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1 **Analysis of SNP variation associated with important economic and CT measured**
2 **traits in Texel sheep**

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16 Analysis of SNP variation in Texel Sheep

17 **Abstract**

18 Sheep are an important part of the global agricultural economy. Growth and meat
19 production traits are significant economic traits in sheep. The Texel breed is the most
20 popular terminal sire breed in the UK, mainly selected for muscle growth and lean
21 carcasses. This is a study based on a genome-wide association approach that
22 investigates the links between some economically important traits, including Computed
23 Tomography (CT) measurements, and molecular polymorphisms in UK Texel sheep.
24 Our main aim was to identify Single Nucleotide Polymorphisms (SNP) associated with
25 growth, carcass, health and welfare traits of the Texel sheep breed. This study used
26 data from 384 Texel rams. Data comprised 10 traits, including 2 CT measured traits.
27 The phenotypic data were placed in four categories: growth traits, carcass traits, health
28 traits and welfare traits. De-regressed estimated breeding values (EBV) for these traits
29 together with sire genotypes derived with the Ovine 50K SNP array of Illumina were
30 jointly analysed in a genome wide association analysis. Eight novel chromosome-wise
31 significant associations were found for carcass, growth, health and welfare traits. Three
32 significant markers were intronic variants and the remainder intergenic variants. This
33 study is a first step to search for genomic regions controlling CT based productivity
34 traits related to body and carcass composition in a terminal sire sheep breed using a
35 50K SNP genome-wide array. Results are important for the further development of
36 strategies to identify causal variants associated with CT measures and other
37 commercial traits in sheep. Independent studies are needed to confirm these results
38 and identify candidate genes for the studied traits.

39 **Keywords:** Sheep, Texel, CT, Associated, GWAS.

40 **Implications**

41 Sheep are an important part of the global agricultural economy. To the best of our
42 knowledge GWAS for CT based productivity traits, for a UK terminal sire breed, has not
43 been widely researched. The main aim of this work was to exploit improved genotypic
44 tools, specifically the Illumina OvineSNP50 chip, allowing a simultaneous genotyping
45 for up to 54,241 SNPs to identify those SNPs associated with growth, carcass
46 composition, health and welfare traits of Texel sheep using de-regressed estimated
47 breeding values of rams.

48 **Introduction**

49 Sheep are an important part of the global agricultural economy. They are particularly
50 well adapted to convert short herbage to meat, milk and wool and they are very
51 important to meet global needs for food security for an increasing population around
52 the world (Hopkins and Lobley, 2009).

53 Currently the Texel breed is the most popular terminal sire breed in the UK accounting
54 for 30% of all purebred rams used for crosses to maternal sheep breeds (Pollott, 2014)
55 and is mainly selected for muscle growth and lean carcasses (Hopkins and Lobley,
56 2009).

57 There are only a few methods to predict body composition in live sheep. Over the last
58 few decades mainly ultrasound technologies had been used on farm animals for
59 evaluation of carcass composition (Silva, 2016). However, computed tomography (CT),
60 a non-invasive imaging technology, can accurately measure carcass traits *in vivo* such
61 as muscle and fat (Bünger *et al.*, 2011), muscularity (Jones *et al.*, 2002) and tissue
62 weights (Macfarlane *et al.*, 2006). Additionally, it has been evidenced the potential of
63 CT scanning to improve eating quality and tissue distribution of sheep meats
64 (Macfarlane *et al.*, 2009). As CT scanning is however more expensive than ultrasound,
65 a two-step-procedure is recommended. Only the best 15-20% of selection candidate
66 ram lambs measured by ultrasound would be subsequently CT scanned (Lewis, 2004).

67 *Sheep genetics studies*

68 Breeders focus sheep selection on production traits, including carcass composition and
69 growth traits but also integrate other traits such as meat quality, disease resistance,
70 lambing ease and survival (Bünger *et al.*, 2011). According to the animal QTL database

71 there are currently (06/2017) 1,515 sheep QTLs curated in the animal QTL database
72 (Hu *et al.*, 2013) representing 222 different sheep traits, reported in 126 publications.
73 However, one of the main limitations of unscrambling the genetic architecture
74 underlying production traits in sheep has been the relative lack of information on the
75 sheep genome in addition to the lack of accurate phenotypic data obtained (Zhang *et al.*,
76 *et al.*, 2013).

