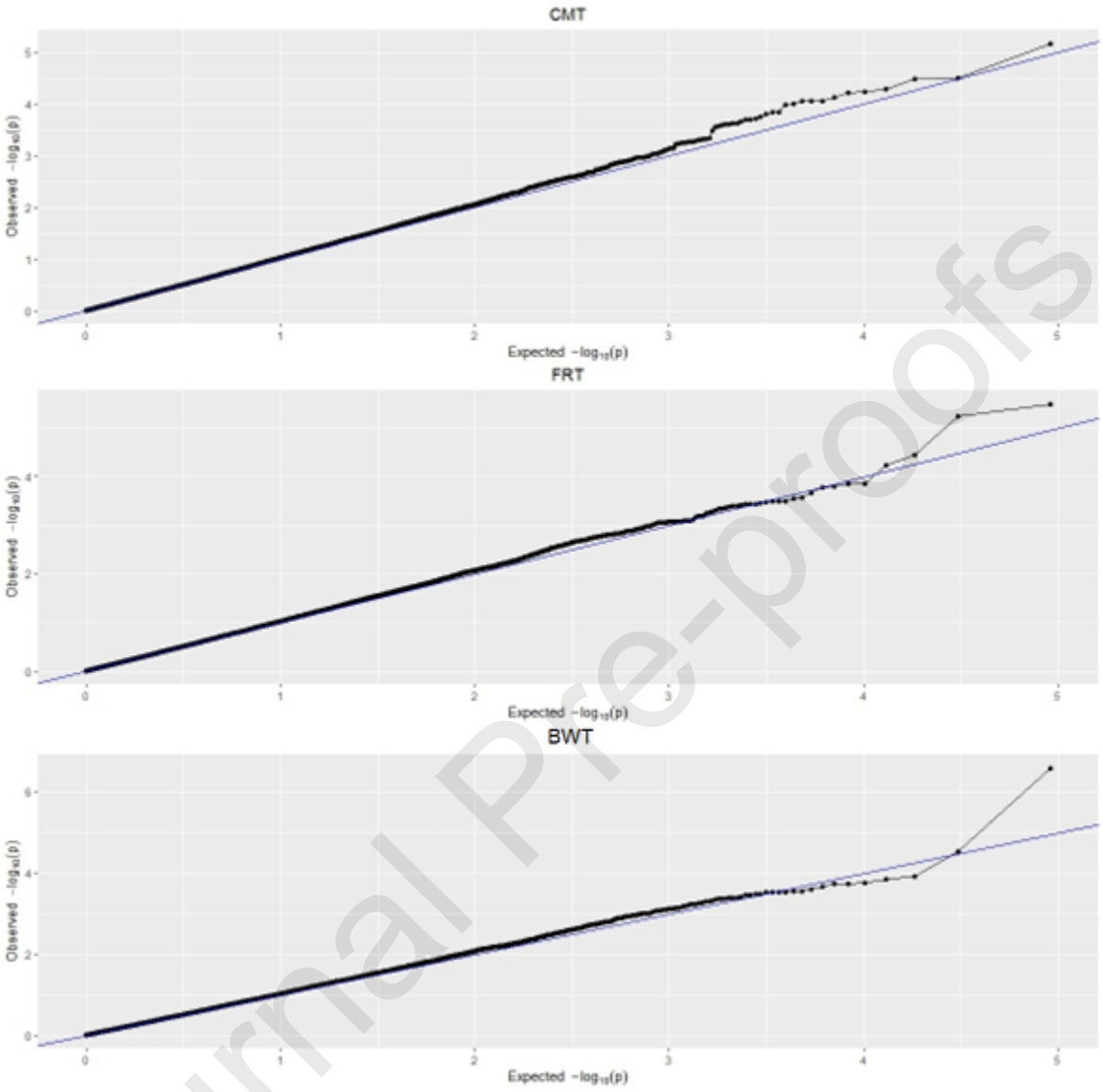
FRT = footrot, CMT - california mastitis test; BWT = birth weight; WW = weaning weight; SWT = scan weight; MD = muscle depth; FD = fat depth; QTL = Quantitative Trait Loci

