Institut für Nutztierwissenschaften, Universität Hohenheim
Fachgebiet Tierzüchtung und Genetik
Prof. Dr. Jörn Bennewitz

Phenotypic and genetic analysis of meat production traits in German Merinoland purebred and crossbred lambs

DISSERTATION

zur Erlangung des Doktorgrades
der Agrarwissenschaften
vorgelegt
der Fakultät Agrarwissenschaften
von

KATJA FRANZISKA SCHILLER
M. Sc. (Agr. Biol.)
aus Freiburg im Breisgau

Hohenheim, 2016

This doctoral thesis was prepared with generous support by the
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ABBREVIATIONS

BCFA	branched chain fatty acids (Me8:0, Me9:0 and Et8:0)
BLUP	best linear unbiased prediction
BHM	German black-headed mutton sheep (purebred)
CH	Charollais x Merinolandschaf- F1-crossbred
EBV	estimated breeding value
GWAS	genome-wide association study
IF	Ile de France x Merinolandschaf- F1- crossbred
MAS	Marker-assisted association study
MQ	meat quality
ML	Merinoland
QTL	Quantitative trait loci
SK	BHM x Merinolandschaf- F1- crossbred
SNP	Single Nucleotide Polymorphism
SU	Suffolk x Merinolandschaf- F1- crossbred
TX	Texel x Merinolandschaf- F1- crossbred

GENERAL SUMMARY (ENGLISH)

The overall aims of the present thesis were to investigate various meat quality (MQ) traits including branched chain fatty acids and their correlation to sensory traits and to perform DNA-based and quantitative genetic analysis for growth, carcass and MQ traits using the data set with about 1600 phenotyped lambs. The lambs were Merinoland (ML) lambs and lambs of five crossbreds of meat type sire breeds and Merinoland ewes. The crosses were CH (Charollais × ML), IF (Ile de France × ML), SK (German black-headed mutton sheep (BHM) × ML), SU (Suffolk × ML) and TX (Texel × ML).

In **chapter one**, growth curves, daily gain and feed conversion of ML sheep and the five ML crosses were investigated via mixed linear models. Linear and Gompertz models were fitted and the quality of fit was assessed. Differences in the model parameters were detected between crosses, genders and birth types. According to the parameters, coefficient of determination and mean square error, the Gompertz provided a better fit compared to the linear model. Additionally feed conversion rate and daily gain were observed, with only the crosses IF and TX showing significant superiority in these traits compared to purebred ML. For practical reasons, however, the common trait daily gain can be recommended to use for breeding purpose, despite if altering the shape of a growth curve is attractive because of e.g. possible lower maintenance costs for a flock.

In **chapter two**, lamb meat and fat of the crosses and ML was investigated for concentration of three branched chain fatty acids (4-Me8:0, 4-ET8:0 and 4-Me9:0) and its correlation to sensory abnormality. Differences between crosses and between sexes were determined, but no significant correlations to sensory traits were found.

In chapters three to five, genetic background and genetic parameters were investigated and a chromosome-wide association study imputing SNP panels was undertaken. Furthermore, the possibilities of implementation of this data to improve breeding programs were discussed. **Chapter three** focuses on genetic parameters of growth, carcass and MQ traits in purebred

ML and crossbred lambs. A series of analyses for twelve traits were performed and heritabilities and genetic correlations were estimated using general linear mixed models. Several significant correlations and low to moderate heritabilities were found, indicating that selection on these traits is possible. In **chapter four**, a targeted association mapping was undertaken with about 330 SNPs using two different statistical models, one with estimation of SNP effects across all crosses and the other with SNP effects per cross. The investigated traits were growth, carcass and MQ traits. In this connection, several weak significant SNPs were revealed. In **chapter five**, F1 lambs were genotyped on selected chromosomes with a very low SNP panel and imputed via Illumina Ovine 50k SNP BeadChip genotypes from the sires and purebred ML. These were included in a haplotype bibliography before. Furthermore, chromosome-wise association analyses using single marker mixed linear models were performed for MQ, carcass, and growth traits. This was done using the imputed genotypes and the trait phenotypes. Several significant associations were detected, e.g. for the traits shoulder width and cutlet area, and these were discussed with regard to other literature reports as well as their use for practical breeding purpose.

The thesis ends with a general discussion.

GENERAL SUMMARY (DEUTSCH)

Die übergeordneten Ziele der vorliegenden Dissertation waren verschiedene Fleisch- und Fleischqualitätsmerkmale inklusive verzweigtkettiger Fettsäuren und deren Korrelation zu sensorischen Merkmalen zu untersuchen und DNA-basierte und quantitative genetische Analysen zu Wachstums-, Schlachtkörper und Fleischqualitätsmerkmalen anhand eines Datensets mit rund 1600 Lämmern durchzuführen. Bei den Lämmern handelte es sich um Merinoland (ML) Lämmer und Lämmer fünf verschiedener Kreuzungen von Fleischschafrassen mit ML Mutterschafen. Die Kreuzungen wurden wie folgt bezeichnet: CH (Charollais × ML), IF (Ile de France × ML), SK (Deutsches Schwarzköpfiges Fleischschaf × ML), SU (Suffolk × ML) und TX (Texel × ML).

In **Kapitel eins** wurden Wachstumskurven, tägliche Zunahmen und Futterverwertung von ML und den fünf ML-Kreuzungen mittels gemischt-linearer Modelle untersucht. Ein lineares und ein Gompertz-Modell wurden angepasst und die Qualität der Anpassung beurteilt. Zwischen den Kreuzungen, Geschlechtern und Geburtstypen wurden Unterschiede in den Modellparametern festgestellt. Gemäß dem Bestimmtheitsmaß und der mittleren quadratischen Abweichung, lieferte das Gompertz-Modell die bessere Anpassung im Vergleich zum linearen Modell. Zusätzlich wurde die Futterverwertung und die tägliche Zunahme betrachtet, wobei nur die Kreuzungen IF und TX verglichen mit den reinrassigen ML eine signifikante Überlegenheit zeigten. Aus praktischen Gründen kann das gebräuchliche Merkmal tägliche Zunahme zur Verwendung für Züchtungszwecke empfohlen werden, obwohl das Umgestalten der Form der Wachstumskurve reizvoll ist, da z.B. geringere Erhaltungskosten für eine Herde möglich wären.

In **Kapitel zwei** wurde Lammfleisch und –fett der Kreuzungen und ML auf Konzentrationen von drei verzweigtkettigen Fettsäuren (4-Me8:0, 4-ET8:0 und 4-Me9:0) und deren Korrelationen zu sensorischen Abnormitäten untersucht. Unterschiede zwischen den

Kreuzungen und den Geschlechtern wurden ermittelt, es konnten aber keine Korrelationen zu sensorischen Merkmalen festgestellt werden.

In den Kapiteln drei bis fünf wurden der genetische Hintergrund und genetische Parameter untersucht sowie eine chromosomenweite Assoziationsstudie mit imputierten SNP Panels durchgeführt. Darüber hinaus wurden die Möglichkeiten diskutiert, ob die Implementierung dieser Daten zur Verbesserung von Zuchtprogrammen beitragen könnte. Das **Kapitel drei** stellt genetische Parameter von Wachstums-, Schlachtkörper-, und Fleischqualitätsmerkmalen bei ML Reinzucht- und Kreuzungslämmern in den Fokus. Dazu wurde eine Serie von Analysen für zwölf Merkmale durchgeführt und Heritabilitäten sowie genetische Korrelationen mittels verallgemeinerten linearen gemischten Modellen geschätzt. Es wurden einige signifikante Korrelationen und gering bis moderat erbliche Heritabilitäten gefunden, welche darauf hinweisen, dass Selektion auf diese Merkmale möglich ist. In **Kapitel vier** wurde eine Assoziationskartierung mit zwei verschiedenen Modellen durchgeführt, wobei die SNP-Effekte über alle Kreuzungen hinweg bzw. für jede Kreuzung einzeln geschätzt wurden. Bei den untersuchten Merkmalen handelte es sich um verschiedene Wachstums-, Schlachtkörper- und Fleischqualitätsmerkmale. Im Zuge der Analysen wurden mehrere schwach signifikante SNPs entdeckt. In **Kapitel fünf** wurden Lämmer anhand ausgewählter Chromosomen mittels eines SNP-Panel sehr geringer Dichte genotypisiert und mittels Illumina Ovine 50k SNP BeadChip-Genotypen ihrer Vatertiere und ML-Reinzuchttieren imputiert. Diese wurden zuvor in eine Haplotypenbibliothek einbezogen. Ferner wurde eine chromosomenweite Assoziationsanalyse für Fleischqualitäts-, Schlachtkörper- und Wachstumsmerkmale durchgeführt, hierbei wurden gemischte lineare Modelle genutzt, die für jeden SNP separat angepasst wurden. Es konnten mehrere signifikante Assoziationen ausfindig gemacht werden, so z.B. für die Merkmale Schulterbreite und Kotelettfläche, welche anschließend in Hinsicht auf Berichte aus der Literatur aber auch auf ihren praktischen Nutzen hin diskutiert wurden.

Die Thesis endet mit einer allgemeinen Diskussion.

GENERAL INTRODUCTION

The Merinoland (ML) is one of various breeds, widespread in Germany and often favored because of their robustness, aseasonal reproduction, good fertility and conformation. In whole of Germany, and also in Baden-Württemberg, ML are the most common breed with approximately 30% of the overall count (VDL, 2005). This breed was developed by crossing Merino sheep imported from Spain with local breeds with the intent of breeding robust sheep to deliver enhanced wool quality (Sambraus, 2011). Currently the routine breeding goal for ML comprises traits for reproduction, growth and meat. Animal performance testing is done on purebred ML sheep on station as well as on farms, but most traits are only recorded for males. The collected phenotypic records are used for estimation of BLUP breeding values (EBV; for ML available in Germany since 2014; Landwirtschaftskammer Niedersachsen, 2014). Additional systematic breeding activities within the ML breed, like e.g. elite matings or even genomic analysis, are currently missing and breeding technologies like artificial insemination are only rarely used. In order to improve growth performance of fattening lambs, and further profit of the proven ML genetics, F1-crossbreeding obtained from mating ML ewes with meat-type terminal sire breeds are frequently performed. The choice of the sire line is of fundamental importance for optimizing F1- crossing systems to provide best possible results. A large crossbred-trial was undertaken by Henseler (2013) with ML lambs and lambs of five ML crosses (ML crossed with Charollais, Ile de France, BHM, Suffolk and Texel). Henseler (2013) investigated crossbred differences compared to purebred ML in growth, carcass, meat and sensory traits and built a dataset with 1600 individuals.

The overall aim of the present dissertation was to investigate various meat and meat quality (MQ) traits including branched chain fatty acids and their correlation to sensory traits as well as to perform DNA-based and quantitative genetic analysis for growth, carcass and MQ traits using the dataset of Henseler (2013).

Evidence indicates that sheep breeds differ in growth curves and that altering of growth curves is possible (Lambe et al., 2006). For meat sheep e.g. a fast but limited growth close to the aimed slaughter weight is desired. Therefore, in **chapter one**, growth curves, daily gain and feed conversion of ML and the mentioned five crosses were investigated via mixed linear models. Linear and Gompertz models were fitted and the quality of fit was assessed. Differences in the model parameters were detected and are discussed.

MQ in all its different aspects like e.g. meat color, water binding capacity, nutritional value and content, food security (Hopkins & Geesink, 2009) but also sensory quality including taste, smell or tenderness is affected by various factors. The most important are genetics, production and processing environment (Hopkins et al., 2011). In contrast to growth and carcass traits, MQ-and sensory quality-traits are more difficult and expensive to measure. This has hindered performance testing and implementation of these traits in breeding programs. Furthermore, often MQ is not included in the direct payment scheme for lamb, though an abnormal smelling food product might be a negative experience for customers. It is sometimes argued that the typical lamb meat taste is caused by some fatty acids accumulating in the fat. Therefore, in **chapter two** lamb meat and fat of the crosses and ML was investigated for concentration of three branched chain fatty acids (4-Me8:0, 4-Et8:0 and 4-Me9:0). The correlation of the concentration of the fatty acids to sensory traits was studied.