77 Currently, knowledge of the major genes or QTL associated with carcass composition
78 and growth traits in sheep is limited (Zhang *et al.*, 2013). Walling *et al.* (2004)
79 pioneered the first accounts of QTL studies for growth and carcass conformation traits
80 in domesticated sheep covering several genomic regions, which led to characterization
81 of the Texel muscling QTL (TM-QTL).

82 With the advent of genome-wide panels of single nucleotide polymorphisms (SNPs)
83 and using the approach of a genome-wide association study (GWAS), it has become
84 possible to identify and localize QTLs for complex traits in many livestock species
85 (Georges, 2007). However, to date, only a small number of GWASs in sheep have
86 been conducted because of either limited information available for the sheep genome
87 and funding. These studies have been mainly focused on sheep growth, ultrasound-
88 measured meat traits and body composition traits (Cavanagh *et al.*, 2010, Zhang *et al.*,
89 2013, Bolormaa *et al.*, 2016, Matika *et al.*, 2016)

90 Moreover, GWAS with high accuracy CT measured body composition traits are still
91 very rare in the literature. Donaldson *et al.* (2014) used spine characteristics measured
92 from X-ray computed tomography (CT) scans in order to investigate if there were any
93 subsequent associations between TM-QTL inheritance and underlying spine
94 characteristics (Donaldson *et al.*, 2014). Also, Cavanagh *et al.* (2010) performed a QTL

95 mapping study in sheep based on in vivo obtained CT data providing predictions for 13
96 traits describing major fat depots, lean muscle, bone, body proportions and body
97 weight; they identified 3 highly significant, 15 significant, and 11 suggestive QTL on
98 eleven chromosomes. But, no tissue-specific QTL were identified. Furthermore, Matika
99 *et al.* (2016) conducted recently a genome-wide association study (GWAS) for carcass
100 composition phenotypes, including bone, fat and muscle components, which were
101 captured using CT. The GWAS analyses revealed multiple SNPs and quantitative trait
102 loci (QTL) that were associated with effects on carcass composition traits and were
103 significant at the genome-wide level.

104 In this study we performed a genome wide association study to identify those SNPs
105 associated with growth, carcass composition, health and welfare traits, including 2 CT
106 measured phenotypes, of Texel sheep using de-regressed EBVs of rams.

107 **Material and Methods**

108 *Traits and phenotypes*

109 A total of 384 Texel rams descended from 252 sires and 351 dams were analysed for
110 10 productivity traits including 2 CT measured traits. These rams represent a group of
111 well-monitored animals as only a proportion (10-20%) of the initial selection candidates
112 will be put forward to CT scanning based on ultrasound results.

113 The phenotypic data were provided by the Signet Sheep breeder Service and
114 comprised EBVs progeny test derived for: birth weight (BW), eight week body weight
115 (EWW) and scan weight (SW), which is the live weight at US scanning at about 21
116 weeks of age. These were considered as growth traits. As carcass traits were used US
117 measured fat depth (FD) and muscle depth (MD) which are obtained by US-scanning at
118 the at the third lumbar vertebra at 90 degrees to the backbone. The CT measured
119 carcass traits: fat weight (FW), CT lean weight (LW) and the muscularity score (MU), a
120 measure of carcass shape (Bünger *et al.*, 2011), were also included. Details on the CT
121 measured traits have been reported earlier (Bünger *et al.*, 2011). Faecal egg count
122 (FEC) as a measure of worm egg count in sample from lambs at 21 weeks of age, and,
123 Lambing ease (LE) as a direct assessment of the ease with which ram progeny will be
124 born.

125 GWAS accuracy can also be affected by systematic environmental effects. De-
126 regressed EBVs are an alternative to raw phenotypic measurements, because they
127 represent aggregate phenotypes adjusted for systematic environmental effect. The
128 phenotypic data used therefore consisted of de-regressed estimated breeding values
129 (EBVs) of standard commercial traits.

