

1 Genetic analysis of meat traits in Merinoland sheep

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3 **Quantitative Genetic and Targeted Association Analyses of Growth,**
4 **Carcass and Meat Quality Traits in German Merinoland and Merinoland-**
5 **Cross Lambs¹**

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ABSTRACT

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In this study, genetic parameters of nine growth, carcass and meat quality (MQ) traits were estimated and targeted association studies were conducted using mixed models. Phenotypic information was collected on 1599 lambs, including both purebred Merinoland animals and five different F1 crosses. The F1 lambs were produced by mating rams of the meat-type breeds Charollais, Ile de France, German Blackheaded Mutton (Deutsches Schwarzköpfiges Fleischschaf), Suffolk, and Texel with Merinoland ewes. Between four and six sires were used per sire breed. The sires and a number of dams were genotyped with the Illumina OvineSNP50 BeadChip. All F1 individuals were genotyped for 289 SNPs located on the chromosomes 1, 2, 3, 18 and 21. These SNPs were used to impute the Illumina Ovine chip SNPs in the F1 individuals. Genetic parameters were estimated and single marker association analysis were performed with breed specific effects.

Moderate heritability estimates (0.15 to 0.40) were found for eye muscle area, shoulder width and many further carcass traits. While heritability for most of the meat quality traits (e.g. cooking loss) was found to be low (< 0.15), shear force showed moderate heritability. In general, low phenotypic and low or moderate genetic correlations were detected between the traits.

Several Bonferroni-corrected significant associations could be identified for shoulder width. A number of additional significant associations were found for other traits. The present study showed that association analyses with imputed SNP chip data are possible with only 289 SNPs distributed on five chromosomes in multiple connected F1 sheep crosses.

Since routine phenotyping is difficult to implement, especially for MQ traits, genomic selection might be a promising tool to improve these traits. The application of genomic selection is also supported by the heritability estimates and the chromosome-wide association results, which

41 point to a quantitative genetic architecture of the traits. However, to confirm the quantitative
42 genetic architecture of MQ the association studies presented should be extended to a genome-
43 wide level and be validated in an independent dataset.

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45 **Key words:** genetic parameters, targeted association study, meat trait, carcass trait, lamb

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INTRODUCTION

48 The Merinoland (ML) sheep is the most common breed in Southern Germany due to its high-
49 quality wool, high fertility, robustness, and its motility. To improve meat quality (MQ), ML
50 ewes are frequently crossed with a sire from a meat type breed. Although meat quality (MQ) is
51 often not included in the direct payment scheme for lamb, there is a growing interest in use of
52 MQ traits in breeding programmes. This is a consequence of consumer demand for improved
53 MQ (Pethick et al., 2011, van der Werf et al., 2010) and the desire to maintain or increase lamb
54 market shares. The most important factors affecting MQ traits include genetics, and production
55 and processing environment (Hopkins et al. 2011). Compared to other livestock species, only
56 few studies have concentrated on MQ traits and their genetic parameters in lamb.

57 Genetic parameters for MQ traits and their genetic correlation to other production traits must
58 be estimated to determine their underlying genetic architecture and to implement them in a
59 breeding program. This is necessary to evaluate the potential impact of selection for MQ on
60 productivity traits and other traits of economic importance (Mortimer et al., 2014; Simm et al.,
61 2009) and to subsequently select the most suitable breeding strategy.

62 In this study, ML ewes were mated with sires from six meat type breeds to generate F1 lambs
63 with improved meat quality. Founder rams and several founder ewes were genotyped with the
64 Illumina Ovine SNP50 BeadChip, and F1 lambs were genotyped for 384 SNPs. Following the

65 encouraging imputation results in multiple sheep breeds (Hayes et al., 2011; Bolormaa et al.,
66 2015) and in pigs (Wellmann et al., 2013), genotypes were imputed for the F1 lambs and
67 subsequent association analyses for growth, carcass and meat quality traits on selected
68 chromosomes were conducted (Hu et al. 2016).

69 The objectives of the present paper were to investigate genetic parameters of growth, carcass
70 and MQ traits in purebred ML and ML crossbred lambs, to impute SNP chip genotypes of F1
71 crossbred lambs, and to conduct association analysis for growth, carcass and MQ traits on
72 selected chromosomes. Potential possibilities to implement findings in current breeding
73 systems are also discussed.

74

75 **MATERIAL AND METHODS**

76 The research protocol was approved by the German Ethical Commission of Animal Welfare of
77 the Provincial Government of Baden-Wuerttemberg. Care of the animals used in this
78 experiment was in accordance with the guidelines issued by the German Regulation for Care
79 and Treatments of Animals

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81 **Animal and data collection**

82 The dataset included 1599 purebred ML and F1-crossbred lambs (meat type sire x ML ewe).
83 As sires, rams of Charollais, Ile de France, German black-headed mutton sheep (Deutsches
84 Schwarzköpfiges Fleischschaf), Suffolk, and Texel were used. Between four and six sires were
85 used per sire breed. For breed abbreviations, number of lambs and number of sires per cross see
86 Table 1. Mating, birth (summer 2011 and autumn 2012) and rearing of lambs until weaning
87 took place on seven farms with purebred ML flocks. Lambs were run with their mothers on
88 pasture with free access to concentrate until weaning (ca. 17 kg bodyweight (BW) and at least