Compared to other livestock species, only few studies have analyzed MQ traits and their genetic background. Therefore, **chapter three** focuses on genetic parameters, especially of carcass and MQ traits in purebred ML and crossbred lambs. A series of analyses for twelve traits was done and heritabilities and genetic correlations were estimated with general linear mixed models. In **chapter four**, a targeted association mapping was undertaken using a very low density SNP panel with two different models: one with estimation of SNP effects across all crosses and the other with SNP effects per cross. The investigated traits were growth, carcass and MQ traits. In **chapter five**, the very low SNP panel and the Illumina Ovine 50k SNP BeadChip genotypes from the sires and purebred ML included in a haplotype bibliography

were used to impute genotypes on selected chromosomes into the F1 lambs. Furthermore, chromosome wide association analysis using single marker mixed linear models were performed for MQ carcass and growth traits using these impute genotypes and the trait phenotypes.

The thesis ends with a general discussion.

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CHAPTER ONE

Analysis of growth and feed conversion in purebred and crossbred German Merinolandschaf lambs

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Abstract In this study, ewes of “Merinolandschaf”, a breed widespread in southern Germany, were crossed with rams of five meat breed types (Ile de France, Charollais, German black-headed mutton sheep (Deutsches Schwarzköpfiges Fleischschaf), Suffolk, Texel) and Merinolandschaf rams. The resulting lambs (179 individuals) were fattened intensively from 55.3 days and body weight of 20.4 kg until 121.7 days and a weight of 40.9 kg. While fattening, feed intake was recorded and lambs were weighed weekly. Ile de France × Merinolandschaf and Texel × Merinolandschaf seem to be of greatest economic interest for intensive fattening because they showed the best feed conversion rate and energetic feed conversion rate. Only these crosses were significantly superior compared to purebred Merinolandschaf in feed conversion rate and also in daily body weight gain during the fattening period. Except Charollais × Merinolandschaf, all crosses showed at least a tendency of improvement in all three traits compared to Merinolandschaf, although this is not always significant. This underlines the advantage of one-way cross-breeding for efficiently producing lamb meat. The growth was modelled with a linear model and the Gompertz model. The results showed that both models fit the data well, although the average R^2 was slightly higher and the average mean square error was slightly lower for the Gompertz model. In addition, the use of the Gompertz model provided some interesting biological insights concerning the growth of lambs and differences between the crosses, even though the lambs were slaughtered before reaching their mature body weight.

1 Introduction

The “Merinolandschaf” (ML) is a typical widespread breed of sheep in southern Germany. Sheep of this breed are completely white, polled, with a wooled forehead and broad hanging ears. Body weight (BW) for adult is 80–90 kg for ewes and 120–140 kg for rams. These sheep have aseasonal reproduction and good fertility. This breed was originally developed by crossing Merino sheep imported from Spain with local breeds with the intent of breeding robust sheep able to travel the summer to winter pastures routes but also which deliver improved wool quality (Sambraus, 2011).

However, due to the currently high costs for shearing and low wool prices, lamb meat production is an important source of income from sheep (Strittmatter, 2005). In order to improve the growth performance of fattening lambs, ML dams are frequently mated with a meat breed type sire to obtain F1 hybrid progeny. Naturally, the choice of the sire

line is of fundamental importance for optimising this oneway crossing system. In a previous study, five sire breeds were tested for their ability to produce high-quality F1 hybrid lambs (Henseler et al., 2014a, b). However, the important trait feed conversion rate was not considered in that study.

Growth can be described by a single parameter, e.g. daily body weight gain (DG). However, the trajectory of growth over the entire lifetime might be of interest as well. Different models have been used from different authors for modelling growth of sheep. As an example, Daskiran et al. (2010) used Gompertz, Bertalanffy, Brody, logistic and negative exponential models, and Lambe et al. (2006) used Gompertz, Richards, exponential and logistic models. Growth models are usually able to summarise the pattern of growth in two to four parameters. Lambe et al. (2006) investigated several growth models to describe the growth of lambs. Among the models tested, the Gompertz model fit the data best. Additionally these authors have shown genetic variability within and between breeds and discussed the use of this variability for breeding purposes.

The aim of the present study was to investigate the ability of six sire breeds to produce F1 hybrid lambs with ML. The two important traits, DG and feed conversion rate (FCR), were

considered. A further aim was to fit growth curves and to compare growth model parameters among the F1 hybrids.

2 Material and Methods

2.1 Animals, feed and management

The experiment took place at the Oberer Lindenhof experimental station (moderate climate, 600 m above sea level, annual rainfall 752 mm) of the University of Hohenheim, Germany. In total 134 ML ewes were crossed with rams of six breeds: Charollais, Ile de France, German black-headed mutton sheep (Deutsches Schwarzköpfiges Fleischschaf), Suffolk, Texel and ML. Each sire breed was represented by one ram. The ram was progeny tested in an earlier study with around 50 progeny produced with ML ewes (Henseler et al., 2014a). The average progeny yield for DG and other growth and meat traits of the selected rams was close to the mean of the respective breed. Hence, it is assumed that the selected rams are a representative sample of their breeds. Unfortunately it was not possible to include multiple rams per sire breed because there were no additional progeny-tested sires available.

The number of lambs as well as number of singletons and males per cross is shown in Table 1. Lambs were born in July and August 2012. During the fattening period, lambs were weighed weekly. Lambs were fed with hay (daily 200–300 g animal $^{-1}$, 7 MJ ME (metabolisable energy) and 63 g kg $^{-1}$ CP (crude protein)) and concentrate (11 MJ ME and 188 g kg $^{-1}$ CP) ad libitum. Total feed intake of hay and of concentrate, and the sum of both, were determined. Due to limited space, six lambs from each F1 hybrid were housed in individual pens and the remaining lambs were housed in groups of 17 to 30 individuals. Lambs were slaughtered when reaching a finishing weight of approximately 41 kg BW.

2.2 Statistical analysis

Daily body weight gain over the lifetime (DG_L) and during the fattening period (DG_F) were recorded for each lamb and were analysed using the following statistical model:

$$y_{ijkml} = \mu + SB_j + BT_k + SEX_l + dam_m + e_{ijklm} \quad (1)$$

where y_{ijkml} is the trait record of lamb *i* (kg), SB*j* is the fixed effect of sire breed j , BT_k and SEX_l are the fixed effects of birth type *k* (single or twin) and of sex *l*, respectively, and dam_m is the random effect of the dam. The dams were assumed to be unrelated. The model was fitted using the MIXED procedure of SAS (9.2, SAS Institute, Inc., Cary, NC, USA). The feed conversion rate traits (FCR, kg dry matter (DM) feed intake kg^{-1} DG_F) and energetic FCR (eFCR, MJ kg^{-1} DG_F) were analysed as follows. The means of the F1 hybrid were calculated from the corresponding group means and the variances were calculated from the trait values of the six lambs housed in the individual pens. The standard errors of the group means were approximated using these two parameters and the number of lambs in the groups. This way of estimating the standard errors was chosen because only six lambs per cross could be housed in individual pens and the remaining lambs had to be housed in groups. Differences between the means of the F1 hybrids were tested for significance using the Welch test. Two types of growth curves were fitted to the weight records. The first one is the Gompertz model, for which the notation of Lambe et al. (2006) was used.

$$y(t) = A \exp\left[-\exp\left(B e \frac{C-t}{A}\right)\right] \quad (2)$$

where *t* is the age in days when the weight *y* (kg) was recorded, *A* is the estimated mature body weight (kg), *B* is the maximum DG (kg), *C* is the age at maximum DG_F (days) and *e* denotes the Euler number. The second model is a linear model,

$$y(t) = INT + bt \quad (3)$$

where *b* is the average DG (kg) and INT is the birth weight (kg). The growth curves were fitted to the data of each individual using the NLIN procedure of SAS version 9.2. This resulted in three parameter estimates and their standard errors for the Gompertz model and two for the linear model for each lamb. The fit of the two models was analysed by calculating the mean square errors and the R^2 values for each lamb and then averaged over all lambs. The parameter *(A, B, C,* INT and *b*) estimates were analysed using model (1), but using the

reciprocal of the error variance of the estimated parameters (i.e. standard error squared) as weighting factors to ensure that individuals with more repeated measurements and hence lower standard errors where weighted stronger.

3 Results

3.1 Descriptive statistics of observations

The average birth weights are shown in Table 1. TX (Texel × ML) showed the highest birth weight, and IF (Ile de France × ML) and SK (German black-headed mutton sheep × ML) the lowest. Weaning BW, weaning age, BW and age at finishing are shown in Table 1. Weaning BW was at a similar level for all crosses. The same holds true for finishing BW. More variability can be observed in the age at finishing. The highest age was observed for CH (Charollais × ML), ML and SU (Suffolk × ML) and the lowest for IF, with a difference between them of around 15 days.

3.2 Feed conversion and growth performance

The feed intake means are shown in Table 2. They varied significantly across the crosses for all three components considered (hay, concentrate and total). The highest (lowest) total feed consumption was observed for IF (ML). The feed conversion rates are shown in Table 3. Both FCR and eFCR varied significantly across the crosses. The lowest FCR was determined for IF and TX (4.5) and the highest for CH (5.5). The eFCR was found to be the lowest for TX (50.7) but without a significant difference from IF; the highest was found for CH (63.2). The least square means of DG_F and DG_L are shown in Table 3. DG_F is consistently above DG_L, except for CH. The daily body weight gain during the fattening period and DG_L varied significantly across the crosses. The lowest values were observed for CH and ML and the highest for IF, though for all three crosses, differences from other crosses are sometimes not significant for DG_F and DG_L.

3.3 Growth models

The estimated parameters of the Gompertz model are shown in Table 4. Parameter *A* (estimated mature body weight) was more or less constant for all crosses. Only for CH is the estimated mature body weight significantly lower compared to the other crosses. Parameter *B* (maximum daily gain) and *C* (age at maximum daily gain) showed more variability between the six crosses. The numerically highest *B* value was estimated for IF and the lowest for ML. Lowest *C* value was observed for CH and highest for SU. Males and twins (Table 4) compared to females and singletons respectively, showed higher estimated mature body weight. The same holds true for parameter *C*. Maximum daily gain is higher for males and for singletons. The Gompertz model fit the data well, as indicated by the high average R^2 value of 0.994 and low average MSE of 0.789.

The results of parameters of the linear model (INT and *b*) are shown in Table 5. Both parameters varied significantly across the crosses. The lowest birth weight (parameter INT) was estimated for SU and SK and the highest for CH and TX. The highest average daily gain (parameter *b*) was estimated for IF and the lowest for ML. Males and twins in particular showed lower estimated birth weights (Table 5). Males also showed a higher estimated DG; the same holds true for singletons. The goodness of fit of the model was also high with an average R^2 value of 0.987 and average MSE of 1.521. However, the fit was slightly poorer than the fit of the Gompertz model, which becomes especially obvious when comparing the MSE of both models.

4 Discussion

First of all, the weakness of the experimental design has to be acknowledged. It was not possible to include more rams per sire breed because there were no additional progeny tested sires available. In addition, it would have been better to house all lambs in individual pens, which was however not possible due to the limited test capacity on the research farm.

4.1 Describing parameters at birth, weaning and finishing

The low range of BW and age at weaning across the crosses (Table 1) indicate that there were no big differences in growth before the fattening period started. Also, the finishing weight, which is highly dependent on the decisions of the producer or responsible scientist, did not show much variance. In contrast, differences were found in finishing age, which indicates an influence of cross on the age of lamb reaching slaughter weight.

4.2 Feed conversion and growth performance

There are significant differences in feed intake (Table 2). Higher feed intake indicates a higher potential of nutrient intake. This might be an advantage under extensive conditions because a lower energy content of the feed can be compensated for by a higher amount of consumed feed. IF and TX seem to have the highest growth potential because they showed highest DG_F and DGL. The daily body weight gain during the fattening period of purebred male individuals of meat breeds and ML under similar conditions were reported to be higher in other studies than found in this study (Table 3). Engelhart and Eckl (2012), who considered only purebred male lambs, reported a DG_F of 362 g day^{-1} for Texel, 438 g day^{-1} for ML, 445 g day^{-1} for German black-headed mutton sheep, 458 g day^{-1} for Ile de France, and 468 g day^{-1} Suffolk. Bildungs- und Wissenszentrum Aulendorf (2005) reported a DG_F of 360 g day^{-1} for ML and CH, 359 g $day^{-1}$for TX and 409 g day^{-1} for SU.