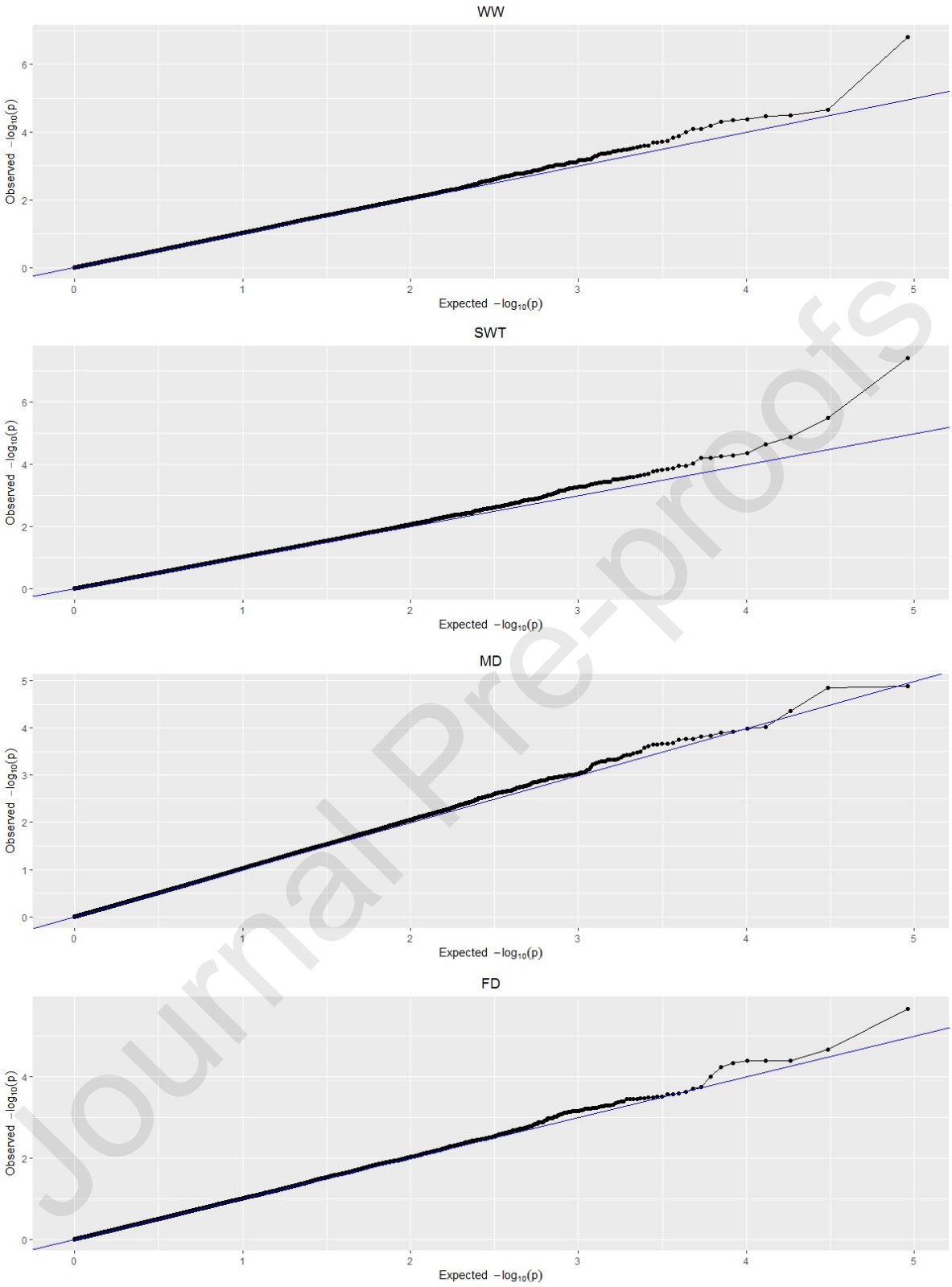
Figure 1: Distribution of de-regressed Estimated Breeding Values used as input to Genome-Wide Association Study for UK Texel sheep



FRT = footrot; CMT = California Mastitis Test; BWT = birth weight; WW = weaning weight; SWT = scan weight; MD = muscle depth; FD = fat depth