130

131 *Statistical model for de-regressed breeding values*

132 The official Texel EBVs were used, those breeding values were derived from the
133 following model:

134
$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

135 where \mathbf{y} is the vector of phenotypic observations for one of the analysed traits, \mathbf{b} is the
136 vector of fixed effects with design matrix \mathbf{X} (relating observations to fixed effects), which
137 varied depending on the trait, \mathbf{a} is the vector of random animal effects, with design
138 matrix \mathbf{Z} (relating observations to random effects) and \mathbf{e} is the vector of random
139 residuals. The list of effects is summarized in Supplementary Table S1.

140 Random effects are assumed to be normally distributed with zero means and the
141 following covariance structure:

142
$$\text{Var} \begin{bmatrix} \mathbf{a} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_a^2 & 0 \\ 0 & \mathbf{I}\sigma_e^2 \end{bmatrix}$$

143 where \mathbf{A} is the pedigree-based relationship matrix, σ_a^2 is the genetic variance, and σ_e^2
144 is the residual variance.

145 The software package MIX99 was used for de-regression (Lidauer M, 2011), using a
146 full animal pedigree with effective offspring contributions (EOC) as weighting factors.

147 The de-regression procedure was based on the method published by Jairath *et al.*
148 (1998), involving solving the mixed model equations with a full pedigree to obtain the
149 right-hand side or de-regressed EBVs. Thus DRPs represent daughters averages
150 adjusted for fixed effects and contributions from parents and relatives in the pedigree
151 (Jairath *et al.*, 1998).

152

153

154 EOC were calculated as:

$$EOC_i = \frac{rel_i \cdot kdau}{1 - rel_i}$$
$$kdau = \frac{4 - h^2}{h^2}$$

156 where rel_i is the reliability of EBV for animal i and h^2 is the heritability of one of the
157 analysed traits.

158 The use of effective daughter or progeny contribution as a weighting factor is used to
159 avoid biases in sire variances (Fikse and Banos, 2001). The EOC provides a measure
160 of the precision of the daughter information used to compute the de-regressed EBV of
161 the animal as the estimates of reliability used in the computation accounts for factors
162 such as contemporary group (CG) structure for the ram's daughters, the correlation
163 between observations on the same daughter and the reliability of the performance of
164 the daughters' dams.

165 A Shapiro and Wilk's W -statistic test, conducted using the R-package (R Core Team,
166 2013) was used to test data distribution for normality (Royston, 1995). Traits not
167 normally distributed were rank transformed to a normal distribution for their use in
168 subsequent analysis. This rank-transformation method has been reported to give a
169 consistent performance in identifying causal polymorphisms with a slight increase in
170 false positive rate (Goh *et al.*, 2009). This method was used because according to Goh
171 *et al.* (2009) for small sample size or genetic effects, the improvement in sensitivity for
172 rank transformation outweighs the slight increase in false positive rate.

173 *Genotyping*

174 All rams were genotyped with the ovine 50k SNP chip (54,241 SNPs across the
175 genome with an average of 20.4 SNPs per Mb) by AgResearch. The order of the SNPs
176 was based on the *Ovis_aries_4.0* assembly released by the International Sheep
177 Genomics Consortium (Jiang et al., 2014).

178 Quality control (QC) was performed with the GenABEL R package by considering
179 genotypes of all rams (Aulchenko *et al.*, 2007). The QC excluded 1,564 SNPs with call
180 rates lower than 95%, 3,891 SNPs with minor allele frequencies less than 1%, 98 X-
181 linked SNPs that were likely to be autosomal (cut off odds > 1000) and 777 SNPs not in
182 Hardy-Weinberg equilibrium (p-value <1x10e⁻⁵). The call rate per individual was always
183 higher than 90% so no animal was removed from the analysis. After applying these
184 quality control criteria 48,433 SNPs (89%) located on 26 autosomes and on the X
185 chromosome were used in the subsequent analyses.