89 eight weeks of age). Fattening was conducted on a single farm in order to standardize
90 environmental conditions. Feeding rations consisted of 200-300 g hay per animal and
91 concentrate *ad libitum*. Lambs were slaughtered at 39-45 kg. The final decision for slaughtering
92 was made by manual scanning. Animals were slaughtered at a commercial abattoir within 35
93 days and were fasted prior to slaughter. The lambs had a mean BW at slaughter of 43.14 ± 3.78
94 kg at an age of 102 to 161 days. During exsanguination, carcasses were electrically stimulated
95 to improve tenderness and prevent cold shortening. Carcasses were chilled on individual hooks
96 at 1 to 3°C. Nine traits of three groups (growth, carcass quality and MQ) were considered in
97 this study (see Table 2 for summary statistics). Hot carcass weight (including kidney and kidney
98 fat) was used to calculate dressing percentage (DRESS), kidney fat weight (KFW) and carcass
99 length (CarL). Shoulder width (SW) was measured 24 h post mortem (p.m.). After
100 measurements, chops of the 10th and 11th rib (M. longissimus thoracis et lumborum) with a
101 thickness of 2 cm were cut, which resulted in samples of about 350 g per animal. Chops were
102 transported to the laboratory and stored at 4°C until MQ testing, which started 48 h p.m..
103 Subcutaneous fat thickness (FAT), cooking loss (COOK) and outlet area (CA) were determined.
104 Subcutaneous fat thickness was calculated as the mean depth of fat cover at four measuring
105 points (one and three cm left and right of the spine at the 11th rib). Cooking loss was defined as
106 the weight difference of the boned chop before and after cooking, done via heating up to a core
107 temperature of 85°C. For measurement of shear force (SF) a cylindrical piece of cooked chop
108 with a diameter of 1.5 cm was punched out and stored at 4°C. After 24 hours, SF was measured
109 with a Warner Bratzler device cutting the meat sample perpendicular to the muscle fibers. All
110 other traits were calculated from the measured data.

111

112 **Genotypes**

113 Blood samples (20ml EDTA whole blood) of every individual were taken during
114 exsanguination directly after slaughter. At day of slaughter an aliquot was taken for DNA
115 extraction and all retained samples were frozen at -20°C. For paternity control, all samples were
116 genotyped for 384 SNP via BeadXpress® using the VeraCode Golden Gate Genotyping
117 Assay® (Illumina, Inc., San Diego, USA). SNPs were excluded if they had a minor allele
118 frequency <3%, and a call rate <95%. A total of 289 SNP, located on the chromosomes 1, 2, 3,
119 18 and 21, passed the data filtering. The chromosomes were chosen in order to focus on QTL
120 for meat performance traits that have been reported in the literature (Hu et al. 2016).
121 To assign the sire to a given individual, parent-child errors (PCEs) were counted for each sire,
122 i.e. the number of SNPs where individual and potential sire had different homozygous
123 genotypes. All but one combination of one individual and all potential sires led to PCEs in the
124 range of 40 to 60, whereas the remaining combinations showed no, or only few PCEs due to
125 genotyping errors. The corresponding potential sire was assumed to be the true sire.
126 Furthermore, all 29 sires and all 359 purebred ML lambs (phenotyped for the traits) used in the
127 experiment, as well as 61 purebred ML from different breeders were genotyped with the
128 Illumina OvineSNP50 BeadChip (Illumina Inc., CA, USA), containing 54,977 SNP. The same
129 genotype filtering criteria were used as described above. Additional, SNPs were removed from
130 the analysis if the linkage disequilibrium with another SNP on the array was >0.99. The total
131 number of SNPs on the targeted chromosomes was 16,534 (16k), whereof 5,202, 4,876, 4,427,
132 1,245, and 784 were located on the chromosomes 1, 2, 3, 18 and 21, respectively. The SNP
133 alleles were coded as 0-allele and 1-allele.
134 The 16k SNP chip genotypes were imputed from 289 SNPs using family and linkage
135 disequilibrium information. The paternal inherited alleles of the lambs were imputed from their
136 16K genotyped sires, whereas the maternal inherited alleles were imputed from a haplotype
137 library, which was built up using the 16K genotypes from ML individuals. For imputation the

138 method of Wellmann et al. (2013) was applied, because it leads to low error rates even for less
139 density marker panels, which was shown by the authors in a pig breeding dataset.

140

141 **Variance component estimation**

142 Variance component were estimated with linear mixed models. The model was

$$143 \quad y = Xb + Z_{sl}sl + Z_a a + e$$

144 where y is the vector of observations, b is a vector of fixed effects including sex, cross, and the

145 covariable weight at slaughter nested within cross, sl is a vector with random effects of day of

146 slaughter (35 levels), a is a vector with the random additive-genetic effects of the individuals,

147 X , Z_{sl} and Z_a are corresponding known design matrixes, and e denotes the residual. The

148 covariance structure of the random animal effect was $\text{var}(a) = A * \sigma_a^2$, with A being the

149 numerator relationship matrix and σ_a^2 the additive genetic variance. The variance of the

150 random day of slaughter effect was $\text{var}(sl) = I * \sigma_{sl}^2$, where σ_{sl}^2 is the slaughter-day variance.

151 The variance of the random residual effect was assumed to be heterogeneous across crosses,

152 i.e. $\text{var}(e) = X'DX$, with X being a known design matrix that assigns each observation to a cross

153 i , and $D = \text{Diag}\{\sigma_{e_i}^2\}$. The modelling of the heterogeneous residual variance led to cross-

154 specific heritability, calculated as $h_i^2 = \frac{\sigma_a^2}{\sigma_a^2 + \sigma_{sl}^2 + \sigma_{e_i}^2}$. The median heritability was calculated

155 as the median of the six cross specific heritabilities.

156 Univariate analyses were performed to estimate the heritability of the traits. Phenotypic and

157 genetic correlations between traits were estimated from a series of bivariate analyses using the

158 same model, but assuming the residual variance to be homogeneous across traits. The statistical

159 analyses were performed using ASReml software (Gilmour et al., 2009).

