Genetic parameter estimates and targeted association analyses of growth, carcass, and meat quality traits in German Merinoland and Merinoland-cross lambs¹

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ABSTRACT: 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 1,599 lambs, including both purebred Merinoland (ML) 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 ML ewes. Between four and six sires were used per sire breed. In total, 29 sires and 298 purebred ML sheep 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 SNPs on five chromosomes of the Illumina Ovine chip in the

F1 individuals. Several Bonferroni-corrected significant associations were identified for shoulder width. A number of additional significant associations were found for other traits. Genetic parameters were estimated and single-marker association analyses were performed with breed-specific effects. Moderate heritability estimates were found for average daily gain (0.23), kidney fat weight (0.19), carcass length (0.15), shoulder width (0.33), subcutaneous fat thickness (0.22), and cutlet area (0.36). While heritability for cooking loss was found to be low (0.07), shear force (0.17) and dressing percentage (0.20) showed moderate heritability, and thus might be candidate traits to be included in the selection index in the population. In general, low phenotypic and low or moderate genetic correlations were detected between the traits.

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

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INTRODUCTION

The Merinoland (ML) sheep is the most common breed in Southern Germany due to its high-quality wool, high fertility, and robustness. To improve meat quality (MQ), ML ewes are frequently crossed with a sire from a meat-type breed. Although MQ traits are often not included in the direct payment scheme for lamb, there is a

growing interest in the use of MQ traits in breeding programs (van der Werf et al., 2010; Pethick et al., 2011). Factors affecting MQ traits include genetics, production, and processing environment (Hopkins et al., 2011). Compared with other livestock species, only few studies have concentrated on MQ traits and their genetic parameters in lamb.

Genetic parameters for MQ traits and their genetic correlation to carcass and growth traits must be estimated to determine their underlying genetic architecture and to implement them in a breeding program. This is necessary to evaluate the potential impact of selection for MQ on productivity and economically important traits (Simm

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et al., 2009; Mortimer et al., 2014) and to subsequently select the most suitable breeding strategy.

In this study, ML ewes were mated with sires from six meat-type breeds to generate purebred ML lambs and F1 lambs. Founder rams and several founder ewes were genotyped with the Illumina Ovine SNP50 BeadChip, and F1 lambs were genotyped for 384 SNPs. Following the encouraging imputation results in multiple sheep breeds (Hayes et al., 2011; Bolormaa et al., 2015) and in pigs (Wellmann et al., 2013), genotypes were imputed for the F1 lambs, and subsequent association analyses for meat performance traits on selected chromosomes were conducted (Hu et al. 2005). We used the method of Wellmann et al. (2013) because they imputed SNP chip genotypes in offspring using only 768 SNPs with an error rate of 8%, provided that boars were genotyped with the porcine 60k SNP chip, and family and linkage disequilibrium was used for imputation.

The objectives of this article were to investigate genetic parameters of growth, carcass, and MQ traits in purebred ML and ML crossbred lambs, to impute SNP chip genotypes of F1 crossbred lambs, and to conduct association analysis on selected chromosomes. Potential possibilities to implement findings in current breeding systems are also discussed.

MATERIALS AND METHODS

The research protocol was approved by the German Ethical Commission of Animal Welfare of the Provincial Government of Baden-Wuerttemberg. The investigation began in autumn and ended in summer 2011. Care of the animals used in this experiment was in accordance with the guidelines issued by the German Regulation for Care and Treatments of Animals.

Animal and Data Collection

The dataset included 1,599 purebred ML and F1-crossbred lambs (meat-type sire x ML ewe). As