186 *Statistical Model for GWAS*

187 A Multidimensional Scaling Analysis (MDS) was performed first to evaluate the genetic
188 structure of the population. For each trait, SNP effects were then tested, by a single
189 marker regression, with a mixed animal model including the genomic kinship matrix
190 (identity by state) between the genotyped animals, adjusted for allele frequencies.
191 Kinship was computed based on the method proposed by Astle and Balding (2009),
192 using GenABEL, to control for population structure or polygenic effect (Astle and
193 Balding, 2009). The following model was used:

$$194 \quad \mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}\mathbf{u} + \mathbf{e}$$

195 where \mathbf{y} is the vector of de-regressed EBV of rams, $\boldsymbol{\beta}$ is a vector of coefficients for the
196 SNP effects, \mathbf{u} is the vector of random animal effects, \mathbf{e} is the vector of random residual
197 effects, and \mathbf{X} and \mathbf{Z} are incidence matrices relating observations to fixed and random

198 animal effects, respectively. Random animal effect followed a normal distribution
199 $MVN(0, \mathbf{G}\sigma_u^2)$ where \mathbf{G} is the genomic kinship matrix and σ_u^2 is the polygenic variance;
200 and the random residual effects of the model was assumed to be $MVN(0, \mathbf{I}\sigma_e^2)$, where
201 σ_e^2 is the residual variance and \mathbf{I} is an identity matrix. Each trait was analysed
202 separately and all analyses were run with GenABEL.

203 This procedure consisted of two steps: firstly it estimated the polygenic and residual
204 variance, not accounting for marker effects and fitting the genomic kinship matrix in the
205 model. Secondly, these estimated variance components were used to estimate all the
206 marker effects (fitting in the model the genotypes and the previously estimated
207 residuals). The j -th marker was fitted in the single-marker-based linear mixed model
208 without removing the j -th marker from the \mathbf{G} matrix. Evidence has shown analytically
209 that, if variance components are kept constant, the estimation of the regression of
210 phenotype on m markers is invariant with respect to whether or not the marker(s) tested
211 for association is(are) included when constructing the **G matrix** (Gianola *et al.*, 2016).

212 Significance of the results was tested at genome-wise and chromosome-wise levels,
213 including a strict Bonferroni correction for multiple-testing, corresponding to 1×10^{-6} and
214 3.5×10^{-5} , respectively.

215 In order to address possible population stratification problems, the inflation in the test
216 statistic was monitored with factor lambda, which does not depend on allele
217 frequencies (Aulchenko *et al.*, 2007). The allele effects estimated by GenABEL refer to
218 the least frequent allele in the population and are expressed in trait phenotypic
219 standard deviation (STD) units. Genes located on or around the identified SNPs were
220 examined using the ENSEMBL database and the *Ovis_aries_3.1* and *4.0* assembly
221 released by the International Sheep Genomics Consortium (Jiang *et al.*, 2014). And

222 finally JBrowse was used to identify previously associated QTLs in the tagged regions
223 (Skinner *et al.*, 2009).

224 **Results**

225

226 *Descriptive statistics*

227 For the 10 analysed traits (de-regressed EBVs) the means and standard deviations are
228 shown in Table 1. The normal distributions of the 10 traits were tested with the Shapiro-
229 Wilk's test (Table 1). For EWW, FD, FW, FEC and LE traits the null hypothesis of
230 following a normal distribution was rejected according to a p value ≤ 0.1 , which has
231 been previously suggested as an acceptable threshold for this type of analysis
232 (Royston, 1995). These records were rank-transformed to a normal distribution for their
233 use in the subsequent analyses.

234

235 *Genome Wide Association Analysis*

236 A multidimensional scaling analysis using the GenABEL package showed that no
237 genetic stratification was present in this population. Also, the average inflation factor (λ)
238 was 1.008 ± 0.007 , with a maximum value of 1.021 for FEC and a minimum of 1 for FD,
239 FW and MU. Therefore, the population structure is not expected to affect the results of
240 GWAS in the present study.

241 No genome-wise significant associations were found between any SNP and trait.
242 However, 8 chromosome-wise significant SNPs were found for EWW, FD, MD, LW,
243 FEC, and LE (Figure 1). These SNPs were located on chromosomes 3, 4, 6, 11, 16
244 and 17, respectively (Table 2). None of the associated SNPs found had been
245 previously associated with any trait in sheep.