160

161 **Targeted association analysis**

162 Single-marker models were used to conduct association analysis on the selected chromosomes
163 for the 16k SNPs with the R-package stats. The model included the same fixed effects as for
164 the variance component estimation. Instead of using the pedigree to model the population
165 structure, the first 10 principal components (PC) of the gene content matrix of the dam alleles
166 and 10 PC of the sire alleles were included if they were significant (p-value < 0.05).
167 Additionally, the breed effect, breed specific effects of the paternal inherited allele, and an
168 effect of the maternal inherited allele were included.

169

170 **Hypothesis testing**

171 For analysing a particular SNP, an effect of the 1-allele originating from the mother and sire-
172 breed specific effects of the 1-allele originating from the sire was estimated, whereby the effect
173 of the 0-allele was set to 0 in both cases. Following this parameterization, three F-tests were
174 performed. In the first test, the null hypothesis was that all effects of the markers are equal to
175 zero. Experiment-wise significant markers were identified using Bonferroni to correct for
176 multiple testing. A SNP was declared significant if the Bonferroni corrected p-value < 0.05. In
177 the second and third tests, breed specific effects of the paternal and maternal allele were tested
178 for significance, respectively. The null hypothesis was that all breed specific effects are equal
179 to zero. If the null hypothesis was rejected because of experiment-wise significance of the SNP,
180 Dunnett's linear contrast test was performed for the breed specific effects of the paternal allele
181 to determine the sire breed in which the marker had a significant effect, i.e. the effects of the 1-
182 alleles were tested against the effect of the 0-allele which was used as a control.

183

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RESULTS AND DISCUSSION

185 **Cross means, genetic variation and heritability estimates**

186 The least square means of the cross effects are shown in Table 2. Similar values have been
187 reported by Henseler et al. (2014), who used a subset of this data. Additive genetic variance,
188 slaughter-day variance, range of residual variance and the range of heritability across crosses
189 as well as the median of the heritability estimates are shown in Table 3. The traits ADG,
190 DRESS, KFW, CarL, SW, FAT, SF and CA showed moderate (0.15 to 0.36) heritability
191 estimates in this study.

192 Heritability estimates for ADG are supported by several authors and for different breeds (Bibé
193 et al., 2002; Botkin et al., 1969; Safari and Fogarty, 2003). A moderate h^2 of 0.20 was found
194 for DRESS in the present study, which corresponds to findings of other authors, although some
195 report numerically higher results (Bennett et al., 1991; Botkin et al., 1969; Fogarty et al., 2003;
196 Greeff et al., 2008). Differences in h^2 compared to those found in the present study might be
197 due to population differences, or also differences in measurement and calculation methods.
198 Reported values of Botkin et al. (1969) for KFW are in agreement with the h^2 value found for
199 KFW in the present study. Botkin et al. (1969) reported $h^2=0.50$ for carcass length (measured
200 from the anterior edge of the first rib to the anterior edge of the aitch bone). This estimate was
201 distinctly higher than our estimates for CarL.

202 The heritability estimated for FAT in the present study was 0.22 which is in agreement with the
203 results of e.g. Mortimer et al. (2010), Greeff et al. (2008) and Bennett et al. (1991), who
204 measured FAT at different points of the carcass. Although h^2 values of MQ traits estimated in
205 the present study were low to moderate, genetic improvement would be possible with
206 implementation of routine performance testing. For SF, a low heritability was estimated which
207 is in contrast with the studies of Botkin et al., (1969), Hopkins et al., (2011) and Mortimer et
208 al. (2010) who reported moderate heritability of SF. The differences to the present study might
209 be explained by differences in genetics, carcass weights, and aging time.

210 Cutlet area can be used as an indicator trait for muscling and represents a highly valued part of
211 the carcass. For CA the highest h^2 was estimated. Results are supported by the findings of other
212 studies (Bennett et al., 1991; Fogarty et al., 2003; Greeff et al., 2008; Mortimer et al., 2010).
213 Factors affecting difference in estimates may have a genetic basis, but might also be due to
214 different measurement methods (direct measurement vs. estimation of the muscle area by 80%
215 of the product of eye muscle depth and length, measuring points, etc.).

216

217 **Phenotypic and genetic correlations**

218 Results of phenotypic and genetic correlations are shown in Table 4. The high SE values
219 indicate that caution should be used when interpreting these results. The weakness of the data
220 structure is the limited number of sires for each cross (Table 1).

221 Phenotypic correlations between most traits were low and often close to zero. Dawson et al.
222 (2002) investigated phenotypic correlations of different carcass and MQ traits and generally
223 found moderate correlations. Greeff et al. (2008) and Fogarty et al. (2003) both reported very
224 low phenotypic correlations for dressing, eye muscle area and two fat depth traits, which is
225 supported by the findings of the present study.

226 The genetic correlations were higher, and in some cases showed a different sign compared to
227 phenotypic correlations. Genetic correlations between ADG and DRESS were found to be
228 positive. Bennett et al. (1991) found a higher correlation for post weaning gain and DRESS.
229 Moderate to high positive genetic correlations of ADG with CarE, SW, SF and FAT were
230 observed. Genetically advantageous correlations were also found between ADG and SF in some
231 muscles (Hopkins et al., 2007), between ADG and tenderness (Hopkins et al., 2006), and
232 between ADG and reduced feed intake (Peeters et al., 1995). Traits that are expected to be
233 muscling indicators (e.g. CA) and therefore should be positively correlated with ADG. Such

234 traits showed only phenotypic correlations close to zero and low genetic correlations,
235 supporting findings of Bibé et al. (2002).

