Quantitative Genetic and Targeted Association Analyses of Growth, Carcass and Meat Quality Traits in German Merinoland and Merinoland-Cross Lambs[1]

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[2]K.F.S. was supported by the *H. Wilhelm Schaumann Stiftung*, Hamburg, Germany.

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 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

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

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

INTRODUCTION

The Merinoland (ML) sheep is the most common breed in Southern Germany due to its high-quality wool, high fertility, robustness, and its motility. To improve meat quality (MQ), ML ewes are frequently crossed with a sire from a meat type breed. Although meat quality (MQ) is often not included in the direct payment scheme for lamb, there is a growing interest in use of MQ traits in breeding programmes. This is a consequence of consumer demand for improved MQ (Pethick et al., 2011, van der Werf et al., 2010) and the desire to maintain or increase lamb market shares. The most important factors affecting MQ traits include genetics, and production and processing environment (Hopkins et al. 2011). Compared to 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 other production 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 traits and other traits of economic importance (Mortimer et al., 2014; Simm et al., 2009) 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 F1 lambs with improved meat quality. 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 growth, carcass and meat quality traits on selected chromosomes were conducted (Hu et al. 2016).

The objectives of the present paper 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 for growth, carcass and MQ traits on selected chromosomes. Potential possibilities to implement findings in current breeding systems are also discussed.

MATERIAL AND METHODS

The research protocol was approved by the German Ethical Commission of Animal Welfare of the Provincial Government of Baden-Wuerttemberg. 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 1599 purebred ML and F1-crossbred lambs (meat type sire x ML ewe). As sires, rams of Charollais, Ile de France, German black-headed mutton sheep (Deutsches Schwarzköpfiges Fleischschaf), Suffolk, and Texel 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

eight weeks of age). Fattening was conducted on a single farm in order to standardize environmental conditions. Feeding rations consisted of 200-300 g hay per animal and concentrate *ad libitum*. Lambs were slaughtered at 39-45 kg. The final decision for slaughtering was made by manual scanning. Animals were slaughtered at a commercial abattoir within 35 days and were fasted prior to slaughter. 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 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 post mortem (p.m.). After measurements, chops of the 10^{th} and 11^{th} 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. Subcutaneous fat thickness was calculated as the mean depth of fat cover at four measuring points (one and three cm left and right of the spine at the 11^{th} rib). Cooking loss was defined as the weight difference of the boned chop 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 hours, 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 (20ml 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, USA). SNPs were excluded if they had a minor allele frequency <3%, and a call rate <95%. A total of 289 SNP, 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. 2016).

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 359 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., CA, USA), 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 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. For imputation the

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

Variance component estimation

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

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

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. $\text{var}(e) = X'DX$, with *X* being a known design matrix that assigns each observation to a cross *i*, and $D = Diag\{\sigma_{e_i}^2\}$. The modelling of the heterogeneous residual variance led to cross-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 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, but assuming the residual variance to be homogeneous across traits. The statistical analyses were performed using ASReml software (Gilmour et al., 2009).

Targeted association analysis

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-value < 0.05). Additionally, the breed effect, breed specific effects of the paternal inherited allele, and an effect of the maternal inherited allele were included.

Hypothesis testing

For analysing 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, three 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 and third tests, breed specific effects of the paternal and maternal 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 which 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 and the range of heritability across crosses as well as the median of the heritability estimates are shown in Table 3. The traits ADG, DRESS, KFW, CarL, SW, FAT, SF and CA showed moderate (0.15 to 0.36) heritability estimates in this study.

Heritability estimates for ADG are supported by several authors and for different breeds (Bibé et al., 2002; Botkin et al., 1969; Safari and Fogarty, 2003). A moderate h^2 of 0.20 was found for DRESS in the present study, which corresponds to findings of other authors, although some report numerically higher results (Bennett et al., 1991; Botkin et al., 1969; Fogarty et al., 2003; Greeff et al., 2008). Differences in h^2 compared to those found in the present 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 the present 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 the present study was 0.22 which is in agreement with the results of e.g. 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 the present study were low to moderate, genetic improvement would be possible with implementation of routine performance testing. For SF, a low heritability was estimated which is in contrast with the studies of Botkin et al., (1969), Hopkins et al., (2011) and Mortimer et al. (2010) who reported moderate heritability of SF. The differences to the present study might be explained by differences in genetics, carcass weights, and aging time.

Cutlet area can be used as an indicator trait for muscling and represents a highly valued part of the carcass. For CA the highest h^2 was estimated. 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. The weakness of the data structure is the limited number of sires for each cross (Table 1).

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 the present study.

The genetic correlations were higher, and in some cases showed a different sign compared to phenotypic correlations. Genetic correlations between ADG and DRESS were found to be positive. Bennett et al. (1991) found a higher correlation for post weaning gain and DRESS. Moderate to high positive genetic correlations of ADG with CarE, 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 the current study SF and ADG were genetically moderately positive correlated as well as 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 unfavourable negative genetic correlation between COOK and SF was observed. Sensory studies with lamb meat have shown that acceptable palatability requires low shear force 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 favourable effect on shear force (Hopkins et al. 2011). In the present study there was no clear tendency showing a relationship between SF and FAT (genetic correlation near zero). In literature positive correlations between fat depths (e.g. Mortimer et al., 2010) and percentage of carcass fat (Lorentzen and Vangen, 2012) with IMF, and negative correlations between IMF and SF (Jacob and Pethick, 2014; Mortimer et al., 2010, 2014; Warner et al., 2010) 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 the current 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).

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

Cooking loss 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.

Subcutaneous fat thickness 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. Concerning CarE, it is striking that this trait is genetically negatively correlated with CarL but positively with SW and CA (phenotypic correlations denote the same tendency), indicating that shorter but broader and more muscular carcasses are evaluated better.

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. A comparison with literature reports (Hu et al. 2016) showed that most significant associations are located in well-known QTL regions. 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. 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 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.

Implementation in breeding programmes

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 does not hold always 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 of the heritability estimates are listed in Table 3. If breeding values are to be estimated in a multivariate setting, the 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.

In some breeding programmes for ML and for some of the tested sire lines ADG, CA, FAT and SW are already implemented. Results of the current 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 programmes. For MQ traits, data recording is cost-prohibitive and time consuming (Mortimer et al., 2010; Simm et al., 2009); 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 programmes (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 (e.g. 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 the present 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 cross bred animals compared to 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. The data collected in the present study might serve as an initial reference population, which has to be augmented by additional data points and, of course, by genomic data.

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

Table 2. Tait, trait abbreviation, unit, number of observations (n), mean, standard deviation (sd), and means of the crosses (standard error in 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	[cm²]	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)

[1] after two days of aging

[2] one day after cooking

[3] For cross/breed abbreviations see Table 1

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

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

[1] For trait abbreviations see Table 2

Table 5. Significant SNP trait associations with chromosome (Chr), position in bp/10^6 (Pos), SNP name, and p-values for the tests. For SNPs with experiment-wise significant sire effects (Test 2) the adjusted *p*-values are shown for which of the sire breeds[1] the SNP has significant effects

				p-value[1]		Sire breed abbreviations[2]					
Chr	Pos	SNP name	Trait	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**

[1] See text for the corresponding null hypothesis.

[2] ML Merinoland, IF Ille de France, CH Charollais, SK German Blackheaded Mutton (Deutsches Schwarzköpfiges Fleischschaf), SU Suffolk, TX Texel

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

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