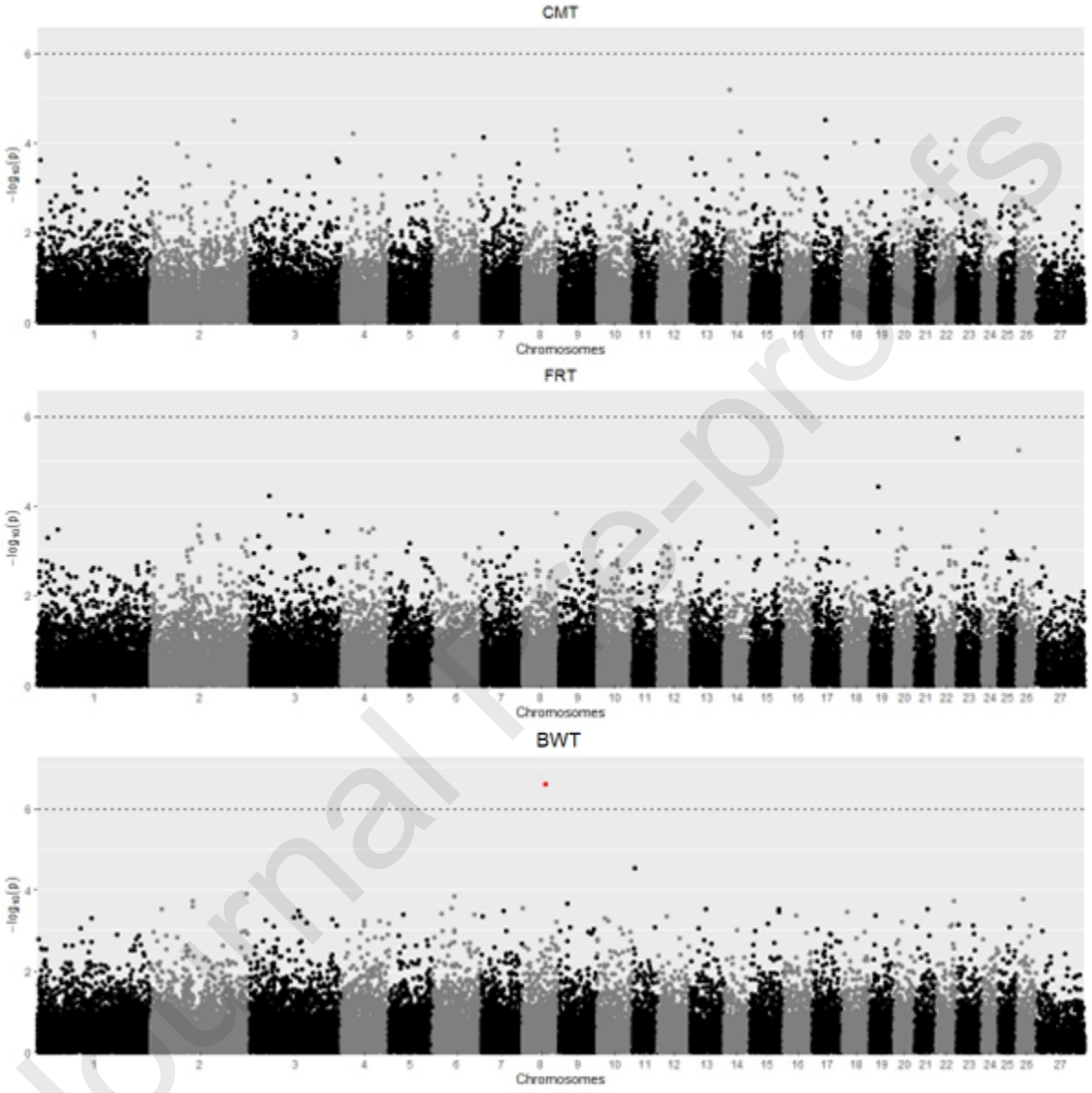
Figure 2: Quantile-quantile (Q-Q) plots of genome-wise association results for health and production traits for UK Texel sheep