236 As mentioned, in the current study SF and ADG were genetically moderately positive correlated
237 as well as SF with CA. Mortimer et al. (2010) reported moderate correlation for body weight at
238 weaning, but low genetic correlations of SF to eye muscle depth. A moderate and unfavourable
239 negative genetic correlation between COOK and SF was observed. Sensory studies with lamb
240 meat have shown that acceptable palatability requires low shear force values and an
241 intramuscular fat (IMF) content of at least 5% (Hopkins et al. 2006). Furthermore, selection for
242 increasing IMF is expected to have a favourable effect on shear force (Hopkins et al. 2011). In
243 the present study there was no clear tendency showing a relationship between SF and FAT
244 (genetic correlation near zero). In literature positive correlations between fat depths (e.g.
245 Mortimer et al., 2010) and percentage of carcass fat (Lorentzen and Vangen, 2012) with IMF,
246 and negative correlations between IMF and SF (Jacob and Pethick, 2014; Mortimer et al., 2010,
247 2014; Warner et al., 2010) are reported. Also Mortimer et al. (2010) reported a low genetic
248 correlation between SF and FAT. McPhee et al. (2008) and Hopkins et al. (2007) found age,
249 breed and cross influencing IMF. The rather lean carcasses and the low age of lambs in the
250 current study might be influencing factors preventing more clear results with regards to the
251 relationship between IMF and SF. The low slaughter age is considered desirable by
252 slaughterers, retailers and consumers. Breeding for leanness can indirectly affect MQ in an
253 undesired way, so a certain fat content of carcasses and muscles needs to be preserved (Pethick
254 et al., 2006; Wood et al., 2008). The challenge will be to breed animals with high lean meat,
255 high IMF and low SF (Jacob and Pethick, 2014; Pannier et al., 2014).

256 Kidney Fat Weight showed a low but positive genetic correlation to FAT. Phenotypic
257 correlations showed the same tendencies, indicating that animals with less kidney fat have better
258 hind limbs.

259 Cooking loss showed several moderate and high genetic correlations of different sign to
260 different traits. A moderate negative correlations to FAT and SF, and a high negative correlation
261 to DRESS. This implies that well evaluated carcasses, as well as those with broad haunches,
262 have higher COOK, which is actually not desired, while fatter, tougher and individuals with
263 better DRESS have less COOK. The negative correlation between DRESS and COOK is
264 desired, because it would serve the producer as well as the consumer. On the other hand,
265 biological reasons for these relationships remain unclear and verification is necessary.

266 Subcutaneous fat thickness showed moderately positive genetic correlations to ADG, DRESS
267 and CarL and a negative correlation of -0.51 to CA. The correlation of FAT and DRESS is
268 supported by a similar estimated phenotypic correlation. Greeff et al. (2008) investigated two
269 different carcass fat depths and reported moderate genetic correlations to DRESS as well as low
270 correlations of different sign to CA. The distinct differences are most likely caused by
271 differences of measurement points, illustrating the problem of comparability. Concerning CarE,
272 it is striking that this trait is genetically negatively correlated with CarL but positively with SW
273 and CA (phenotypic correlations denote the same tendency), indicating that shorter but broader
274 and more muscular carcasses are evaluated better.

275

276 **Targeted association analysis**

277 The results of the association analysis are shown in Table 5. For the traits SW, CA, COOK, and
278 SF experiment-wise significant SNPs could be detected. A comparison with literature reports
279 (Hu et al. 2016) showed that most significant associations are located in well-known QTL
280 regions. For the low heritable MQ traits, only one SNP on chromosome 2 was experiment-wise
281 significant for COOK. On chromosome 2, QTL were also found for DRESS in the literature
282 (Laville et al., 2004; Johnson et al., 2009). For the traits with the highest heritability estimates,
283 CA and SW, the most experiment-wise significant SNPs were identified. For CA and SW four

284 and eight significant SNPs were found. One QTL on chromosome 2 was found for longissimus
285 muscle width (Johnson et al., 2005), which supports our findings on chromosome 2 for SW.
286 Although experiment-wise significant SNPs were found, no clear signal with consecutive
287 significant SNPs could be detected. This might be because the significance is due to the alleles
288 inherited from the Texel sire breed and the number of lambs from this sire breed is only 150,
289 thus representing the smallest F1 cross. For all experiment-wise significant associations, the
290 Texel breed origin alleles were significant ($p < 0.05$). Thus, the power to map these significant
291 SNPs is mainly due to the Texel F1 cross and the other F1 cross did not add much to the power.
292 The breed specific effect of the maternal alleles is not shown, because it was not experiment-
293 wise significant.

294

295 **Implementation in breeding programmes**

296 The cross means (Table 2) show that for the growth and carcass traits, the crossbred lambs are
297 superior to the purebred ML lambs, but this does not hold always for MQ traits. Hence, if
298 growth and carcass traits are to be improved, crossbreeding ML sheep with a meat type sire
299 breed is recommended, but this will likely not improve MQ traits substantially.

300 Single heritability estimates are not shown for the different F1 crosses because the number of
301 sires within crosses is low. Instead of showing cross-specific heritability estimates, the medians
302 of the heritability estimates are listed in Table 3. If breeding values are to be estimated in a
303 multivariate setting, the genetic correlations reported in this study should not be used due to
304 their high SE. In addition, if both purebred ML data and F1 crossbred data is to be used for
305 routine genetic evaluations, more reliable genetic parameters must be estimated using a larger,
306 better structured data set.

307 In some breeding programmes for ML and for some of the tested sire lines ADG, CA, FAT and
308 SW are already implemented. Results of the current study support this choice of traits because

309 of the moderate heritability estimates and the genetic and phenotypic correlations found. The
310 integration of muscling and fat parameters is particularly important to control leanness. For
311 further improvement of MQ and palatability traits, inclusion of SF and COOK in a breeding
312 program can be recommended.