sires, rams of Charollais (**CH**), Ile de France (**IDF**), German blackheaded mutton sheep (Deutsches Schwarzköpfiges Fleischschaf, **SK**), Suffolk (**SU**), and Texel (**TX**) were used. Between four and six sires were used per sire breed. For breed abbreviations, number of lambs, and number of sires per cross, see Table 1. Mating, birth (summer 2011 and autumn 2012), and rearing of lambs until weaning took place on seven farms with purebred ML flocks. Lambs were run with their mothers on pasture with free access to concentrate until weaning (ca. 17 kg bodyweight [BW] and at least 8 wk of age). Fattening was conducted on a single farm in order to standardize environmental conditions. Feeding rations consisted of 200 to 300 g hay per animal and concentrate *ad libitum*. Lambs were harvested to be slaughtered at 39 to 45 kg. The final decision for slaughtering was made by visual appraisal. The lambs had a mean BW at slaughter of 43.14 ± 3.78 kg at an age of 102 to 161 days. During exsanguination, carcasses were electrically stimulated to improve tenderness and prevent cold shortening. Carcasses were chilled on individual hooks at 1 °C to 3 °C. Nine traits of three groups (growth, carcass quality, and MQ) were considered in this study (see Table 2 for summary statistics). Hot carcass weight (including kidney and kidney fat) was used to calculate dressing percentage (**DRESS**), kidney fat weight (**KFW**), and carcass length (**CarL**). Shoulder width (**SW**) was measured 24 h postmortem (**p.m.**). After measurements, chops of the 10th and 11th rib (M. longissimus thoracis et lumborum) with a thickness of 2 cm were cut, which resulted in samples of about 350 g per animal. Chops were transported to the laboratory and stored at 4 °C until MQ testing, which started 48 h p.m. Subcutaneous fat thickness (**FAT**), cooking loss (**COOK**), and cutlet area (**CA**) were determined. **FAT** was calculated as the mean depth of fat cover at four measuring points (1 and 3 cm left and right of the spine at the 11th rib). **COOK** was defined as the weight difference of the boned chop

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

Cross	Abbreviation	<i>n</i> lambs	<i>n</i> sires
Charollais x ML	CH	324	5
Ile de France x ML	IF	359	5
ML x ML	ML	237	4
German blackheaded mutton x ML	SK	250	5
Suffolk x ML	SU	279	4
Texel x ML	TX	150	6

ML, German Merinoland sheep; German blackheaded mutton, Deutsches Schwarzköpfiges Fleischschaf.

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

Trait	Abbreviation	<i>n</i>	mean	SD	Cross ^a					
					CH	IF	ML	SK	SU	TX
Average daily gain (fattening), g/d	ADG	1,582	329.96	67.55	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	1,551	48.96	2.37	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, g	KFW	1,590	235.22	114.11	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, cm	CarL	1,592	40.46	2.45	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, cm	SW	1,589	19.06	1.11	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, mm	FAT	1,592	4.49	1.47	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, %	COOK ^b	1,598	32.53	4.07	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, N	SF ^c	1,514	65.07	24.62	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, cm ²	CA	1,592	12.34	1.64	12.25 (0.22)	12.68 (0.22)	11.95 (0.24)	12.26 (0.22)	12.18 (0.24)	13.23 (0.26)

^a For cross per breed abbreviations, see Table 1.

^b After two days of aging.

^c One day after cooking.

before and after cooking, done via heating up to a core temperature of 85 °C. For measurement of shear force (SF), a cylindrical piece of cooked chop with a diameter of 1.5 cm was punched out and stored at 4 °C. After 24 h, SF was measured with a Warner Bratzler device cutting the meat sample perpendicular to the muscle fibers. All other traits were calculated from the measured data.

Genotypes

Blood samples (20 mL EDTA whole blood) of every individual were taken during exsanguination directly after slaughter. At day of slaughter, an aliquot was taken for DNA extraction, and all retained samples were frozen at −20 °C. For paternity control, all samples were genotyped for 384 SNP via BeadXpress using the VeraCode Golden Gate Genotyping Assay (Illumina, Inc., San Diego, CA). SNPs were excluded if they had a minor allele frequency <3% and a call rate <95%. A total of 289 SNP, whereof 94, 83, 66, 31, and 15 were located on the chromosomes 1, 2, 3, 18 and 21, passed the data filtering. The chromosomes were chosen in order to focus on QTL for meat performance traits that have been reported in the literature (Hu et al., 2005).

To assign the sire to a given individual, parent–child errors (PCEs) were counted for each sire, i.e., the number of SNPs where individual and potential sire had different homozygous genotypes. All but one combination of one individual and all potential sires led to PCEs in the range of 40 to 60, whereas

the remaining combinations showed no or only few PCEs due to genotyping errors. The corresponding potential sire was assumed to be the true sire.