Depending on the diet and breed, different FCR for sheep have been reported in the literature, e.g. 8.8 to 17.8 kg feed per kg bodyweight gain for different selection lines of Merino and different diets (6.3 to 9.2 MJ ME kg^{-1} DM) (Doyle et al., 2011). Fahmy et al. (1992) determined FCR of 4.99 to 5.76 kg DM kg^{-1} weight gain for different breeds and crosses including Booroola Merino and Suffolk with feeds of different protein qualities. Engelhart and Eckl (2012) tested purebred male individuals of several meat breed types. The eFCR varied between means of 30.9 for Texel to 32.9 for German black-headed mutton sheep. These figures are below those values found in this study (Table 3), probably because Engelhart and Eckl (2012) considered only purebred male lambs which were expected to be above the mean of a population.

4.3 Growth models

As can be seen from the MSE and R^2, the fit of the Gompertz model was improved compared to the linear model, although both fit the data well. In contrast, Daskiran et al. (2010) reported the best R^2 results for logistic model. Gbangboche et al. (2008) determined Brody to be the best fitting model, but reported a lower R^2 for all models than in this study and also used a slightly different Gompertz model. Topal et al. (2004) determined a better fit of the Gompertz model compared to Brody, Logistic and Bertalanffy models for growth of Morkaraman sheep, but for Awassi sheep, the Brody model showed better fit. On the other hand, Yildiz et al. (2009) and Lambe et al. (2006), who used the same model as used in this study, came to the result that the Gompertz model described the growth of their lambs best compared to various other linear and non-linear models.

The good fit of the linear model in our study indicates that individuals used in the dataset were still in the phase of almost linear growth. This is illustrated by the average growth curves fitted to the observed weights (Fig. 1). Observations of older animals are missing and hence the data are truncated. This has implications for the interpretation of the parameters of the Gompertz model. The parameter *A* usually is interpreted as mature BW. Lambe et al. (2006) used also truncated data from lambs and interpreted the parameter *A* as finishing weight at the end of fattening. LS means of the Gompertz model parameters are shown in Table 4. Mature BWs of purebred ML are reported to be higher (VDL, 2005) for ML than the estimate of *A* for ML (Table 4). Hence, parameter *A* seems to underestimate true mature BW, probably due to the truncated data.

The estimate of parameter *B* (Table 4), which is interpreted as maximum DG, is higher than the observed average DG (Table 3). This indicates that B might reflect the true maximum DG even though the data were truncated. The lowest estimate was found for ML. Hence, all crosses were superior in maximum DG compared to ML (although not always significantly).

Parameter *C*, which is interpreted as the age at maximum DG, is the lowest for TX and CH (Table 4). This indicates that TX and especially CH reached the maximum DG at a younger age compared to the other crosses. This may cause some problems if this maximum DG takes

place around weaning. First, because weaning as a stress factor might cause growth depression, sometimes called post-weaning depression (e.g. Peeters et al., 1995). Second, this early maximum DG must be supported by the milk of the ewes. Reduced milk yield of the ewes might result in a reduced maximum DG of the lambs. This is less problematic for lambs that mainly grow later in life during the fattening period, i.e. showing a higher *C* value (SU and IF in our study, Table 4). The parameter INT from the linear model underestimates the average birth weight for all crosses except CH (Tables 1 and 5 and Fig. 1). As expected, the estimated (parameter *b*, Table 5) and observed DG (Table 3) are in close agreement for all crosses.

The influence of sex and birth type on growth in sheep (Tables 4 and 5) was also found by others (Hassen et al., 2002 and Analla et al., 1998, respectively). Daskiran et al. (2010) reported on influences on growth curve parameters. Peeters et al. (1995) not only detected influences on growth, but also on FCR and age of finishing. Additionally, it is well known that males have a higher mature weight than females of the same breed. As expected, significant differences between sexes and birth types were detected in this study. Mature BW (parameter *A*, Table 4) shows differences between sexes, even though absolute values are underestimated as already discussed above. Males are estimated to be significantly heavier. Estimations for DG (*B* and *b*, Tables 4 and 5) were higher for males and singletons compared to females and twins. Female lambs are younger at maximum DG (parameter *C*, Table 5) than males.

In conclusion, IF and TX seem to be of greatest economic interest for intensive fattening because they showed the best FCR and eFCR. Only these crosses were significantly superior compared to purebred ML in FCR, eFCR and also in DG_F. This underlines the advantage of one-way crossbreeding for efficiently producing lamb meat.

Both growth models were well suited to model the data, but the fit of the Gompertz model was slightly better. In addition, the use of the Gompertz model provided some interesting biological insights of the growth of lambs and differences between the crosses, even though the lambs were slaughtered before reaching mature BW.

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Table 1 Crosses of sheep breeds, number of lambs and means and standard deviation of birth weight, bodyweight and age at weaning and finishing of fattening lambs.

Cross	Abb	*N*	*N* male	*N* single	Birth BW, kg		Weaning BW, kg		Weaning age, days		Finishing BW, kg		Finishing age, days	
					MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD	MEAN	SD
Charollais × ML[1]	CH	35	13	16	5.2	0.8	20.7	3.3	53.9	6.9	40.7	1.6	125.6	18.9
Ile de France × ML	IF	23	10	7	5.0	1.1	20.3	3.3	51.3	8.5	41.2	3.2	110.8	16.0
ML × ML	ML	36	19	18	5.3	0.8	20.7	3.4	56.0	7.9	40.9	1.6	125.6	18.0
German black headed mutton sheep × ML	SK	25	12	6	5.0	0.7	20.1	3.3	56.8	7.8	40.8	1.4	122.0	15.9
Suffolk × ML	SU	36	11	9	5.1	1.0	19.6	2.7	57.2	9.4	40.7	1.3	125.9	19.7
Texel × ML	TX	24	12	10	6.0	1.0	21.2	4.2	55.6	10.3	40.9	2.1	114.2	21.6

[1] ML=German Merinoland sheep

Table 2 Effect of cross on daily feed intake (g) of hay, concentrate and sum of both during the fattening period of lambs.

Cross	Hay		Concentrate		Hay + concentrates	
	MEAN	SE	MEAN	SE	MEAN	SE
CH	246 [a]	7	1418 [c]	9	1664 [c]	15
IF	241 [a]	10	1475 [d]	21	1715 [d]	22
ML	298 [b]	11	1246 [a]	28	1543 [a]	24
SK	249 [a]	15	1327 [ab]	30	1575 [ab]	27
SU	309 [b]	11	1291 [ab]	26	1601 [abc]	30
TX	293 [b]	10	1330 [b]	15	1623 [b]	15

[abcd] Within a column, values with different superscript letters (a–d) differ significantly at $P \leq 0.05$.

Table 3 Effect of cross on FCR, eFCR, DG during the fattening period and over the lifetime of fattening lambs.

	FCR, kg DM kg^{-1}		eFCR, MJ ME kg^{-1}*		DG_F**		DG_L***	
Cross	MEAN	SE	MEAN	SE	LS mean	SE	LS mean	SE
CH	5.5 [d]	0.2	63.2 [c]	2.0	297.4 [c]	7.2	298.7 [cd]	6.1
IF	4.5 [a]	0.1	51.2 [a]	1.5	374.1 [a]	8.9	345.3 [a]	7.5
ML	5.0 [c]	0.1	55.8 [b]	1.5	294.0 [c]	7.1	288.5 [d]	5.9
SK	4.6 [b]	0.2	52.6 [ab]	1.8	329.2 [b]	8.7	312.8 [bc]	7.3
SU	4.9 [c]	0.1	54.5 [ab]	0.8	338.1 [b]	7.4	313.5[bc]	6.1
TX	4.5 [a]	0.2	50.7 [a]	1.8	350.3 [ab]	8.7	322.1 [b]	7.3

* MJ ME = megajoule metabolisable energy, ** results from model (1) effect of the sire breed $P < 0.0001$, *** results from model (1) effect of the sire breed $P < 0.0001$, abcd Within a column values with different superscript letters (a–d)
differ significantly at $P \leq 0.05$.

Table 4 Effect of cross, sex and birth type on Gompertz parameters A (estimated mature body weight), B (maximum daily gain) and C (age at maximum daily gain) modelled for fattening lambs.

Cross/ Sex/	*A*		*B*		*C*	
Birth Type	LS mean	SE	LS mean	SE	LS mean	SE
CH	57.4 [b]	1.6	0.340 [cd]	0.009	53.7 [a]	2.9
IF	66.2 [a]	2.6	0.387 [a]	0.012	62.6 [ab]	4.5
ML	62.8 [a]	2.0	0.329 [d]	0.009	61.2 [ab]	3.5
SK	62.2 [a]	2.0	0.349 [bcd]	0.010	60.1 [ab]	3.6
SU	64.2 [a]	1.9	0.358 [abc]	0.009	63.1 [b]	3.4
TX	64.6 [a]	2.2	0.374 [ab]	0.011	55.4 [ab]	3.8
male	69.3 [a]	1.8	0.391 [a]	0.006	64.3 [a]	2.7
female	56.5 [b]	0.9	0.322 [b]	0.005	54.3 [b]	1.6
singleton	59.8 [a]	1.2	0.370 [a]	0.006	47.0 [a]	2.1
twin	66.0 [b]	1.3	0.342 [b]	0.006	71.6 [b]	2.3

abcd Within a column values and given the same aspect (cross, sex or birth type), values with different superscript letters (a–d) differ significantly at P ≤ 0.05.

Table 5 Effect of cross, sex and birth type on parameters INT and *b* of linear regression modelled for fattening lambs.

Cross/ Sex/	INT		*b*	
Birth type	LS mean	SE	LS mean	SE
CH	5.8 [c]	0.2	0.296 [ab]	0.007
IF	4.8 [abc]	0.3	0.339 [d]	0.009
ML	4.7 [ab]	0.2	0.287 [a]	0.006
SK	4.4 [a]	0.3	0.309 [bc]	0.008
SU	4.2 [a]	0.3	0.315 [c]	0.007
TX	5.2 [bc]	0.3	0.318 [cd]	0.008
male	4.5 [a]	0.2	0.337 [a]	0.005
female	5.2 [b]	0.1	0.284 [b]	0.004
singleton	6.2 [a]	0.2	0.327 [a]	0.005
twin	3.5 [b]	0.2	0.294 [b]	0.004

abcd Within a column values and given the same aspect (cross, sex or birth type), values with different superscript letters (a–d) differ significantly at P ≤ 0.05.