313 In general, growth and carcass traits are relatively easy to measure (so called “easy to measure
314 traits”) at acceptable costs. Therefore they are often already implemented in breeding
315 programmes. For MQ traits, data recording is cost-prohibitive and time consuming (Mortimer
316 et al., 2010; Simm et al., 2009); these traits are classical “hard to measure” traits. Because lambs
317 are often paid by weight, and not by MQ or palatability, high phenotyping costs are the main
318 barrier of inclusion of quality traits to breeding programmes (Simm et al., 2009). Hayes et al.
319 (2013) recommended genomic selection for the improvement of traits that are too expensive to
320 measure routinely in selection candidates, and genomic selection has been introduced in some
321 sheep breeding schemes (e.g. Daetwyler et al., 2012). Genomic selection, however, needs a
322 large reference population with genotyped and phenotyped individuals in order to reliably
323 predict breeding values. Establishing such reference populations is challenging, but is probably
324 the most efficient way to improve MQ traits, as shown by Daetwyler et al. (2012). The
325 phenotypic data collected in the present study, supplemented by genomic data, may serve as an
326 initial reference population, but has to be augmented by additional data sets.

327

328

CONCLUSION

329 For growth and carcass traits, it is beneficial to produce F1 cross bred animals compared to
330 purebred ML lambs. The heritability estimates show that it is generally possible to achieve
331 selection response for the traits included in this study. From the chromosome wide association

332 results, it seems that the method used to model SNP effects is important due to different linkage
333 disequilibrium structures between SNP and causal mutations in different crosses.

334 While growth and some carcass traits are considered in some ML breeding schemes, MQ traits
335 are usually not included in the breeding goal due to high cost of data recording in conventional
336 routine breeding schemes. Although the quantitative genetic background of MQ traits is
337 supported by the heritability estimates and association results, a validation in an independent
338 dataset, as well as an extension of the association studies on a genome-wide level, is needed.

339 The data collected in the present study might serve as an initial reference population, which has
340 to be augmented by additional data points and, of course, by genomic data.

341

342 **Table 1.** Sheep breed crosses, cross abbreviations, number of lambs per cross (n lambs) and
 343 number of sires per cross (n sires)

Cross	Abbreviation	n lambs	n sires
Charolais x ML ¹	CH	324	5
Ile de France x ML	IF	359	5
ML x ML	ML	237	4
German black headed mutton ² x ML	SK	250	5
Suffolk x ML	SU	279	4
Texel x ML	TX	150	6

344 ¹ ML=German Merinoland sheep

345 ² German black headed mutton = Deutsches Schwarzköpfiges Fleischschaf

346 **Table 2.** Trait, trait abbreviation, unit, number of observations (n), mean, standard deviation (sd), and means of the crosses (standard error in
 347 parenthesis)

Trait	abbreviation	unit	n	mean	Cross ³					
					CH	IF	ML	SK	SU	TX
Average daily gain (fattening)	ADG	[g/d]	1582	329.96	323.88 (8.30)	340.81 (8.22)	320.93 (8.87)	337.85 (8.30)	337.84 (8.91)	336.27 (8.76)
Dressing Percentage	DRESS	[%]	1551	48.96	49.29 (0.33)	49.45 (0.32)	48.70 (0.36)	48.67 (0.32)	48.18 (0.35)	49.31 (0.37)
Kidney Fat Weight	KFW	[g]	1590	235.22	219.87 (17.81)	262.29 (17.77)	247.29 (18.97)	246.69 (17.99)	235.88 (19.07)	222.53 (18.62)
Carcass length	CarL	[cm]	1592	40.46	39.85 (0.32)	39.86 (0.32)	41.50 (0.34)	41.02 (0.32)	40.85 (0.34)	39.63 (0.34)
Shoulder Width	SW	[cm]	1589	19.06	19.26 (0.12)	19.43 (0.12)	18.62 (0.13)	18.93 (0.11)	18.81 (0.13)	19.15 (0.14)
Subcutaneous fat thickness	FAT	[mm]	1592	4.49	4.68 (0.16)	5.05 (0.16)	4.15 (0.18)	4.37 (0.16)	4.31 (0.18)	3.80 (0.18)
Cooking loss ¹	COOK	[%]	1598	32.53	32.35 (0.40)	32.94 (0.38)	30.98 (0.45)	31.57 (0.41)	32.62 (0.43)	32.87 (0.47)
Warner-Bratzler shear force ²	SF	[N]	1514	65.07	61.24 (3.59)	66.62 (3.56)	64.46 (3.84)	63.56 (3.70)	67.64 (3.86)	70.13 (4.06)
Cutlet area	CA	[cm ²]	1592	12.34	12.25 (0.22)	12.68 (0.22)	11.95 (0.24)	12.26 (0.22)	12.18 (0.24)	13.23 (0.26)

348 ¹ after two days of aging

349 ² one day after cooking

350 ³ For cross/breed abbreviations see Table 1

351

352 **Table 3.** Additive genetic variance (σ_a^2), slaughter day variance (σ_{SD}^2), range of residual
 353 variance across the crosses ($\sigma_{e_i}^2$) and median of the heritability estimates. (standard error in
 354 parenthesis)

Trait ¹	σ_a^2	σ_{SD}^2	$\sigma_{e_i}^2$	h^2
			min – max	median
ADG	611.63 (288.62)	1134.27 (229.95)	478.20 - 1004.02 (≤ 218.09)	0.23
DRESS	1.09 (0.45)	1.19 (0.32)	2.15 - 3.82 (≤ 0.56)	0.20
KFW	2444.95 (5.58)	6021.66 (3.99)	1661.40 - 5064.67 (≤ 5.25)	0.19
CarL	0.70 (0.28)	1.97 (0.50)	1.52 - 1.95 (≤ 0.36)	0.15
SW	0.19 (0.07)	0.09 (0.02)	0.25 - 0.50 (≤ 0.08)	0.33
FAT	0.32 (0.14)	0.18 (0.05)	0.65 - 1.07 (≤ 0.16)	0.22
COOK	1.04 (0.72)	1.73 (0.52)	11.46 - 16.50 (≤ 1.72)	0.07
SF	109.12 (46.83)	199.08 (51.84)	237.08 - 361.65 (≤ 64.70)	0.17
CA	0.72 (0.27)	0.22 (0.06)	0.73 - 1.35 (≤ 0.30)	0.36