Furthermore, all 29 sires and all 237 purebred ML lambs (phenotyped for the traits) used in the experiment, as well as 61 purebred ML from different breeders were genotyped with the Illumina OvineSNP50 BeadChip (Illumina Inc.), containing 54,977 SNP. The same genotype filtering criteria were used as described above. Additional, SNPs were removed from the analysis if the linkage disequilibrium with another SNP on the array was >0.99. The SNP with a higher number of missing genotypes was removed.

The total number of SNPs on the targeted chromosomes was 16,534 (16k), whereof 5,202, 4,876, 4,427, 1,245, and 784 were located on the chromosomes 1, 2, 3, 18 and 21, respectively. The SNP alleles were coded as 0-allele and 1-allele.

The 16k SNP chip genotypes were imputed from 289 SNPs using family and linkage disequilibrium information. The paternal inherited alleles of the lambs were imputed from their 16K genotyped sires, whereas the maternal inherited alleles were imputed from a haplotype library, which was built up using the 16K genotypes from ML individuals. The imputation method is described in detail in Wellmann et al. (2013), and only essentials are given in the following. Naturally, imputation of the alleles inherited from the dams was less accurate since the dams had no pedigrees and were to a large extent not genotyped, and the breed has a high effective population size.

To improve imputation from the haplotype library, phantom parents were added to the pedigree. That is, the unknown dams of lambs were modeled to be the same for all lambs born at one farm because of the higher relationships between animals originating from the same farm. As a consequence, high-density genotyped sheep were favored to impute a particular lamb if they originated from the same herd as the lamb. This approach utilizes the common family structures in flocks and improved the imputation accuracy.

Variance Component Estimation

Variance components were estimated with linear mixed models. The model was as follows:

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

where y is the vector of observations, b is a vector of fixed effects including sex, cross, and the covariable weight at slaughter nested within cross, sl is a vector with random effects of day of slaughter (35 levels), a is a vector with the random additive genetic effects of the individuals, X , Z_{sl} , and Z_a are corresponding known design matrixes, and e denotes the residual. The covariance structure of the random animal effect was $\text{var}(a) = A * \sigma_a^2$, with A being the numerator relationship matrix and σ_a^2 the additive genetic variance. The variance of the random day of slaughter effect was $\text{var}(sl) = I * \sigma_{sl}^2$, where σ_{sl}^2 is the slaughter-day variance. The variance of the random residual effect was assumed to be heterogeneous across crosses, i.e., $\text{var}(e) = C'DC$, with C being a known design matrix that assigns each observation to a cross i , and $D = \text{Diag}(\sigma_{e_i}^2)$. The modeling of the heterogeneous residual variance led to cross-specific heritability, calculated as $h_i^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_{sl}^2 + \sigma_{e_i}^2)$. The median heritability was calculated as the median of the six cross-specific heritabilities.

Univariate analyses were performed to estimate the heritability of the traits. Phenotypic and genetic correlations between traits were estimated from a series of bivariate analyses using the same model. The statistical analyses were performed using ASReml software (Gilmour et al., 2009).

Targeted Association Analysis and Hypothesis Testing

Single-marker models were used to conduct association analysis on the selected chromosomes for the 16k SNPs with the R-package stats. The model

included the same fixed effects as for the variance component estimation. Instead of using the pedigree to model the population structure, the first 10 principal components (PC) of the gene content matrix of the dam alleles and 10 PC of the sire alleles were included if they were significant ($P < 0.05$). Ten PCs were fitted separately, to account for the structure of the cross design, where five sire breeds were crossed with an unrelated dam breed (ML) to produce half-sib families. Additionally, the breed effect was included.

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

RESULTS AND DISCUSSION

Cross Means, Genetic Variation, and Heritability Estimates

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

Heritability estimates for ADG are supported by several authors and for different breeds (Botkin et al., 1969; Bibé et al., 2002; Safari and Fogarty, 2003). A moderate h^2 of 0.20 was found for DRESS in this study, which corresponds to findings of