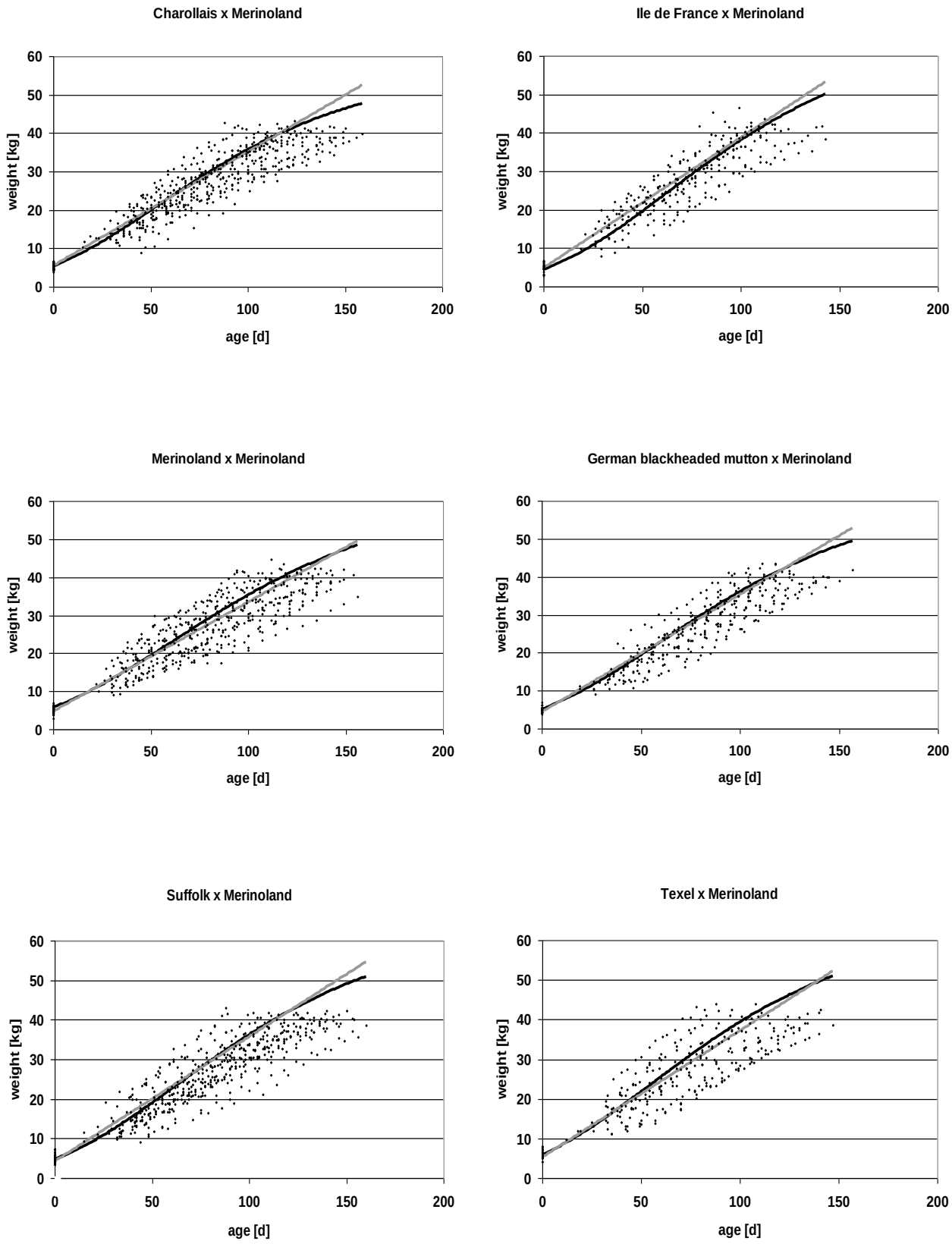

Figure 1 Estimated growth function for Gompertz (black) and linear model (grey) for different crossbred lambs and purebred Merinolandschaf lambs; body weight (kg) plotted against age (days).

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CHAPTER TWO

Short Communication:

Concentration of three branched-chain fatty acids in adipose tissue does not affect meat sensory traits in crossbred and purebred German “Merinolandschaf” lambs

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Concentration of three branched-chain fatty acids in adipose tissue does not affect meat sensory traits in crossbred and purebred German "Merinolandschaf" lambs

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Abstract Intense sheep odour and flavour in lamb is often associated with lower consumer acceptance. Branched-chain fatty acids (BCFAs) are suggested as possible reasons. Therefore, muscle and subcutaneous adipose tissue samples of 98 lamb chops were analysed for three BCFAs (4-methyloctanoic, 4-ethyloctanoic and 4-methylnonanoic fatty acid). Samples were derived from a previous study, in which lambs were raised and fattened under intensive conditions and tested for sensory quality. BCFA contents of fat extracts from muscle tissue were very low and quantification was not possible. In subcutaneous adipose tissue different concentrations of BCFA and differences between crosses were detected. The sex of lambs had a significant influence. The BCFA correlations were significant, while correlations between BCFA of adipose tissue and sensory traits were not significant. Therefore, it seems likely that BCFA concentrations were too low and/or other substances are involved in causing the lamb flavour detected through sensory analysis.

1 Introduction

"Merinolandschaf" (ML) represent a widespread sheep breed in Germany. In order to improve growth performance of fattening lambs, F1-crossbreeding obtained from mating ML ewes with a meat-type terminal-sire breed is frequently performed. The choice of the sire line is of fundamental importance for optimizing F1-crossing systems to provide the best possible quality.

Typical sheep odour and flavour is often associated with an unpleasant smell and therefore lower consumer acceptance of sheep products such as lamb (Prescott et al., 2001; Rhee and Ziprin, 1996; Wong et al., 1975). For lamb production, choosing a certain terminal-sire breed would be a rather simple and practicable opportunity to achieve better consumer acceptance if this reduced species-specific odour and flavour. In the sensory analysis of Henseler et al. (2014), differences in lamb flavour between crosses were detected. Since feeding conditions were comparable for the crosses, a genetic influence of crossing was assumed. The branched chain fatty acids (BCFAs) 4-methyloctanoic acid (4-Me-8:0), 4-methylnonanoic acid (4-Me-9:0) (Wong et al., 1975) and 4-ethyloctanoic acid (4-Et-8:0) (Ha and Lindsay, 1990) were thought to be mainly responsible for species-related flavour. Prescott et al. (2001) mentioned 4-Me-8:0, in particular, as a strong candidate. The authors reported that an increase in BCFA content in meat, reached by adding different amounts of 4-Me-8:0 and 4-Me-9:0, resulted in decreased acceptance of the meat on the part of consumers. As medium-chain fatty acids might have a more decisive role than longer chained fatty acids in sensory analysis, due to their higher volatility, we focused on three medium-sized BCFAs, namely 4-Me- 8:0, 4-Me-9:0 and 4-Et-8:0.

Feed was found to have a strong impact on the concentrations of BCFA in lamb tissue. According to Duncan and Garton (1978), carbohydrate-rich feed (barley-based) results in higher BCFA concentrations in subcutaneous adipose tissue than grass feeding. Busboom et al. (1981) reported higher BCFA concentrations for high- compared to low-energy diets. For pasture feeding, lower concentrations of 4-Me-8:0 and 4-Me-9:0 were reported compared to concentrate feeding (Priolo et al., 2001; Young et al., 2003). Similar results were reported for other BCFAs, such as 4-Me-10:0, 4-Me-12:0 and 4-Me-14:0 (Miller et al., 1986), even though only low amounts of BCFA could be found in plants (Diedrich and Henschel, 1990). BCFAs are formed mainly from microbial metabolism in the rumen (Chilliard et al., 2003). Through this fermentation, acetate, propionate and butyrate are produced, and, especially at high propionate concentrations, BCFA formation increases (Lindsay, 1996).

The aim of the present study was to investigate the occurrence and concentrations of the branched-chain fatty acids 4-Me-8:0, 4-Me-9:0 and 4-Et-8:0 in five different F1-crossbreeds and purebred ML. Intense feeding conditions were chosen because BCFA concentrations were expected to be higher than for pasture feeding and feeding differences could be minimized. A further aim was to investigate the relationship between the branched-chain fatty acids tested and several sensory traits.

2 Material and Methods

2.1 Animals and sensory data set

The tissues analysed were from chops of the 10/11th rib obtained from 98 lambs. All lambs were purebred ML or F1-crossbred lambs which were produced to test five meat-type terminal-sire breeds (Charolais, Ile de France, German blackheaded mutton sheep, Suffolk and Texel) on ML ewes. Crosses and cross abbreviations are listed in Table 1. Intensive feeding conditions were chosen. Lambs were raised on seven farms until weaning at a body weight (BW) of 17 kg with free access to concentrate (soy- and barley-based) and roughage. Fattening was centralized and took place in group housing with 200–300 g hay day^{-1} per animal and concentrate ad libitum. Lambs were slaughtered at 43.14±3:78 kg body weight and at an age of 102–161 days. After slaughter the carcasses were chilled to 1–3 °C and dissected; adipose and muscle tissue of the chops were separated and frozen (-20°C) 48 h post mortem. To ensure enough sample material for analysis, lambs needed to weigh at least 36 kg at slaughter and show medium fat coverage. Lambs were chosen at random from animals fulfilling these criteria. All samples were homogenized after 222–530 days of storage (disperser Ultra Turrax T18-10, IKAWerke, Staufen, Germany), and muscle tissue was lyophilized (freeze dryer Gamma 1- 20 LMC2, Martin Christ, Osterode, Germany) at 2.6 mbar for 72 h. Samples were frozen (-20°C) until preparation for analysis.

In a previous study, chops of the same animals as used for this study were tested for their sensory meat quality (Henseler et al., 2014). The traits tested were overall appraisal, lamb flavour, flavour quality, odour, juiciness and tenderness. Traits were evaluated by a trained

sensory panel of 21 persons of different sex and ages. Fifteen sensory tests were conducted on 15 days; a duplicate was included in every test for every tester. The chops tested were 2 cm thick and unseasoned, and subcutaneous fat was removed. They were grilled on a contact grill at 170 °C and subsequently left to simmer for 2:20 min wrapped in aluminium foil. For tasting, the chops were sliced in 0.7 cm broad sections, and the inner and outer sections were discarded. The data set of the sensory analysis was used for determining possible relations between BCFA concentrations and sensory traits.

2.2 Analysis of BCFA

The fat extracts of raw muscle tissue of *musculus longissimus thoracis et lumborum* and subcutaneous adipose tissue of the same chop (without bones) were analysed separately. The preparation of the samples was undertaken according to the method of Kaffarnik et al. (2014). Subcutaneous fat samples were directly transesterified to result in fatty acid methyl esters (FAMEs).

The fat of muscle tissue samples (dried homogenized muscle tissue, subcutaneous fat removed) was extracted by means of a Soxtherm apparatus (Kaffarnik et al., 2014). The sample extracts were concentrated to 10 mL, and an aliquot was used for the formation of FAMEs. FAMEs were analysed by gas chromatography coupled with mass spectrometry in selected ion monitoring mode (GC–MS-SIM). Quantification was performed using the internal standards undecenoic acid methyl ester (11 V 1*n*-1) and tetradecanoic acid ethyl ester (14 V 0). The limit of detection was 1.1–1.4 ng g^{-1}, and the limit of quantification was 3.6–4.8 pg (Kaffarnik et al., 2014).

Additionally, it was tested whether lyophilization had any influence on the results. For this purpose, 1.43 g fresh muscle tissue was pulverized and mixed with sodium sulfate (ratio 2:6 : 1); the remaining procedure was as described above. For another test three adipose tissue samples were lyophilized. The dry samples and their condensates, derived from the drying process, were directly esterified and analysed.

2.3 Statistical analysis

The concentrations of BCFA found were recorded for each chop and analysed using the following statistical model:

$$y_{ijk} = \mu + C_j + SEX_k + C_j \times SEX_k + e_{ijk} \quad (1)$$

where $y_{...}$ is the amount of BCFA of lamb *i* (ng mg^{-1}), C_j is the fixed effect of cross *j* and SEX_k is the fixed effect of sex *k*. $C_j \times SEX_k$ represents the interaction of cross *j* and SEX *k*. The model was fitted using the MIXED procedure of SAS (9.2, SAS Inst. Inc., Cary, NC). For the calculation of correlation, data of subcutaneous adipose tissue and the sensory analysis from Henseler et al. (2014) were used.

3 Results

3.1 Muscle tissue

Muscle tissue samples from 17 lambs showed concentrations below the limit of quantification or below the limit of detection for all three BCFAs investigated (data not shown). This was also valid for the non-lyophilized fresh muscle tissue tested. Due to these results the amount of samples was limited to 17 because a sample with BCFA sufficient for quantification was not expected to be found. Losses in BCFA concentration arising from lyophilization under the conditions applied were not detectable. In collected fatty condensates, developed during lyophilization, no BCFAs were detectable.

3.2 Adipose tissue

Significant differences between crosses were detected for all three fatty acids tested (shown in Table 1). Concentrations of 4-Me-8:0 ranged between 56.9 and 103.0 ng mg^{-1}, while those of 4-Et-8:0 (13.3–19.7 ng mg^{-1}) and for 4-Me-9:0 (17.3–46.6 ng mg^{-1}) were lower. Only CH and SK showed significant differences in 4-Me-8:0 and 4-Me-9:0 concentrations compared to ML. For 4-Me-9:0, two groups were distinguishable, with CH, SK and SU having significantly higher values. For 4-Et-8:0, none of the crosses tested showed significant differences compared to purebred ML. A significant ($P \leq 0.001$) influence of sex was identified for concentrations of 4-

Me-8:0 and 4-Me-9:0 but not for 4-Et- 8:0 (Table 1). The cross–sex interaction effect was significant for 4-Me-8:0 and 4-Me-9:0 at $P \leq 0.05$. These interaction effects resulted in scaling effects, i.e. the differences between the crosses and between sexes varied numerically but without a re-ranking. For 4-Et-8:0, the interaction effect was not significant.