355 ¹ For trait abbreviations see Table 2

356

357 **Table 4.** Genetic (upper diagonal) and phenotypic (lower diagonal) correlations of growth-, carcass- and meat quality traits (standard errors are
 358 in parenthesis)

Trait ¹	ADG	DRESS	KFW	CarL	SW	FAT	COOK	SF	CA
ADG		0.16 (0.28)	-0.03 (0.27)	0.10 (0.28)	0.36 (0.24)	0.36 (0.26)	0.14 (0.37)	0.50 (0.23)	0.11 (0.26)
DRESS	-0.13 (0.06)		-0.01 (0.29)	0.07 (0.29)	0.13 (0.27)	0.35 (0.26)	-0.62 (0.36)	0.16 (0.30)	0.19 (0.26)
KFW	-0.19 (0.08)	0.21 (0.06)		-0.18 (0.28)	-0.23 (0.27)	0.12 (0.28)	-0.13 (0.38)	-0.20 (0.28)	-0.25 (0.26)
CarL	-0.21 (0.07)	0.05 (0.06)	0.14 (0.08)		-0.26 (0.27)	0.27 (0.28)	-0.21 (0.39)	-0.13 (0.30)	-0.28 (0.26)
SW	0.03 (0.05)	0.46 (0.03)	0.04 (0.05)	-0.11 (0.05)		-0.04 (0.29)	0.01 (0.39)	0.27 (0.28)	0.26 (0.25)
FAT	0.02 (0.05)	0.29 (0.04)	0.15 (0.05)	-0.04 (0.05)	0.17 (0.04)		-0.47 (0.34)	0.09 (0.30)	-0.51 (0.22)
COOK	0.04 (0.05)	-0.01 (0.04)	-0.08 (0.05)	-0.02 (0.05)	-0.03 (0.04)	0.04 (0.03)		-0.49 (0.36)	-0.15 (0.36)
SF	0.07 (0.07)	-0.01 (0.06)	-0.11 (0.07)	-0.17 (0.07)	0.05 (0.05)	-0.16 (0.04)	-0.01 (0.04)		0.42 (0.25)
CA	0.08 (0.05)	0.38 (0.04)	-0.01 (0.05)	-0.13 (0.05)	0.35 (0.03)	-0.14 (0.04)	0.03 (0.03)	0.26 (0.04)	

359 ¹For trait abbreviations see Table 2

360 **Table 5.** Significant SNP trait associations with chromosome (Chr), position in bp/10⁶ (Pos), SNP name, and p-values for the tests.

361 For SNPs with experiment-wise significant sire effects (Test 2) the adjusted *p*-values are shown for which of the sire breeds¹ the SNP has

362 significant effects

Chr	Pos	SNP name	Trait	<i>p</i> -value ¹			Sire breed abbreviations ²				
				Test 1	Test 2	ML	IF	CH	SK	SU	TX
1	82.021	OAR1_82021326.1	SW	3.74E-07	2.96E-07	0.668	< 0.001	0.154	0.259	0.111	NA
1	150.184	OAR1_150183526.1	SW	3.47E-06	1.53E-06	1.000	0.006	0.998	0.926	0.557	< 0.001
1	150.193	OAR1_150193285.1	SW	1.88E-06	1.50E-06	1.000	0.011	0.986	0.517	0.811	< 0.001
1	173.225	s21244.1	SW	3.00E-06	1.16E-06	0.053	0.364	0.400	0.932	0.016	< 0.001
1	225.403	OAR1_225402747.1	CA	4.09E-07	2.27E-06	0.461	0.249	0.009	0.289	0.121	0.025
2	52.308	OAR2_52308410.1	SW	4.51E-08	2.36E-08	1.000	0.247	0.119	0.014	0.173	< 0.001
2	80.474	OAR2_80474394.1	COOK	2.27E-06	1.77E-06	0.002	0.001	0.032	1.000	0.873	0.317
3	7.255	s62569.1	CA	7.68E-07	3.30E-07	1.000	0.433	0.157	0.992	1.000	< 0.001
3	137.712	OAR3_137712214.1	SW	3.59E-08	1.26E-08	0.807	0.012	0.016	0.019	0.837	< 0.001
3	231.664	s36196.1	CA	1.50E-06	2.31E-06	0.003	0.894	0.006	0.794	1.000	0.001
21	27.861	s12930.1	SW	9.34E-08	8.55E-08	0.003	0.059	1.000	0.953	0.933	< 0.001
21	36.067	OAR21_36067273.1	SW	3.30E-06	1.41E-06	0.004	0.676	0.484	0.739	0.389	0.001
21	44.494	OAR21_44493640.1	CA	2.54E-07	9.08E-08	0.926	0.857	0.581	0.751	0.427	0.002
21	51.128	OAR21_51127739.1	SF	1.81E-07	6.67E-08	0.204	0.768	0.010	0.001	0.978	0.001

363 ¹ See text for the corresponding null hypothesis.