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

Trait ^a	σ_a^2	σ_{SD}^2	$\sigma_{e_i}^2$	h_i^2	h^2
			Min – Max	Min – Max	Median
ADG	611.63 (288.62)	1134.27 (229.95)	478.20 – 1004.02 (≤ 218.09)	0.22 – 0.28 (≤ 0.10)	0.23
DRESS	1.09 (0.45)	1.19 (0.32)	2.15 – 3.82 (≤ 0.56)	0.18 – 0.25 (≤ 0.10)	0.20
KFW	2444.95 (5.58)	6021.66 (3.99)	1661.40 – 5064.67 (≤ 5.25)	0.18 – 0.24 (≤ 0.10)	0.19
CarL	0.70 (0.28)	1.97 (0.50)	1.52 – 1.95 (≤ 0.36)	0.13 – 0.17 (≤ 0.07)	0.15
SW	0.19 (0.07)	0.09 (0.02)	0.25 – 0.50 (≤ 0.08)	0.25 – 0.36 (≤ 0.13)	0.33
FAT	0.32 (0.14)	0.18 (0.05)	0.65 – 1.07 (≤ 0.16)	0.17 – 0.28 (≤ 0.11)	0.22
COOK	1.04 (0.72)	1.73 (0.52)	11.46 – 16.50 (≤ 1.72)	0.05 – 0.07 (≤ 0.05)	0.07
SF	109.12 (46.83)	199.08 (51.84)	237.08 – 361.65 (≤ 64.70)	0.16 – 0.20 (≤ 0.08)	0.17
CA	0.72 (0.27)	0.22 (0.06)	0.73 – 1.35 (≤ 0.30)	0.31 – 0.43 (≤ 0.11)	0.36

^a For trait abbreviations, see Table 2.

other authors, although some report numerically higher results (Botkin et al., 1969; Bennett et al., 1991; Fogarty et al., 2003; Greeff et al., 2008). Differences in h^2 compared with those found in this study might be due to population differences, or also differences in measurement and calculation methods. Reported values of Botkin et al. (1969) for KFW are in agreement with the h^2 value found for KFW in this study. Botkin et al. (1969) reported $h^2 = 0.50$ for carcass length (measured from the anterior edge of the first rib to the anterior edge of the aitch bone). This estimate was distinctly higher than our estimates for CarL.

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

CA can be used as an indicator trait for muscling and represents a highly valued part of the carcass. The highest h^2 in our study was estimated for CA. Results are supported by the findings of other studies (Bennett et al., 1991; Fogarty et al., 2003; Greeff et al., 2008; Mortimer et al., 2010). Factors affecting difference in estimates may have a genetic basis, but might also be due to different measurement methods (direct measurement vs. estimation

of the muscle area by 80% of the product of eye muscle depth and length, measuring points, etc.).

Phenotypic and Genetic Correlations

Results of phenotypic and genetic correlations are shown in Table 4. The high SE values indicate that caution should be used when interpreting these results. Phenotypic correlations between most traits were low and often close to zero. Dawson et al. (2002) investigated phenotypic correlations of different carcass and MQ traits and generally found moderate correlations. Greeff et al. (2008) and Fogarty et al. (2003) both reported very low phenotypic correlations for dressing, eye muscle area, and two fat depth traits, which is supported by the findings of this study.

The genetic correlations were higher and in some cases showed a different sign compared with phenotypic correlations. Genetic correlations between ADG and DRESS were found to be positive. Bennett et al. (1991) found a higher correlation for postweaning gain and DRESS. Moderate to high positive genetic correlations of ADG with SW, SF, and FAT were observed. Genetically advantageous correlations were also found between ADG and SF in some muscles (Hopkins et al., 2007), between ADG and tenderness (Hopkins et al., 2006), and between ADG and reduced feed intake (Peeters et al., 1995). Traits that are expected to be muscling indicators (e.g., CA) and therefore should be positively correlated with ADG. Such traits showed only phenotypic correlations close to zero and low genetic correlations, supporting findings of Bibé et al. (2002).