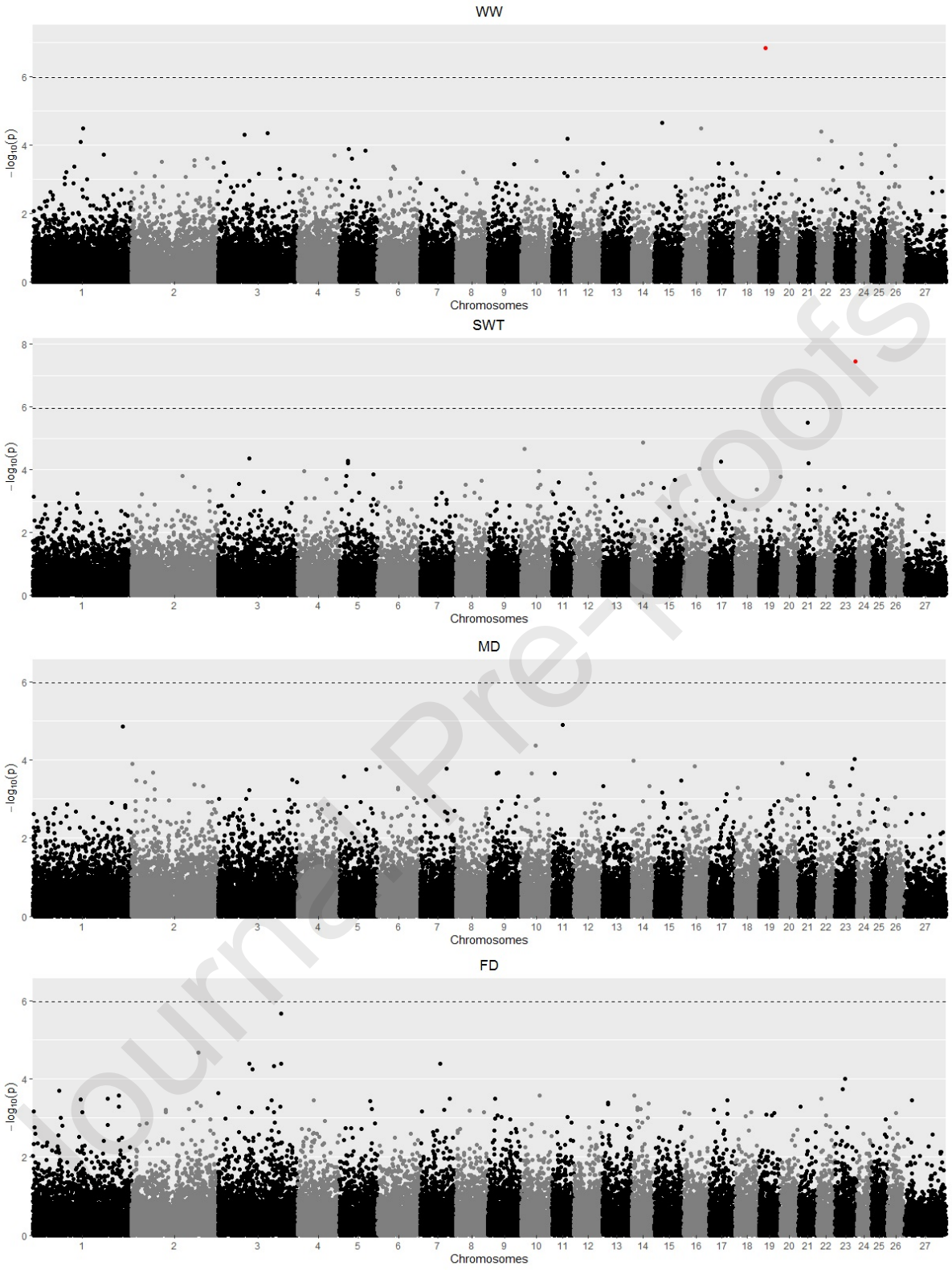




FRT = footrot; CMT = California Mastitis Test; BWT = birth weight; WW = weaning weight; SWT = scan weight; MD = muscle depth; FD = fat depth

Figure 3: Manhattan plots of genome wide association study for health and production traits in Texel sheep. −log10(P-values) for each marker are shown on the vertical axis, chromosome numbers are indicated on the horizontal axis. The dashed black line indicates the genome-wise significance threshold (5.96). Red dots indicate significant SNP (above the threshold).





FRT = footrot; CMT = California Mastitis Test; BWT = birth weight; WW = weaning weight; SWT = scan weight; MD = muscle depth; FD = fat depth

Highlights

- This study analysed the genetic basis of footrot, mastitis and production traits.
- Results showed these traits to be highly polygenic with complex genetic architecture.
- A total of 12 significant Single Nucleotide Polymorphisms were associated with production traits.
- A subsequent five significant Single Nucleotide Polymorphisms were associated with health traits.
- The use of such whole genomic information enhances selection decision-making.