3.3 Correlations of BCFA concentrations and sensory analysis

Significant ($P \leq 0.01$) correlations were detected between the BCFAs tested (see Table 2), indicating, in particular, that concentrations of 4-Me-8:0 and 4-Me-9:0 are closely related. Correlations between the amounts of BCFAs in adipose tissue and the sensory traits were not significant.

4 Discussion

The quantification of the fat extracts of muscle tissue (MEAT) samples turned out to be more problematic than for subcutaneous adipose tissue (FAT). Quantification for MEAT was not possible, while for corresponding FAT from the same individual quantification was possible. FAT samples showed analysable results despite the concentration of injection being lower than for MEAT. Brennand and Lindsay (1992) reported higher concentrations of 4-Me-8:0, 4-Et-8:0 and 4- Me-9:0 in FAT than in MEAT, which supports the results of the present study. Miller et al. (1986) reported lower levels of other BCFAs (4-Me-10:0, 4-Me-12:0 and 4-Me-14:0) in MEAT than in FAT, partly below the limit of quantification.

For all three BCFAs, significant differences between specific crosses were detected. The smallest differences were detected for 4-Et-8:0. Busboom et al. (1981) tested several BCFAs (4-Me-10:0 until 4-Me-17:0 and 4-Me-17:1) and reported small and nonsignificant breed effects. Also, Duckett and Kuber (2001) determined that breed or the breed of terminal sire seems to have a minor impact on the intensity of lamb flavour. Apart from the detected breed effects in the present study, a highly significant ($P \leq 0:001$) influence of sex was detected for two of the BCFAs investigated (Table 1). This is supported by results in Watkins et al. (2010), who detected influences of sex and age for 4-Me-8:0, 4-Et-8:0 and 4-Me-9:0. The influence of

age at slaughter was tested but was not significant in the present study, most likely because age variation was low.

As summarized by Young and Braggins (1998), it seems probable that other substances, such as phenols and sulfur-containing compounds, could play a role besides BCFA for the lamb or sheep-like odour and flavour. According to Resconi et al. (2010), lamb flavour in grilled loins is related to the concentration of heptan-2-one and oct-1-en-3-one. Priolo et al. (2001) suggested that 3-methylindole (skatole), in addition to its own flavour, might increase the perception of sheep-like flavour caused by BCFA. Another factor might be the concentration of linoleic and α-linolenic acid, which, according to Sañudo et al. (2000), influence lamb flavour intensity. The presence of some of the substances mentioned might explain the results of Henseler et al. (2014), where lamb flavour was noticed by the sensory panel although BCFA levels detected in the present study were very low in fat extracts of muscle tissue.

A lack of significant results concerning correlations could be due to other substances besides the three BCFAs tested being involved in lamb flavour. Another possibility would be a different fatty acid composition in subcutaneous as opposed to intramuscular fat as observed for some fatty acids and reviewed by Wood et al. (2008). Differences in the fatty acid composition of subcutaneous and intramuscular fat with regard to BCFA remain unclear but might be an interesting objective for further studies.

5 Conclusions

Differences in concentrations of 4-Me-8:0, 4-Et-8:0 and 4-Me-9:0 were detected in subcutaneous adipose tissue of different crosses. For fat extracts from muscle tissue, concentrations of the fatty acids investigated could not be quantified. In adipose tissue samples significant correlations were found between BCFAs. Correlations between the amount of BCFAs in adipose tissue and meat sensory traits were not significant, possibly because of other substances involved or differences in the fatty acid composition of intramuscular fat and adipose tissue.

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Table 1 Crosses, cross abbreviations (abbrev.), number (n) of muscle tissue samples (MEAT), number of subcutaneous adipose tissue samples (FAT) per cross and sex and concentrations of 4-Me-8:0, 4-Et-8:0 and 4-Me-9:0 (ng mg^{-1}) in subcutaneous adipose tissue of different crosses of sheep.

Cross/ sex	Abb.	*n*		4-Me 8:0 (ng mg^{-1})		4-Et 8:0 (ng mg^{-1})		4-Me 9:0 (ng mg^{-1})	
		MEAT	FAT	LSmean	SE	LSmean	SE	LSmean	SE
Charolais x ML*	CH	4	14	103.0 ^{c}	13.1	19.7 ^{b}	2.3	46.6 ^{b}	9.3
Ile de France x ML	IF	3	18	67.0 ^{ab}	11.6	19.4 ^{b}	2.1	18.7 ^{a}	8.2
ML x ML	ML	3	15	57.3 ^{a}	12.7	15.4 ^{ab}	2.3	18.3 ^{a}	9.0
German blackheaded mutton sheep** x ML	SK	2	18	99.1 ^{bc}	11.6	18.4 ^{ab}	2.1	44.6 ^{b}	8.3
Suffolk x ML	SU	3	16	87.9 ^{abc}	12.3	13.3 ^{a}	2.2	46.6 ^{b}	8.7
Texel x ML	TX	2	17	56.9 ^{a}	12.0	18.2 ^{ab}	2.1	17.3 ^{a}	8.5
Male	m	8	44	99.7 ^{a}	7.4	15.5 ^{a}	1.3	48.5 ^{a}	5.3
Female	f	9	54	57.3 ^{b}	6.7	18.3 ^{a}	1.2	15.6 ^{b}	4.8

* ML is “Merinolandschaf”; ** German blackheaded mutton sheep is “Deutsches Schwarzköpfiges Fleischschaf”; $^{a;b;c;d}$ within a column and same effect (cross or sex), values with different superscript letters (a-d) differ significantly at $P \leq 0:05$.

Table 2 Correlation coefficients of concentrations of the fatty acids 4-Me-8:0, 4-Et-8:0 and 4-Me-9:0 (ng mg^{-1}) in sheep subcutaneous adipose tissue and six sensory traits (Henseler et al., 2014).

	4-Me 8:0	4-Et 8:0	4-Me 9:0
4-Me 8:0	1		
4-Et 8:0	**0.335 ***	1	
4-Me 9:0	**0.878 ***	0.080	1
Overall appraisal	-0.156	-0.044	-0.045
Lamb flavour	-0.005	0.072	-0.073
Flavour quality	-0.088	-0.058	-0.026
Odour	-0.104	-0.060	-0.012
Juiciness	0.034	-0.097	0.128
Tenderness	-0.189	0.037	-0.144

* Significant at $P \leq 0:01$.

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CHAPTER THREE

Genetic Analyses of Growth, Carcass and Meat Quality Traits in German Merinoland and Merinoland-Cross Lambs

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Submitted

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Abstract Increased consumer interest in meat quality (MQ) and meat taste could spark changes in breeding goals of lamb producers and breeders. However there is limited information available on the genetic parameters of MQ traits and their relationship to growth or carcass characteristics. In this study genetic parameters of growth, carcass and MQ traits were estimated using mixed models. Data were collected for twelve traits. Phenotypic information was collected on 1599 lambs, including both purebred Merinoland animals and five different F1 crosses. Moderate heritability (0.15 to 0.40) was found for eye muscle area, shoulder width and many further carcass traits. While heritability for most of the MQ 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. Since especially for MQ traits a routine phenotyping is difficult to implement, genomic selection might be a promising tool to improve these traits. The data collected in the present study might serve as an initial reference population.

Keywords: heritability, genetic correlation, meat trait, carcass trait, lamb

1 Introduction

Lean meat yield (the amount of meat that can be boned out from a carcass) is the key productivity driver of meat supply chains (Pethick et al., 2011). As a result, sheep breeders have mainly focused on growth and carcass traits to produce leaner slaughter animals and thereby increase profitability. Although selection based on increased lean meat yield is negatively correlated with palatability (eg. Hopkins et al., 2006, Karamichou et al., 2006, 2007; Lorentzen and Vangen, 2012), the trend towards leaner lamb has continued over the past several decades. This trend has been accompanied by a decline in European lamb consumption: in Western Europe, lamb stocks declined by 24% between 2000 and 2013 (FAO, 2014). Genetic improvement programmes could provide a long term, sustainable solution for simultaneous improvement of both yield and quality in lamb production.

Meat quality (MQ) is affected by various factors, the most important of which 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. In contrast to growth and carcass traits, MQ traits are more difficult and expensive to measure, which has hindered performance testing and implementation of these traits in breeding programmes. Furthermore, MQ often is not included in the direct payment scheme for lamb. Nevertheless, sheep breeders are becoming more interested in application of MQ traits in breeding programmes. This is likely a consequence of a larger 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.

Before MQ traits can be implemented in a breeding program, genetic parameters for MQ traits and their genetic correlation to other production traits must be estimated. 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). Some studies on MQ traits have been published, most of which involve colour, pH and intramuscular fat (see Mortimer et al., 2010 for a review). These studies were mainly conducted on Australian Merino and Merino

cross populations. Recent studies additionally cope with mineral contents (e.g. Daetwyler et al., 2012) or specific fatty acids (e.g. Schiller et al., 2015a).

In Southern Germany, the Merinoland (ML, also “Wurttemberger”) sheep is the most common breed due to its high-quality wool, high fertility, robustness, and its motility (Sambraus, 2011). The breeding goal comprises traits for reproduction, growth and meat. Animal performance testing is done on purebred ML sheep on station as well as on farms. The collected phenotypic records are used for a BLUP breeding value estimation. Additional systematic breeding activities within the ML breed, like e.g. elite matings or even genomic analysis, are currently missing. Due to the increased importance of meat production (Fogarty et al., 2003; Greeff et al., 2008; Strittmatter, 2005), meat type terminal sires are commonly crossed with ML ewes in order to produce F1 lambs with an improved growth rate and feed conversion (Schiller et al., 2015b). Until now, MQ traits are not included in the breeding goal. The objective of the present paper was to investigate genetic parameters of selected growth, carcass and MQ traits and their relations in purebred ML and ML crossbred lambs. Potential possibilities to implement findings in current breeding systems are also discussed.

2 Material and methods

2.1 Animal material 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. For breed abbreviations and 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 and 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 in 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. Twelve traits of three groups (growth, carcass quality and MQ) were considered in this study. See Table 2 for a summary statistics. Hot carcass weight (including kidney and kidney fat) used to calculate dressing percentage (DRESS), kidney fat weight (KFW), carcass length (CarL) and carcass evaluation (CarE) were recorded on hot carcasses. Shoulder width (SW), Haunch width (HW) and Haunch circumference (HC) were 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. FAT (subcutaneous fat thickness), COOK (cooking loss) and EMA (eye muscle area) were determined. FAT 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). COOK was defined as the weighting difference of the boned chop before and after cooking, done via heating up to a core temperature of 85°C. For measurement of 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 shear force 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.

2.2 Parentage Testing

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 at 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 313 SNP passed the data filtering. 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 combination showed no, or due to genotyping errors, only a few PCEs. The corresponding potential sire was assumed to be the true sire.

2.3 Statistical Analyses

The statistical analyses were conducted 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 for the residual term. The covariance structure of the random animal effect was $\mathrm{var}(a) = A * \sigma_a^2$, 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 $\mathrm{var}(sl) = I * \sigma_{sl}^2$, 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. $\mathrm{var}(e) = X'DX$, 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).

3 Results and Discussion

3.1 Cross means, genetic variation and heritability estimates

The least square means of the cross effects are shown in Table 3. 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 4. The traits ADG, DRESS, KFW, CarL, CarE, SW, FAT, SF and EMA showed moderate (0.15 to 0.40) heritability in this study. For ADG this is supported by several authors and for different breeds (Bibé et al., 2002; Botkin et al., 1969; Safari and Fogarty, 2003). For DRESS in the present study moderate h^2 of 0.18 to 0.25 were found, 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 the present work 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 values 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.

Estimates of h^2 for FAT in the present study ranged from 0.19 to 0.27. These values are in agreement with results of e.g. Mortimer et al. (2010), Greeff et al. (2008) and Bennett et al. (1991), measuring at different points of the carcass. Haunch traits HC and HW both showed low h^2. 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. Traits such as SF, the MQ trait with the highest heritability in the present study, showed lower values than found in studies with similar aging time. Still, moderate heritabilities are reported for SF (Botkin et al., 1969; Hopkins et al., 2011; Mortimer et al., 2010). The differences to the present study might be explained by differences in genetics, carcass weights, preparation, and aging time.

EMA can be seen as an indicator for muscling and represents a highly valued part of carcass. For EMA 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 vs. estimation of the muscle area by 80% of the product of eye muscle depth and length, measuring points etc.).