As mentioned, in this study, SF and ADG were genetically moderately positive correlated as well as

Table 4. Genetic (upper diagonal) and phenotypic (lower diagonal) correlations of growth, carcass, and meat quality traits

Trait ^a	ADG	DRESS	KFW	CarL	SW	FAT	COOK	SF	CA
ADG		0.16	-0.03	0.10	0.36	0.36	0.14	0.50	0.11
DRESS	-0.13		-0.01	0.07	0.13	0.35	-0.62	0.16	0.19
KFW	-0.19	0.21		-0.18	-0.23	0.12	-0.13	-0.20	-0.25
CarL	-0.21	0.05	0.14		-0.26	0.27	-0.21	-0.13	-0.28
SW	0.03	0.46	0.04	-0.11		-0.04	0.01	0.27	0.26
FAT	0.02	0.29	0.15	-0.04	0.17		-0.47	0.09	-0.51
COOK	0.04	-0.01	-0.08	-0.02	-0.03	0.04		-0.49	-0.15
SF	0.07	-0.01	-0.11	-0.17	0.05	-0.16	-0.01		0.42
CA	0.08	0.38	-0.01	-0.13	0.35	-0.14	0.03	0.26	

Standard errors for the genetic correlations range from 0.24 to 0.39; standard errors for the phenotypic correlations range from 0.03 to 0.09.

^a For trait abbreviations, see Table 2.

SF with CA. Mortimer et al. (2010) reported moderate correlation for body weight at weaning, but low genetic correlations of SF to eye muscle depth. A moderate and unfavorable negative genetic correlation between COOK and SF was observed. Sensory studies with lamb meat have shown that acceptable palatability requires low SF values and an intramuscular fat (IMF) content of at least 5% (Hopkins et al., 2006). Furthermore, selection for increasing IMF is expected to have a favorable effect on SF (Hopkins et al., 2011). In this study, there was no clear tendency showing a relationship between SF and FAT (genetic correlation near zero). In literature, positive correlations between fat depths (Mortimer et al., 2010) and percentage of carcass fat (Lorentzen and Vangen, 2012) with IMF, and negative correlations between IMF and SF (Mortimer et al., 2010, 2014; Warner et al., 2010; Jacob and Pethick, 2014) are reported. Also Mortimer et al. (2010) reported a low genetic correlation between SF and FAT. McPhee et al. (2008) and Hopkins et al. (2007) found age, breed, and cross influencing IMF. The rather lean carcasses and the low age of lambs in this study might be influencing factors preventing more clear results with regards to the relationship between IMF and SF. The low slaughter age is considered desirable by slaughterers, retailers, and consumers. Breeding for leanness can indirectly affect MQ in an undesired way, so a certain fat content of carcasses and muscles needs to be preserved (Pethick et al., 2006; Wood et al., 2008). The challenge will be to breed animals with high lean meat, high IMF, and low SF (Jacob and Pethick, 2014; Pannier et al., 2014).

KFW showed a low but positive genetic correlation to FAT. Phenotypic correlations showed the same tendencies, indicating that animals with less kidney fat have less subcutaneous fat.

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

FAT showed moderately positive genetic correlations to ADG, DRESS, and CarL, and a negative correlation of -0.51 to CA. The correlation of FAT and DRESS is supported by a similar estimated phenotypic correlation. Greeff et al. (2008) investigated two different carcass fat depths and reported moderate genetic correlations to DRESS as well as low correlations of different sign to CA. The distinct differences are most likely caused by differences of measurement points, illustrating the problem of comparability.

Targeted Association Analysis

The results of the association analysis are shown in Table 5. For the traits SW, CA, COOK, and SF, experiment-wise significant SNPs could be detected. Although experiment-wise significant SNPs were found, no clear signal with consecutive significant SNPs could be detected. This might be because the significance is due to the alleles inherited from the Texel sire breed, and the number of lambs from this sire breed is only 150, thus representing the smallest F1 cross. For all experiment-wise significant associations, the Texel breed

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

Chr	Pos	SNP name	Trait	<i>P</i> value ^a		Sire breed abbreviations ^b						
				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	

For SNPs with experiment-wise significant sire effects (Test 2), the adjusted *P* values are shown for which of the sire breeds^b the SNP has significant effects. Significant breed-specific effects of the paternal allele are written in bold.

ML, Merinoland; IF, Ille de France; CH, Charollais; SK, German blackheaded mutton (Deutsches Schwarzköpfiges Fleischschaf); SU, Suffolk; TX, Texel.

^a See text for the corresponding null hypothesis.

origin alleles were significant ($P < 0.05$). Thus, the power to map these significant SNPs is mainly due to the Texel F1 cross, and the other F1 cross did not add much to the power. The breed-specific effect of the maternal alleles is not shown because it was not experiment-wise significant.