364 ² ML Merinoland, IF Ile de France, CH Charollais, SK German Blackheaded Mutton (Deutsches Schwarzköpfiges Fleischschaf), SU Suffolk,

365 TX Texel

366 Significant breed specific effects of the paternal allele are written in bold

367

LITERATURE CITED

- 368 Bennett, G.L., D.L. Johnson, A.H. Kirton, and A.H. Cartes. 1991. Genetic and
369 environmental effects on carcass characteristics of Southdown x Romney lambs:
370 II. Genetic and phenotypic variation. *J. Anim. Sci.* 69, 1864–1874.
- 371 Bibé, B., J.C. Brunel, Y. Bourdillon, D., Loradoux, M.H. Gordy, J.L. Weisbecker, and J.
372 Bouix. 2002. Genetic parameters of growth and carcass quality of lambs at the
373 french progeny-test station Berrytest. *Proceeding of the 7th World Congr. Genet.*
374 *Appl. to Livest. Prod. Genomic.*, Montpellier.
- 375 Bolormaa, S., K. Gore, J.H.J. van der Werf, B.J. Hayes, and H.D. Daetwyler. 2015.
376 Design of a low-density SNP chip for the main Australian sheep breeds and its
377 effect on imputation and genomic prediction accuracy. *Animal Genetics* 46, 544-
378 556.
- 379 Botkin, M.P., R.A. Field, M.L. Riley, J.C.J. Nolan, and G.P. Roehrkaase. 1969.
380 Heritability of Carcass Traits in Lambs. *J. Anim. Sci.* 29, 251–255.
- 381 Daetwyler, H.D., A.A. Swan, J.H.J. van der Werf, and B.J. Hayes. 2012. Accuracy of
382 pedigree and genomic predictions of carcass and novel meat quality traits in multi-
383 breed sheep data assessed by cross-validation. *Genet. Sel. Evol.* 44, 33.
- 384 Dawson, L.E.R., A.F. Carson, and B.W. Moss. 2002. Effects of crossbred ewe
385 genotype and ram genotype on lamb meat quality from the lowland sheep flock.
386 *J. Agric. Sci.* 139, 195–204.

387 FAO, Food and Agriculture Organization of the United Nations. 2014. FAOSTAT.
388 Rome, Italy. Retrieved May 20, 2015, from
389 <http://faostat3.fao.org/download/Q/QA/E>.

390 Fogarty, N.M., E. Safari, P.J. Taylor, and W. Murray. 2003. Genetic parameters for
391 meat quality and carcass traits and their correlation with wool traits in Australian
392 Merino sheep. *Aust. J. Agric. Res.* 54, 715–722.

393 Gilmour, A.R., B.J. Gogel, B.R. Cullis, and R. Thompson. 2009. ASReml User Guide
394 Release 3.0 VSN International Ltd., Hemel Hempstead, HP1 1ES, UK.

395 Greeff, J.C., E. Safari, N.M. Fogarty, D.L. Hopkins, F.D. Brien, K.D. Atkins, S.I.
396 Mortimer, and J.H.J. Van Der Werf. 2008. Genetic parameters for carcass and
397 meat quality traits and their relationships to liveweight and wool production in
398 hogget Merino rams. *J. Anim. Breed. Genet.* 125, 205–215.

399 Hayes, B.J., P.J. Bowman, H.D. Daetwyler, J.W. Kijas, and J.H.J. van der Werf. 2011.
400 Accuracy of genotype imputation in sheep breeds. *Animal Genetics* 43, 72-80.

401 Hayes, B.J., H.A. Lewin, and M.E. Goddard. 2013. The future of livestock breeding:
402 Genomic selection for efficiency, reduced emissions intensity, and adaptation.
403 *Trends Genet.* 29, 206–214.

404 Henseler, S., S. Preuss, and J. Bennewitz. 2014. Fleischerzeugung mit
405 Merinolandschaf-Gebrauchskreuzungen – 1. Mitteilung, Analyse der Schlacht-
406 und Fleischqualität. *Züchtungskunde* 86, 95–103.

407 Hopkins, D.L., N.M. Fogarty, and S.I. Mortimer. 2011. Genetic related effects on sheep
408 meat quality. *Small Rumin. Res.* 101, 160–172.

409 Hopkins, D.L., R.S. Hegarty, P.J. Walker, and D.W. Pethick. 2006. Relationship
410 between animal age, intramuscular fat, cooking loss, pH, shear force and eating
411 quality of aged meat from sheep. *Aust. J. Exp. Agric.* 46, 879.

412 Hopkins, D.L., D.F. Stanley, L.C. Martin, E.S. Toohey, and A.R.C. Gilmour. 2007.
413 Genotype and age effects on sheep meat production 3. Meat quality. *Aust. J. Exp.*
414 *Agric.* 47, 1155–1164.

415 Hu, Z. L., C.A. Park, and J. M. Reecy. 2005. A QTL resource and comparison tool for
416 pigs: PigQTLDB. *Mammalian Genome* 16: 792-800.

417 Jacob, R.H., and D.W. Pethick. 2014. Animal factors affecting the meat quality of
418 Australian lamb meat. *Meat Sci.* 96, 1120–1123.

419 Johnson, P.L., K.G. Dodds, W.E. Bain, G.J. Greer, N.J. McLean, R.J. McLaren, S.M.
420 Galloway, T.C. van Stijn, and J.C. McEwan. 2009. Investigations into the GDF8
421 g+6723G-A polymorphism in new zealand texel sheep. *J. Anim. Sci.* 87(6): 1856-
422 1864. doi: 10.2527/jas.2008-1508

423 Johnson, P. L., J. C. McEwan, K. G. Dodds, R. W. Purchas, and H. T. Blair. 2005. A
424 directed search in the region of GDF8 for quantitative trait loci affecting carcass
425 traits in texel sheep. *J. Anim. Sci.* 83(9): 1988-2000.