3.2 Phenotypic and genetic correlations

Results of phenotypic and genetic correlations are shown in Table 5. 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, which is around 5 per 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 found in general 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. ADG and DRESS were found to be genetically positive correlated. 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. EMA) 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 work SF and ADG were genetically moderately positive correlated as well as SF with EMA. 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 is 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. As far as breeding on 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. More distinct genetic correlations are the negative correlations of KFW to HW and HC. Phenotypic correlations showed the same tendencies, indicating that animals with less kidney fat have better hind limbs.

COOK, showed several moderate and high genetic correlations of different sign to different traits. A high positive genetic correlation was detected to CarE and HW, 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 cooking losses, which is actually not desired, while fatter, tougher and individuals with better dressing percentage have less cooking losses. 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, a moderate negative correlation to HW and a negative correlation of -0.51 to EMA. 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 EMA. 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, HW and EMA (phenotypic correlations denote the same tendency), indicating that shorter but broader and more muscular carcasses are evaluated better.

3.3 Implementation in breeding programmes

The cross means (Table 3) 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 to be recommended, but this will likely not improve MQ traits substantially.

The heritability estimates show moderate SE, and thus could be used, with cautions, for univariate routine breeding value evaluations. If, however, 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 next to purebred ML data also F1 crossbred data should be used for routine genetic evaluations, more reliable genetic parameters have to be estimated using a larger data set that is better structured.

In some breeding programmes for ML and for some of the tested sire lines ADG, EMA, FAT and SW are already implemented (Engelhart and Eckl, 2012). Results of the current study support this choice of traits, because of 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, shear force and cooking loss 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-intense and time consuming (Mortimer et al., 2010; Simm et al., 2009). Hence, these traits are classical “hard to measure” traits. Because lambs are often paid by weight, and not MQ or palatability, the high phenotyping costs are the main barrier of inclusion of MQ traits to breeding programmes (Simm et al., 2009). Genomic selection has been introduced in some sheep breeding schemes (e.g. Daetwyler et al., 2012). Hayes et al. (2013) recommended genomic selection for the improvement of traits that are too expensive to measure routinely in selection candidates. Genomic selection, however, needs a large reference population with genotyped and phenotyped individuals in order to predict reliable breeding values. Establishing this reference population 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.

4 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 in general possible to achieve selection response for the traits included in this study. 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 in data recording in a conventional routine breeding scheme. Genomic selection might be a promising tool to improve MQ traits. 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.

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

Cross	Abbrev.	*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

[1] ML=German Merinoland sheep

[2] German black headed mutton = Deutsches Schwarzköpfiges Fleischschaf

Table 2 Tait, trait abbreviation, unit, number of observations (n), mean, standard deviation (SD), and the percentiles 10 (p10) and 90 (p90).

Trait	Abbrev.	unit	*n*	MEAN	SD	p10	p90
Average daily gain (fattening)	ADG	[g/d]	1582	329.96	67.55	247.00	418.00
Dressing Percentage	DRESS	[%]	1551	48.96	2.37	50.70	56.40
Kidney Fat Weight	KFW	[g]	1590	235.22	114.11	121.00	377.50
Carcass length	CarL	[cm]	1592	40.46	2.45	37.50	43.50
Carcass evaluation	CarE	1-5	1487	3.36	0.73	3.00	4.00
Shoulder Width	SW	[cm]	1589	19.06	1.11	17.70	20.40
Haunch Width	HW	[cm]	1593	21.65	1.05	20.30	22.90
Haunch circumference	HC	[cm]	1591	63.91	2.62	60.50	67.00
Subcutaneous fat thickness	FAT	[mm]	1592	4.49	1.47	2.83	6.47
Cooking loss [1]	COOK	[%]	1598	32.53	4.07	27.00	37.20
Warner-Bratzler shear force [2]	SF	[N]	1514	65.07	24.62	39.33	95.23
Eye muscle area	EMA	[cm²]	1592	12.34	1.64	10.35	14.45

[1] after two days of aging

[2] one day after cooking

Table 3 Adjusted means of the crosses per trait (standard error in parenthesis).

Trait[2] \ Cross[1]	CH	IF	ML	SK	SU	TX
ADG	323.88 (8.30)	340.81 (8.22)	320.93 (8.87)	337.85 (8.30)	337.84 (8.91)	336.27 (8.76)
DRESS	49.29 (0.33)	49.45 (0.32)	48.70 (0.36)	48.67 (0.32)	48.18 (0.35)	49.31 (0.37)
KFW	219.87 (17.81)	262.29 (17.77)	247.29 (18.97)	246.69 (17.99)	235.88 (19.07)	222.53 (18.62)
CarL	39.85 (0.32)	39.86 (0.32)	41.50 (0.34)	41.02 (0.32)	40.85 (0.34)	39.63 (0.34)
CarE	3.478 (0.09)	3.51 (0.09)	3.09 (0.10)	3.26 (0.09)	3.31 (0.10)	3.40 (0.10)
SW	19.26 (0.12)	19.43 (0.12)	18.62 (0.13)	18.93 (0.11)	18.81 (0.13)	19.15 (0.14)
HW	21.89 (0.09)	21.69 (0.08)	21.69 (0.10)	21.45 (0.09)	21.34 (0.10)	21.75 (0.10)
HC	64.41 (0.22)	64.11 (0.21)	63.46 (0.23)	63.24 (0.22)	63.89 (0.23)	64.80 (0.23)
FAT	4.68 (0.16)	5.05 (0.16)	4.15 (0.18)	4.37 (0.16)	4.31 (0.18)	3.80 (0.18)
COOK	32.35 (0.40)	32.94 (0.38)	30.98 (0.45)	31.57 (0.41)	32.62 (0.43)	32.87 (0.47)
SF	61.24 (3.59)	66.62 (3.56)	64.46 (3.84)	63.56 (3.70)	67.64 (3.86)	70.13 (4.06)
EMA	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] For cross/breed abbreviations see Table 1

[2] For trait abbreviations see Table 2

Table 4 Additive genetic variance (σ_a^2), slaughter day variance (σ_{SD}^2)**,** range of residual variance across the crosses ($\sigma_{e_i}^2$), range of heritability across crosses for the traits (standard error in parenthesis) and median of the estimated heritabilities.

Trait[1]	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
CarE	0.11 (0.05)	0.01 (0.01)	0.24 - 0.32 (≤ 0.06)	0.26 - 0.31 (≤ 0.12)	0.28
SW	0.19 (0.07)	0.09 (0.02)	0.25 - 0.50 (≤ 0.08)	0.25 - 0.36 (≤ 0.13)	0.33
HW	0.08 (0.04)	0.06 (0.02)	0.28 - 0.42 (≤ 0.05)	0.14 - 0.19 (≤ 0.09)	0.15
HC	0.40 (0.19)	0.54 (0.15)	1.20 - 2.39 (≤ 0.25)	0.12 - 0.19 (≤ 0.09)	0.14
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
EMA	0.72 (0.27)	0.22 (0.06)	0.73 - 1.35 (≤ 0.30)	0.31 - 0.43 (≤ 0.11)	0.36

For trait abbreviations see Table 2

Table 5 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	CarE	SW	HW	HC	FAT	COOK	SF	EMA
ADG		0.16 (0.28)	-0.03 (0.27)	0.10 (0.28)	0.57 (0.21)	0.36 (0.24)	-0.12 (0.30)	-0.02 (0.30)	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)	-0.28 (0.27)	0.13 (0.27)	-0.36 (0.28)	0.23 (0.29)	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)	0.13 (0.27)	-0.23 (0.27)	-0.61 (0.22)	-0.75 (0.18)	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)		-0.74 (0.17)	-0.26 (0.27)	-0.61 (0.23)	0.01 (0.32)	0.27 (0.28)	-0.21 (0.39)	-0.13 (0.30)	-0.28 (0.26)
CarE	0.11 (0.04)	0.16 (0.04)	0.08 (0.04)	-0.17 (0.04)		0.66 (0.17)	0.54 (0.25)	-0.30 (0.29)	-0.09 (0.29)	0.66 (0.32)	0.10 (0.30)	0.15 (0.27)
SW	0.03 (0.05)	0.46 (0.03)	0.04 (0.05)	-0.11 (0.05)	0.36 (0.03)		0.19 (0.29)	-0.21 (0.29)	-0.04 (0.29)	0.01 (0.39)	0.27 (0.28)	0.26 (0.25)
HW	0.01 (0.05)	0.19 (0.04)	-0.11 (0.05)	-0.05 (0.05)	0.13 (0.03)	0.13 (0.04)		0.34 (0.30)	-0.38 (0.28)	0.83 (0.28)	-0.16 (0.32)	0.07 (0.30)
HC	0.02 (0.06)	0.50 (0.03)	-0.13 (0.06)	-0.12 (0.06)	0.13 (0.03)	0.27 (0.04)	0.39 (0.03)		-0.18 (0.31)	0.47 (0.39)	0.30 (0.30)	0.46 (0.24)
FAT	0.02 (0.05)	0.29 (0.04)	0.15 (0.05)	-0.04 (0.05)	0.11 (0.03)	0.17 (0.04)	0.02 (0.04)	0.01 (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)	0.05 (0.03)	-0.03 (0.04)	0.05 (0.03)	0.01 (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)	0.03 (0.04)	0.05 (0.05)	-0.11 (0.04)	0.09 (0.05)	-0.16 (0.04)	-0.01 (0.04)		0.42 (0.25)
EMA	0.08 (0.05)	0.38 (0.04)	-0.01 (0.05)	-0.13 (0.05)	0.13 (0.04)	0.35 (0.03)	0.12 (0.04)	0.36 (0.03)	-0.14 (0.04)	0.03 (0.03)	0.26 (0.04)	

[1] For trait abbreviations see Table 2

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CHAPTER FOUR

Targeted Association Mapping in Merinoland Crossbred Lambs

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Targeted Association Mapping in Merinoland Crossbred Lambs

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Abstract: This study reports the results of targeted association analysis in multiple F1 Merinoland crossbred lambs. A number of 384 SNPs in chromosomal regions with reported QTL for growth, carcass and meat quality were genotyped at 1493 crossbred lambs. These lambs were produced from Merinoland ewes and rams from five different meat-type breeds (Charollais, Ile de France, German Blackheaded Mutton, Suffolk, and Texel). Single SNP association analysis was conducted across the crosses or nested within the crosses. The traits daily gain, carcass yield, drip loss, haunch circumference, and fat layer were considered. Modeling SNP effect across the crosses identified weak associations with the same effect sign across the crosses. The nested analysis revealed significant associations with different effects signs in the crosses, which were not detected in the model where SNP effect was fitted across the crosses. Positional and functional candidate genes were identified and discussed.

Keywords: Crossbred sheep, Targeted association analysis, Meat-type, traits

Introduction

The Merinoland (ML) is a widespread breed of sheep in Germany. ML ewes are crossed frequently with a meat-type sire breed in order to produce high quality lamb meat. In a previous study we investigated which sire breed is most appropriate to produce F1 crossbred lambs with ML. Five sire breeds and in addition the ML were used to produce F1 lambs, which were fattened and slaughtered and comprehensively phenotyped for various growth, carcass and meat quality traits (Henseler et al., 2014a; b).

Identifying genetic markers that are associated with economically relevant traits will be helpful to select rams within and across sire breeds. Targeted association study by selecting a low number of SNPs in chromosomal regions that have been frequently reported to harbor genes affecting the traits of interest is a cost effective alternative to genome wide association studies. Especially in situations where the empirical power of the study design is limited (e. g. due to limited number of individuals) it has its advantages due to a lower multiple testing problem.

The aim of the present study was to apply a targeted association study for five meat-type traits using 1493 ML x sire breed F1 crossbred lambs and 384 selected SNPs.