246 The proportion of total variance explained by each SNP was obtained by first scanning
247 using the score test and then reevaluating best hits, individually, using Maximum

248 Likelihood with significant SNP allelic effect fitted as covariate. The variance explained
249 for chromosome wise significant SNP associated with EWW, FD, LW, MD and FEC
250 were 0.029, 0.061, 0.062, 0.060 and 0.051, respectively. And for LE, each significant
251 marker explained a variance of 0.006, 0.038 and 0.013.

252 **Discussion**

253 Until very recently, limited information on the sheep genome and lack of phenotypic
254 data for many important traits have resulted in only a few studies on SNPs associated
255 with production and welfare traits in sheep (Zhang *et al.*, 2013). It has been suggested
256 that the use of more precise phenotypes derived from CT measures will lead to more
257 accurate phenotypes for genetic analyses (Cavanagh *et al.*, 2010).

258 To date, only a small number of GWAS in sheep have been conducted, those have
259 been mainly focused on sheep growth, ultrasound-measured meat traits and body
260 composition traits (Cavanagh *et al.*, 2010, Zhang *et al.*, 2013, Bolormaa *et al.*, 2016,
261 Matika *et al.*, 2016). Moreover, genetic analyses with high accuracy CT-measured body
262 composition traits are still very rare in the literature (Walling *et al.*, 2004, Donaldson *et*
263 *al.*, 2014, Bolormaa *et al.*, 2016, Matika *et al.*, 2016).

264 The main aim of the present study was to identify SNPs associated with traits currently
265 in the selection index for a UK Terminal sire breed (Texel Sheep), including CT based
266 productivity traits. In the UK, CT scanning has been used in sheep breeding programs
267 since 2000. However, as CT scanning is more expensive than ultrasound, a two-step-
268 procedure is recommended. Only the best 15-20% of selection candidate ram lambs
269 measured by ultrasound are usually subsequently CT scanned (Lewis, 2004, Bünger *et*
270 *al.*, 2011).

271 A total of 384 Texel rams were analysed for 10 productivity traits including 2 CT
272 measured traits. It should be noted that the dataset used in the present study was
273 limited in its size, largely due to the restricted availability of CT-measured rams, due to
274 CT costs. However, because this study analysed a small group of preselected animals

275 we acknowledged that the power to detect genome wide significant associations was
276 diminished.

277 *Genome Wide Association Analysis*

278 In the current study no genome-wise significant association for any of the analysed
279 traits was found. However, 8 chromosome-wise significant SNPs were found for: EWW,
280 FD, MD, LW, FEC and LE. These SNPs were located on chromosomes 3, 4, 6, 11, 16
281 and 17, and were found to be either intronic or intergenic variants. None of the
282 significant SNPs had been previously associated with any trait in sheep. However,
283 chromosomes 11 and 16 have been previously tagged by SNPs associated with
284 muscle, body and carcass weight (Cavanagh *et al.*, 2010).

285 We identified as candidate genes, those which were either directly tagged by a
286 significant SNP (intronic variant) or those located within genomic regions of 30 kb up
287 and downstream of an associated marker (Bolormaa *et al.*, 2016). However, due to the
288 current relatively poor status of the ovine genome annotation, little information
289 regarding the function of the tagged genes was obtained.

290 Regions tagged for EWW and LE have not been previously associated with any
291 significant growth or welfare traits. However, two identified markers for LE, on
292 chromosomes 6 and 17 (OAR6_108683365.1 and OAR17_11963200.1), belong to
293 suggestive QTLs previously associated with parasite resistance (Beh *et al.*, 2002,
294 Marshall *et al.*, 2009). Former studies have reported a low to moderate genetic
295 correlation between lambing ease and birth weight (Brown, 2007), while a moderate
296 genetic correlation between birth weight and parasite resistance has been suggested
297 (Verbeek *et al.*, 2011). However, more information would be needed to estimate the
298 genetic correlation between parasite resistance and welfare traits such as LE.