A comparison with literature reports (Hu et al. 2005) showed that most significant associations are located in well-known QTL regions. In the following part, only QTL regions belonging to the same trait complex were discussed. For the low heritable MQ traits, only one SNP on chromosome 2 was experiment-wise significant for COOK. On chromosome 2, QTL were also found for DRESS in the literature (Laville et al., 2004; Johnson et al., 2009). For the traits with the highest heritability estimates, CA and SW, the most experiment-wise significant SNPs were identified. For CA and SW, four and eight significant SNPs were found. One QTL on chromosome 2 was found for longissimus muscle width (Johnson et al., 2005), which supports our findings on chromosome 2 for SW. The myostatin (*MSTN*) gene is located on chromosome 2 between positions 126.318.147 and 126.324.913. *MSTN* is well known for muscular hypertrophy and was first reported by Clop et al. (2006). Haynes et al. (2013) reported that lambs homozygous for the *MSTN* g+6723G>A mutation have changes in carcass characteristics (dressing and total lean), organ weights, and muscle fiber number. The Texel *MSTN* was not part of the

genotypic dataset. There was no significant association in the *MSTN* region.

On chromosome 18, no significant associations were found. A possible explanation can be that inaccurate imputation results can lead to false-negative results. However, there is no possibility to investigate the effect of imputation accuracy on the association results because the F1-crossbred lambs were not genotyped with the Illumina OvineSNP50 BeadChip.

In this study, chromosomes for the targeted association study were chosen in order to focus on QTL for meat performance traits that have been reported in the literature (Hu et al., 2005).

Confirmatory results were assumed by the targeted association analysis. However, only confirmatory results were found for chromosome 2. If genome-wide association studies were applied to the data, we assume that no significant results were expected after multiple testing.

Implementation in Breeding Programs

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

Single heritability estimates are not shown for the different F1 crosses because the number of sires within crosses is low. Instead of showing cross-specific heritability estimates, the medians and the range of the heritability estimates are listed in Table 3. If breeding values are to be estimated, the heritability estimates and genetic correlations reported in this study should not be used due to their high SE. In addition, if both purebred ML data and F1 crossbred data is to be used for routine genetic evaluations, more reliable genetic parameters must be estimated using a larger, better structured data set. That means more F1 crossbred individuals are needed to reduce the high standard errors for the genetic parameter estimates, and more sires are required to lead to more reliable heritability estimates.

In some breeding programs for ML and for some of the tested sire lines, ADG, CA, FAT, and SW are already implemented. Results of this study support this choice of traits because of the moderate heritability estimates and the genetic and phenotypic correlations found. The integration of muscling and fat parameters is particularly important to control leanness. For further improvement of MQ and palatability traits, inclusion of SF and COOK in a breeding program can be recommended.

In general, growth and carcass traits are relatively easy to measure (so called easy to measure traits) at acceptable costs. Therefore, they are often already implemented in breeding programs. For MQ traits, data recording is cost-prohibitive and time consuming (Simm et al., 2009; Mortimer et al., 2010); these traits are classical “hard to measure” traits. Because lambs are often paid by weight, and not by MQ or palatability, high phenotyping costs are the main barrier of inclusion of quality traits to breeding programs (Simm et al., 2009). Hayes et al. (2013) recommended genomic selection for the improvement of traits that are too expensive to measure routinely in selection candidates, and genomic selection has been introduced in some sheep breeding schemes (Daetwyler et al., 2012). Genomic selection, however, needs a large reference population with genotyped and phenotyped individuals in order to reliably predict breeding values. Establishing such reference populations is challenging but is probably the most efficient way to improve MQ traits, as shown by Daetwyler et al. (2012).

The phenotypic data collected in this study, supplemented by genomic data, may serve as an initial reference population, but has to be augmented by additional data sets.

CONCLUSION

For growth and carcass traits, it is beneficial to produce F1 crossbred animals compared with purebred ML lambs. The heritability estimates show that it is generally possible to achieve selection response for the traits included in this study. From the chromosome-wide association results, it seems that the method used to model SNP effects is important due to different linkage disequilibrium structures between SNP and causal mutations in different crosses.

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

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