Materials and Methods

Data. The dataset included 1511 F1 crossbreed and purebred ML-lambs. For production of crossbreed lambs rams of the meat-type breeds Charollais, Ile de France, German Blackheaded Mutton (Deutsches Schwarzköpfiges Fleischschaf), Suffolk, and Texel were crossed with ML ewes. The crosses are listed in Table 1. All lambs were raised, fattened and slaughtered under standardised conditions. Lambs were raised on seven farms till weaning at 17 kg bodyweight (BW). Fattening took place on a single farm in group housing with 200-300 g hay per animal and concentrate *ad libitum*. The lambs had a mean BW at slaughter of 43.14 ± 3.78 kg at an age of 102 to 161 days. During and after slaughter growth, carcass, and meat quality traits were recorded. Details can be found in Henseler et al. (2014a; b). The following traits were considered in this study: daily bodyweight gain during fattening (BWG [g]), carcass yield (CY [%]), haunch circumference (HC [cm]), fat cover (FAT [cm]), and drip loss (DRIP [%]). Lambs were genotyped for 384 SNPs These SNPs were located on chromosome 1, 2, 3, 18 and 21, in order to focus on chromosomes where QTL for these traits have been reported in the literature (Hu et al., 2013).

Statistical analysis. SNP filtering was done using following criteria. A SNP was excluded if it had a minor allele frequency <3%, and a call rate <95%. A number of 313 SNP passed the data filtering. Single marker association mapping was done using two different models. Model one estimated one effect per SNP *k* across all six crosses. The model was

$$y_{ij} = x_{ij}\beta + sire_{ij} + b_k * x_{ijk} + e_{ij} \qquad (1)$$

where y_{ij} is the trait record of individual *j* of cross *i*, the term x_{ij} denotes for the *ij*th row vector of a design matrix linking the phenotypic observation of the individual to some fixed effects stored in β (i. e. the effect of the cross, the sex, and the weight at slaughter). The effect of the SNP *k* was modelled as a regression on the number of copies of the allele with the higher frequency (x = 0, 1, or 2), with b_k being the regression coefficient. Pedigree data were not available. Therefore, the sire effect was included as an uncorrelated random effect to capture some population structure effects. The term e_{ij} is a random residual with heterogeneous variance, i. e. $e_{ij} \sim N(0, \sigma_i^2)$. The null (alternative) hypothesis was that $b_k = 0$ ($b_k \neq 0$). The test statistic was an *F*-test.

In the second model the SNP effects were nested within the crosses, i. e.

$$y_{ij} = x_{ij}\beta + sire_{ij} + b_{ik} * x_{ijk} + e_{ij} \qquad (2)$$

The terms are as defined for the previous model. The null (alternative) hypothesis was that $b_{ik} = 0$ for every cross *i* ($b_{ik} \neq 0$ for at least one cross *i*). The test statistic was a pooled *F*-test. This model was applied, because the marker density was low even in the targeted regions, and hence, the Linkage Disequillibrium (LD) between an SNP and a causal mutation might be different across the crosses. If this LD holds across the crosses, then this model will be of reduced power, because six regression coefficients have to be estimated instead of one (as in model (1)). In order to control for multiple testing an FDR *q*-value was calculated for each test using the software QVALUE (Storey and Tibshirani, 2003). The association analysis was undertaken using ASReml 3.0 (Gilmour et al, 2009).

Gene annotation and ontology. Significant SNPs were arranged in clusters based on trait association. Candidate genes were searched in the vicinity of significant SNPs. The super-set of cDNA sequences for Ovis Aries (taxid:9940) was obtained from Ensembl (Flicek et al., 2014) known, novel and pseudo gene predictions. cDNA sequences were used as queries against the non-redundant protein database using Blast2GO version 2.7.0. A relaxed statistical

significance threshold for reporting matches against database sequences was chosen. The gene matches were used for the gene ontology (GO) term assignment. After gene ID mapping, GO term assignment and annotation augmentation the final annotation file was produced. Results were categorized with respect to the Blast2GO categories Biological Process, Molecular Function and Cellular Component. GO terms were searched at several levels, in order to establish links to considered traits.

Results and Discussion

The number of significant SNPs from both models is shown in Table 2. A low threshold level was chosen because no extensive multiple testing was done and in addition the empirical power of the study is limited. The FDR *q*-values of the significant associations are relatively high (not shown), suggesting a number of false positives. Nearly the same number of significant SNPs was identified by the two models. However, these were not always the same. Model (1) had more power to detect associations with same effect in the crosses. Model (2) detected additional significant associations that showed opposite effect signs in the crosses.

Some of highly significant SNPs and their chromosomal position and candidate genes are shown in Table 3. ATF2 showed significant results for the trait CY and BWG. GO terms of the gene's transcripts are connected to terms like muscle organ development, embryo development, regulation of protein metabolic process and therefore were of functional interest. SNP *OAR18_68269251.1* seemed to be of special interest because of possible homolog functions to the human *DLK1* gene, which is known to be involved in cell differentiation of several cell types also in other species (Appelbe et al., 2013).

Conclusion

Targeted association analysis revealed weak significant SNP associations for all traits. Modeling SNP effects nested within crosses revealed additional significant associations that would have been missed if the SNP would have been fitted solely across the crosses. Interesting candidate genes were identified. The study will be continued using additional

targeted and untargeted SNPs. This will allow also an SNP-based modeling of the population effects.

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Table 1 Crosses, cross abbreviation, number of sires and number of F1 lambs

Cross	Abbrev.	*n* sires	*n* lambs
Charollais x ML[1]	CH	5	298
Ile de France x ML	IF	5	329
ML x ML	ML	4	225
Blackheaded Mutton x ML	SK	5	221
Suffolk x ML	SU	5	277
Texel x ML	TX	4	143

[1]ML = Merinoland sheep

Table 2 Number of significant SNPs, results from both models

	Model (1)		Model (2)	
Trait	p≤0.01	p≤0.001	p≤0.01	p≤0.001
BWG[1]	4	1	3	2
CY[2]	4	1	6	2
HC[3]	8	2	6	2
DRIP[4]	2	0	5	0
FAT[5]	5	0	4	0

[1] BWG = daily bodyweight gain during fattening
[2] CY = carcass yield
[3] HC = haunch circumference
[4] DRIP = drip loss
[5] FAT= fat layer

Table 3 Significant SNPs per trait, candidate genes, error probability (*p*) effect estimates ($\hat{b}$ and $\hat{b}_i$) (standard error in parenthesis), results from both models

Trait[1] (μ ± σP)	SNP bp [2]	candidate gene	Model (1)		Model (2)		
			p	$\hat{b}$	*p*		$\hat{b}_i$
BWG (330.1 ±70.9)	OAR2_142354112.1 133865504	ATF2	<0.001	-5.169 (1.520)	<0.001	CH	- 5.930(3.494)
						IF	- 0.583(2.917)
						ML	2.912(4.255)
						SK	-13.863(4.687)
						SU	- 8.768 (3.200)
						TX	- 7.692 (5.454)
	OAR18_68269251.1 64385940	DLK1, BEGAIN, oar-mir-136	0.394	-1.680 (1.970)	0.001	CH	-12.255(5.873)
						IF	4.721 (5.824)
						ML	15.751(4.879)
						SK	- 5.256 (4.313)
						SU	- 7.370 (3.490)
						TX	- 3.306 (5.987)
CY (53.6 ±4.6)	OAR2_142354112.1 133865504	ATF2	<0.001	-0.331 (0.091)	0.010	CH	-0.320 (0.200)
						IF	-0.464 (0.175)
						ML	-0.548 (0.272)
						SK	-0.328 (0.313)
						SU	-0.092 (0.188)
						TX	-0.227 (0.320)
	OAR2_205872952.1 194324700	PCGEM1	0.145	0.126 (0.086)	<0.001	CH	0.297 (0.174)
						IF	0.341 (0.186)
						ML	0.458 (0.244)
						SK	0.130 (0.218)
						SU	0.057 (0.210)
						TX	-0.905 (0.255)
	OAR3_197402139.1 183368930	DENND5B, FAM60A, CAPRIN2,	0.010	0.227 (0.088)	<0.001	CH	-0.095 (0.192)
						IF	-0.022 (0.202)
						ML	1.043 (0.248)
						SK	0.671 (0.239)
						SU	0.153 (0.184)
						TX	0.087 (0.239)
HC (64.0 ±2.7)	OAR1_140104902.1 129332577	-	<0.001	-0.214 (0.065)	0.053	CH	-0.173 (0.143)
						IF	-0.196 (0.144)
						ML	-0.288 (0.164)
						SK	-0.323 (0.168)
						SU	-0.193 (0.150)
						TX	-0.164 (0.186)
	OAR1_145988855.1 135244346	-	0.990	-0.008 (0.001)	<0.001	CH	0.151 (0.135)
						IF	0.684 (0.168)
						ML	-0.271 (0.172)
						SK	-0.301 (0.151)
						SU	-0.258 (0.152)
						TX	0.014 (0.189)
	OAR2_222903133.1 210644328	ENSOARG 0000001949	<0.001	-0.228 (0.064)	0.035	CH	-0.343 (0.164)
						IF	-0.199 (0.142)
						ML	-0.322 (0.164)
						SK	-0.091 (0.158)
						SU	-0.197 (0.149)
						TX	-0.187 (0.157)
	OAR3_169440758.1 158312976	-	0.305	-0.067 (0.065)	<0.001	CH	-0.502 (0.177)
						IF	-0.113 (0.145)
						ML	-0.219 (0.146)
						SK	0.062 (0.165)
						SU	-0.040 (0.139)
						TX	-0.239 (0.204)

[1] Abbreviations are shown in Table 1 and 2; [2] Flicek et al., 2014

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CHAPTER FIVE

Chromosome-wide association analysis of growth, carcass and meat quality traits in multiple Merinoland sheep crosses using imputed SNP-chip data

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Submitted

Chromosome-wide association analysis of growth, carcass and meat quality traits in multiple Merinoland sheep crosses using imputed SNP-chip data

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Summary The present study reports the results from a chromosome-wide association analyis in multiple F1 sheep crosses for growth, carcass and meat quality traits. The data set included about 1500 F1 crossbreed and purebred Merinoland (ML) -lambs. 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. The sires and a number of dams were genotyped with the Illumina OvineSNP50 BeadChip. All 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, which were located on these chromosomes, in the F1 individuals. Single marker association analysis was performed with sire-breed specific effects and one effect for the common dam breed (i.e. ML). 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.

Keywords: imputation, association analysis, German Merinoland sheep, multiple connected F1 sheep crosses

1. Introduction

In sheep lamb meat production most important traits are growth, carcass and meat quality traits. The Merinoland (ML) sheep is the most common breed in Southern Germany due to its high-quality wool, high fertility, robustness, and its motility (Sambraus, 2011, Schiller et al., 2015). Extensive breeding is practised and no DNA-type information is used for selection. In order to improve lamb meat quality ML ewes are frequently crossed with a sire from a meat type breed. Recently we reported the results from a comparable large scale cross experiment, where ML ewes were mated with sires from six meat type breeds in order to generate F1 lambs with an improved meat quality (Henseler et al., 2014). In that study, parentage testing was conducted with 384 SNPs. In the mean time the founder rams and several founder ewes were genotyped with the Illumina Ovine SNP50 BeadChip. Hayes et al. (2011) and Bolormaa et al. (2015) imputed 50k genotypes using low density SNP panels in multiple breed sheeps. In a pig breeding data set, Wellmann et al. (2013) imputed SNP chip genotypes in offspring using only 768 SNPs with an error rate of 8%, provided that boars were genotyped with the porcine 60 k SNP chip and family and linkage disequillibrium was used for imputation.

Following these encouraging imputation results, the aim of the present study was to impute the SNP chip genotypes into the F1 crossbred lambs and subsequently to use these imputed genotypes for association analysis for growth, carcass and meat quality traits on selected chromosomes.

2. Materials and Methods

The dataset included about 1500 F1 crossbred and purebred ML-lambs. 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. The number of F1 lambs within the crosses varied between about 150 (Texel) and 359 (Ile de France). The lambs were run with their mothers on pasture until weaning (ca. 19 kg bodyweight and at least eight weeks of age). Lambs were slaughtered at 39-45 kg at a commercial abattoir. The lambs had a mean

body weight at slaughter of 41.33 ± 4.81 kg at an age of 102 to 161 days. Summary statistics of the traits considered in the present study are shown in Table 1.

Blood samples were collected at day of slaughtering and the DNA was extracted using standard methods. All samples were genotyped at 384 SNP on 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 passed the data filtering. These SNPs were located on chromosome 1, 2, 3, 18 and 21, in order to focus on chromosomes where QTL for these traits have been reported in the literature (Hu et al., 2016).