426 Laville, E., J. Bouix, T. Sayd, B. Bibé, J.M. Elsen, C. Larzul, F. Eychenne, F. Marcq,
427 and M. Georges. 2004. Effects of a quantitative trait locus for muscle hypertrophy
428 from belgian texel sheep on carcass conformation and muscularity. *J. Anim. Sci.*
429 82(11): 3128-3137.

430 Lorentzen, T.K., and O. Vangen. 2012. Genetic and phenotypic analysis of meat
431 quality traits in lamb and correlations to carcass composition. *Livest. Sci.* 143,
432 201–209.

433 McPhee, M.J., D.L. Hopkins, and D.W. Pethick. 2008. Intramuscular fat levels in
434 sheep muscle during growth. *Aust. J. Exp. Agric.* 48, 904–909.

435 Mortimer, S.I., J.H.J. van der Werf, R.H. Jacob, D.L. Hopkins, L. Pannier, K.L. Pearce,
436 G.E. Gardner, R.D. Warner, G.H. Geesink, J.E. Hocking Edwards, E.N.
437 Ponnampalam, A.J. Ball, A.R. Gilmore, and D.W. Pethick. 2014. Genetic
438 parameters for meat quality traits of Australian lamb meat. *Meat Sci.* 96, 1016–24.

439 Mortimer, S.I., J.H.J. van der Werf, R.H. Jacob, D.W. Pethick, K.L. Pearce, R.D.
440 Warner, G.H. Geesink, J.E. Hocking Edwards, G.E. Gardner, E.N. Ponnampalam,
441 S.M. Kitessa, A.J. Ball, and D.L. Hopkins. 2010. Preliminary estimates of genetic
442 parameters for carcass and meat quality traits in Australian sheep. *Anim. Prod.*
443 *Sci.* 50, 1135 – 1144.

444 Pannier, L., D.W. Pethick, G.H. Geesink, A.J. Ball, R.H. Jacob, and G.E. Gardner.
445 2014. Intramuscular fat in the longissimus muscle is reduced in lambs from sires
446 selected for leanness. *Meat Sci.* 96, 1068–1075.

447 Peeters, R., G. Kox, and J. Van Isterdael. 1995. Environmental and genetic influences
448 on growth performance of lambs in different fattening systems. *Small Rumin. Res.*,
449 18: 57–67.

450 Pethick, D.W., A.J. Ball, R.G. Banks, and J.F. Hocquette. 2011. Current and future
451 issues facing red meat quality in a competitive market and how to manage
452 continuous improvement. *Anim. Prod. Sci.* 51, 13.

453 Pethick, D.W., R.D. Warner, and R.G. Banks. 2006. Genetic improvement of lamb—
454 industry issues and the need for integrated research. *Aust. J. Exp. Agric.* 57, 591–
455 592.

456 Quaas, R.L. 1988. Additive Genetic Model with Groups and Relationships. *J. Dairy Sci.*
457 71, 1338–1345.

458 Safari, A., N.M. Fogarty. 2003. Genetic Parameters for Sheep Production Traits -
459 Estimates from the Literature. *Tech. Bull.* 49, NSW Agriculture Orange Agricultural
460 Institute, Orange NSW.

461 Schiller, K.F., V. Grams, and J. Bennewitz. 2015b. Analysis of growth and feed
462 conversion in purebred and crossbred German Merinolandschaf lambs. *Arch.*
463 *Anim. Breed.* 58, 177–183.

464 Schiller, K.F., S. Preuss, S. Kaffarnik, W. Vetter, M. Rodehutschord, and J. Bennewitz.
465 2015a. Concentration of three branched-chain fatty acids in adipose tissue does
466 not affect meat sensory traits in crossbred and purebred German
467 “Merinolandschaf” lambs. *Arch. Anim. Breed.* 58, 159–163.

468 Simm, G., N.R. Lambe, L. Bünger, E.A. Navajas, and R. Roehe. 2009. Use of meat
469 quality information in breeding programmes, in: Kerry, J.P., David, L. (Eds.),
470 Improving the Sensory and Nutritional quality of fresh meat. Woodhead Publishing
471 Ltd, Great Abington, pp. 265-292.

- 472 Strittmatter, K. 2005. Entwicklung, Stand und Perspektiven der Schafproduktion in
473 Deutschland. Züchtungskunde 77, 496–501.
- 474 Van der Werf, J.H.J., R.G. Banks, S.A. Clark, S.J. Lee, H.D. Daetwyler, B.J. Hayes,
475 and A.A. Swan. 2014. Genomic Selection in Sheep Breeding Programs.
476 Proceeding of the 10th World Congr. Genet. Appl. to Livest. Prod. Genomic.
477 Vancouver.
- 478 Van der Werf, J.H.J., B.P. Kinghorn, and R.G. Banks. 2010. Design and role of an
479 information nucleus in sheep breeding programs. Anim. Prod. Sci. 50, 998–1003.
- 480 Warner, R.D., R.H. Jacob, J.E. Hocking Edwards, M. McDonagh, K. Pearce, G.
481 Geesink, G. Kearny, P. Allingham, D.L. Hopkins, and D.W. Pethick. 2010. Quality
482 of lamb meat from the Information Nucleus Flock. Anim. Prod. Sci. 50, 1123 –
483 1134.
- 484 Wellmann R., S. Preuß, E. Tholen, J. Heinkel, K. Wimmers, and J. Bennewitz. 2013.
485 Genomic selection using low density marker panels with application to a sire line
486 in pigs. Genetics Selection Evolution 45, 28.
- 487 Wood, J.D., M. Enser, A.V. Fisher, G.R. Nute, P.R. Sheard, R.I. Richardson, S.I.
488 Hughes, and F.M. Whittington. 2008. Fat deposition, fatty acid composition and
489 meat quality: A review. Meat Sci. 78, 343–358.