299 The region tagged by OAR16_20147789.1, significantly associated with FD, is an
300 intronic variant of the NDUFAF2 gene, which encodes a NADH dehydrogenase
301 (ubiquinone) complex I, assembly factor 2, a molecular chaperone for mitochondrial
302 complex I assembly. OAR16_20147789.1 is located in a QTL region, which has been
303 previously associated with final body weight, percent lean and subcutaneous fat area
304 (Cavanagh *et al.*, 2010).

305 SNP s26074.1 was found to be significantly associated with LW. This SNP, is an
306 intergenic variant, which is located in a QTL region formerly associated with body and
307 carcass weight (Cavanagh *et al.*, 2010).

308 The region identified by SNP OAR11_12972551.1, was significantly associated with
309 MD. This SNP is an intronic variant of the ACACA gene. ACACA encodes an acetyl-
310 CoA carboxylase alpha, which is considered as a key enzyme of fatty acid synthesis in
311 the mammary gland by catalysing the first step of fatty acid synthesis in mammalian
312 cytosol. This gene has been described as a candidate gene for fat content in sheep,
313 due to an observed significant association with variation in milk fat content, and change
314 of fat composition in several sheep breeds (Bolormaa *et al.*, 2016). Moreover,
315 OAR11_12972551.1 is located in QTL regions associated with body weight (Raadsma
316 *et al.*, 2009), fat synthesis (Bolormaa *et al.*, 2016), internal fat amount and hot carcass
317 weight (Cavanagh *et al.*, 2010).

318 Thus, results of significant associations with carcass traits provide evidence of a
319 possible effect on FD, LW and MD by QTLs previously reported by Raadsma *et al.*
320 (2009), Cavanagh *et al.* (2010) and Bolormaa *et al.* (2016).

321 Finally, SNP s30868.1 associated with FEC, is an intronic variant of the ZNF227 gene,
322 which encodes a zinc finger protein 227, probably involved in transcriptional regulation.

323 This gene is a paralogue of the ZNF229 gene, which has been previously associated
324 with tuberculosis susceptibility in African human populations (Thye *et al.*, 2010). Also,
325 s30868.1 tags a QTL region formerly reported to be associated with Immunoglobulin A
326 level, an antibody that plays a crucial role in the immune function (Atlija *et al.*, 2016).
327 This suggests that there might be a worm resistance QTL on chromosome 4.
328 A large number of QTLs have been identified for traits related to parasite resistance in
329 sheep (Beh *et al.*, 2002, Marshall *et al.*, 2009, Atlija *et al.*, 2016) suggesting that those
330 traits are not determined by individual genes acting alone but rather by complex
331 multigene interactions. Thus, further identification of SNPs in strong LD with the casual
332 variants, could contribute to the implementation of these results in breeding schemes
333 for the Texel breed population.
334 The proportion of total variance explained by the significant SNPs was low, which is in
335 agreement with Hayes and Goddard (2010), who explained that a small number of
336 markers with validated associations would explain a small portion of the genetic
337 variance in complex traits (Hayes and Goddard, 2010). This suggests that if alleles of
338 large effect were present in our data, those would be in such a low frequency that they
339 individually could only explain a small proportion of the variance.
340 Further improvement in sheep GWAS could be achieved by increasing the sample size
341 and using the new ovine 700K HD chip, which has a much denser distribution of SNPs
342 across the genome and thus should have higher LD with the potential QTLs controlling
343 the traits of interest.
344 The present study found 8 chromosome-wise significant SNPs for 6 traits among them
345 a CT measured trait (LW). Tagged regions on chromosomes 4, for worm resistance
346 (FEC), 11 and 16, for carcass traits (MD, LW and FD), are consistent with other

347 studies, where QTL regions have been found for Immunoglobulin A level and meat and
348 carcass traits, respectively. Whereas regions tagged on chromosomes 3, 6 and 17 for
349 LE and EWW can be considered novel.

350 Among the tagged genes ZNF227, ACACA and NDUFAF2 were found. Hence, these
351 genes could be considered as candidate genes for future research to further dissect the
352 genomic architecture of the traits.

353 **Conclusions**

354 This study is one of very few studies using CT-derived carcass traits and other
355 productivity traits already integrated in the selection index for terminal sire sheep
356 breeds. It revealed some significant associations between genomic markers and
357 important traits in sheep production. Further fine mapping the regions around these
358 markers could lead to the identification of causative genes and better molecular
359 predictors of CT based carcass composition, which might help to decrease phenotyping
360 costs in the longer term. Results may also be integrated and inform genomic selection
361 approaches and future SNP chip designs. The result may also guide similar studies in
362 the other important Terminal Sire Breeds in the UK and beyond.

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376

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496 **Tables**497 **Table 1** *Descriptive statistics for the de-regressed EBVs of the analysed traits.*

Trait	Unit	Acronym	Mean	SD	Minimum	Maximum	p value
Growth Traits							
Birth Weight	kg	BW	0.48	0.81	-2.19	2.89	0.88
Eight Week Weight	kg	EWV	3.24	11.30	-27.01	43.26	0.10
Scan Weight	kg	SW	7.17	7.60	-14.69	35.22	0.17
Carcass Traits							
Fat Depth	mm	FD	-0.08	1.74	-6.1	5.78	0.07
Muscle Depth	mm	MD	1.73	3.42	-8.64	12.4	0.16
Fat Weight	kg	FW	0.79	1.75	-4.05	6.50	0.10
Lean Weight	kg	LW	2.17	2.01	-3.53	8.70	0.74
Muscularity	Ratio	MU	3.3	5.85	-12.94	18.14	0.33
Health Trait							
Faecal Egg Count	Log values	FEC	0.12	0.58	-2.72	4.77	< 0.001
Welfare Trait							
Lambing Ease	Score units (1-6)	LE	0.05	11.98	-70.11	24.83	<0.001

498 SD = Phenotypic standard deviation, 384 tested individuals, Significant p values, for Shapiro
499 and Wilk's W-statistic test, ($p \leq 0.1$) in bold. Fat and Lean weights were measured by CT (as
500 described by Bunger *et al.* (2011))

501 **Table 2** *Chromosome-wide significant SNPs associated with important economic traits*
 502 *and size of estimated effects.*

SNP	Chr	Position OAR v3.1 / OAR v4.0	Allele Effect	SD	P-value	Trait	Nearest Gene (Code)	Nearest Gene (Name)
OAR17_22884911.1	17	20425356 / 20428283	- 0.388	0.09	3.9E-05	EWW	PCDH18 [454.22]	Protocadherin 18
OAR16_20147789.1	16	18368560 / 18365229	- 0.439	0.10	1.3E-05	FD	NDUFAF2	Ubiquinone oxidoreductase complex assembly factor 2
s26074.1	11	8271088 / 8261942	0.673	0.15	2.6E-05	LW	CUEDC1 [37.38]	CUE domain containing 1
OAR11_12972551.1	11	13110133 / 13079564	- 1.115	0.25	1.7E-05	MD	ACACA	Acetyl-CoA carboxylase alpha
s30868.1	4	56089343 / 56074079	- 0.336	0.07	2.0E-05	FEC	ZNF227	Zinc finger protein 227
OAR6_108683365.1	6	98702734 / 98597850	0.341	0.07	6.8E-06	LE	NKX6 [193.99]	NK6 homeobox 1

s23722.1	3	178956951 /178727572	0.519	0.11	9.3E-06	LE	MB [92.5]	Myoglobin
OAR17_11963200.1	17	10808289 / 10794783	- 0.363	0.08	1.6E-05	LE	TTC29 [295.07]	Tetratricopeptide repeat domain 29

503 Chr (Chromosome); Allele effect (deviations from the mean); SD (standard deviation) of the
504 allele effect; P-value for the significance of the association; Units for FEC and LE on the
505 transformed scale; SNPs located within known ovine genes are highlighted in bold; the nearest
506 genes were identified using the ENSEMBL Genome Browser; the number in brackets is the
507 distance from SNP to the nearest gene.

508

509 **Figure Captions**

510

511 **Figure 1:** Manhattan plots for EWW, FD, LW, MD, FEC and LE traits, blue line refers to
512 the genome-wise threshold and the red line to the chromosome-wise significance
513 threshold.