Furthermore all 32 sires and all 359 purebred ML lambs (phenotyped for the traits) used in the experiment, as well as a number of 61 purebred ML from different breeders were genotyped with the Illumina OvineSNP50 BeadChip (Illumina Inc., CA, USA), containing 54 977 SNP. SNPs were removed from the analysis if the following quality control measures were not met: A call rate of > 95%, a genotype call (GC) score of > 0.6, minor allele frequency of > 0.01, in Hardy-Weinberg equilibrium (a *P*-value cut-off of 1^{-15}), genome location known, in < 0.99 linkage disequilibrium with another SNP on the array. Thus 46 210 SNP from this SNP chip remained in the data set. The SNP alleles were coded as 0-allele and 1-allele.

The 50k SNP chip genotypes on chromosomes 1, 2, 3, 18 and 21 were imputed using the 289 SNPs using the imputation method of Wellmann et al. (2013). The number of SNPs on these chromosomes was 5202, 4876, 4427, 1245, and 784 respectively. The total number of SNPs was 16 534. The imputation method is described in detail in Wellmann et al. 2013 and only essentials are given in the following. The paternal inherited alleles of the lambs were imputed from their 50K genotyped sires, whereas the maternal inherited alleles were imputed from a haplotype library, which was built up using the 50K genotypes from ML individuals. 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 favoured 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.

Association analysis (AS) on the selected chromosomes for the 16 534 SNPs was done using a single SNP mixed linear model in R with function lm. Since the linear model assumed normally distributed residuals and violation of this assumption can severely affect the power and type I error, the traits deviating from normality were transformed to approximate normality. Traits were transformed by using the logarithm to reduce skewness and the arcustangens to reduce the thickness of the tails, see Table 1. The residuals were tested for normality with the Shapiro test in order to investigate if the transformation was successful.

The mixed model included a fixed breed effect, breed specific effects of the paternal inherited allele, and an effect of the maternal inherited allele. Further explanatory variables were determined for each trait separately. The sex, the weight at arrival at the fattening unit, the weight at slaughter, the season, the herd, and interactions between them were included if they were significant (p-value < 0.05). Additionally 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 had a significant effect on the trait (p-value < 0.05). All explanatory variables were considered as fixed.

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 were included in the model, whereby the effect of the 0-allele was set to 0 in both cases. Following this parameterization, the following three F-tests were performed with the corresponding null hypotheses:

1) All effects of the marker are equal to zero.
2) The breed specific effects of the paternal allele are all equal to zero.
3) The maternal effect of 1-allele is equal to zero.

The first test was used to identify experiment-wise significant markers, whereby Bonferroni was used to correct for multiple testing. A SNP was declared as significant if the Bonferroni corrected *p*-value < 0.05 and if the residuals were approximately normal distributed (*p*-value > 0.0001 from the Shapiro test). If the second test was experiment wise significant then Dunnett's linear contrast test was performed to determine the sire breed in which the marker has 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.

3. Results and Discussion

The results of the association analysis are shown in Table 2. For the traits SW, CA, Cook, H 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. Especially for SW the association analysis was successful in identifying significant SNPs. The plots of the test statistics are shown in Figure 1. For SW the seven significant SNPs are distributed over large chromosomal regions and no clear signal with several consecutive significant SNPs could be detected. This might be due to the fact, that the significance is due to the alleles inherited from the Texel sire breed (results from the linear contrast tests, Table S1) and the number of lambs with this sire breed is only 150 and thus the smallest F1 cross. Also for the other significant associations, the Texel breed origin alleles were significant. 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.

4. Conclusion

To conclude, the present study showed that it is possible to conduct association analysis with imputed SNP chip data in multiple connected F1 sheep crosses with only 289 SNPs. Single SNP association analyses were used with modelling F1 cross specific allelic effects. From the results shown in Table S1 it seems that this way of modelling the SNP effects was important, because the linkage disequilibrium between the SNP and the causal mutations seemed to

differ between the groups. An alternative way of analysing the data would be to use only the SNPs used for imputation and to conduct linkage analysis in the multiple and connected F1 cross groups (Rückert and Bennewitz 2010).

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Table 1 Trait, trait ID, unit, number of observations (n), mean, standard deviation (sd), and heritability[1] (h^2)

Trait	Trait ID	unit	*n*	MEAN	SD	h^2
Daily gain	DG	[g/d]	1466	330.28	67.85	0.23
Dressing Percentage	DRESS	[%]	1436	49.02	2.35	0.20
Kidney Fat Weight	KFW	[g]	1480	236.56	115.21	0.19
Carcass length	CarL	[cm]	1482	40.43	2.47	0.15
Shoulder Width	SW	[cm]	1480	19.57	1.12	0.33
Haunch	H	[cm]	1483	12.14	0.76	0.15
Subcutaneous fat thickness	FAT	[mm]	1482	4.49	1.47	0.22
Cooking loss	COOK	[%]	1401	31.18	3.23	0.07
Warner-Bratzler shear force	SF	[N]	1403	65.10	24.72	0.17
Cutlet area	CA	[cm²]	1482	12.35	1.63	-

[1] Results from a detailed quantitative-genetic analysis of the traits will be described elsewhere.

Table 2 Significant SNP trait associations with chromosome (Chr), position in bp/10^6 (Pos), SNP name, and p-values for tests 1-3.

				p-value[1]		
Chr	Pos	SNP name	Trait	Test 1	Test 2	Test 3
1	82.021	OAR1_82021326.1	SW	3.74E-07	2.96E-07	0.150
1	150.184	OAR1_150183526.1	SW	3.47E-06	1.53E-06	0.525
1	150.193	OAR1_150193285.1	SW	1.88E-06	1.50E-06	0.283
1	173.225	s21244.1	SW	3.00E-06	1.16E-06	0.807
1	225.403	OAR1_225402747.1	CA	4.09E-07	2.27E-06	0.018
2	52.308	OAR2_52308410.1	SW	4.51E-08	2.36E-08	0.177
2	80.474	OAR2_80474394.1	COOK	2.27E-06	1.77E-06	0.095
3	7.255	s62569.1	CA	7.68E-07	3.30E-07	0.349
3	101.25	OAR3_101249671.1	H	3.99E-06	1.51E-06	0.904
3	137.712	OAR3_137712214.1	SW	3.59E-08	1.26E-08	0.427
3	151.078	s68447.1	H	7.65E-07	8.49E-07	0.159
3	231.664	s36196.1	CA	1.50E-06	2.31E-06	0.093
21	27.861	s12930.1	SW	9.34E-08	8.55E-08	0.212
21	36.067	OAR21_36067273.1	SW	3.30E-06	1.41E-06	0.299
21	44.494	OAR21_44493640.1	CA	2.54E-07	9.08E-08	0.930
21	51.128	OAR21_51127739.1	SF	1.81E-07	6.67E-08	0.711

[1] See text for the corresponding null hypothesis.

Table S1 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, with chromosome (Chr), position in bp/10^6 (Pos), and SNP name (significant effects are written in bold).

Chr	Pos	SNP name	Trait	ML	IF	CH	SK	SU	TX
1	82.021	OAR1_82021326.1	SW	0.668	**<0.001**	0.154	0.259	0.111	NA
1	150.183	OAR1_150183526.1	SW	1.000	**0.006**	0.998	0.926	0.557	**<0.001**
1	150.193	OAR1_150193285.1	SW	1.000	**0.011**	0.986	0.517	0.811	**<0.001**
1	173.224	s21244.1	SW	0.053	0.364	0.400	0.932	**0.016**	**<0.001**
1	225.402	OAR1_225402747.1	CA	0.461	0.249	**0.009**	0.289	0.121	**0.025**
2	52.308	OAR2_52308410.1	SW	1.000	0.247	0.119	**0.014**	0.173	**<0.001**
2	80.474	OAR2_80474394.1	COOK	**0.002**	**0.001**	**0.032**	1.000	0.873	0.317
3	7.255	s62569.1	CA	1.000	0.433	0.157	0.992	1.000	**<0.001**
3	101.249	OAR3_101249671.1	H	0.858	0.196	0.722	0.431	**0.001**	**0.002**
3	137.712	OAR3_137712214.1	SW	0.807	**0.012**	**0.016**	**0.019**	0.837	**<0.001**
3	151.077	s68447.1	H	0.736	NA	0.943	**0.000**	NA	**<0.001**
3	231.664	s36196.1	CA	**0.003**	0.894	**0.006**	0.794	1.000	**0.001**
21	27.861	s12930.1	SW	**0.003**	0.059	1.000	0.953	0.933	**<0.001**
21	36.067	OAR21_36067273.1	SW	**0.004**	0.676	0.484	0.739	0.389	**0.001**
21	44.493	OAR21_44493640.1	CA	0.926	0.857	0.581	0.751	0.427	**0.002**
21	51.127	OAR21_51127739.1	SF	0.204	0.768	**0.010**	**0.001**	0.978	**0.001**

[1] Sire breed abbreviations are: ML Merinoland, IF Ile de France, CH Charollais, SK German Blackheaded Mutton (Deutsches Schwarzköpfiges Fleischschaf), SU Suffolk, TX Texel

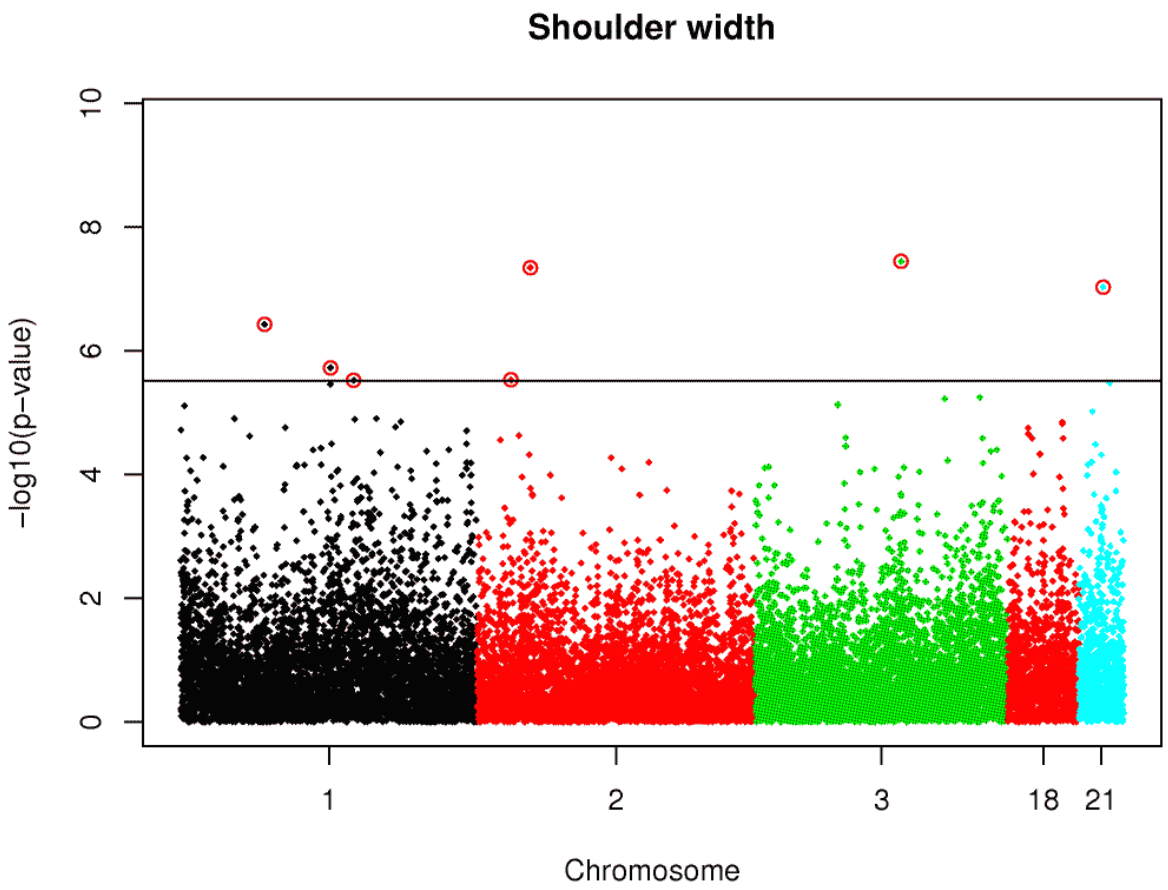

Figure 1 Test statistic profile of SNP effects for shoulder width in the F1-lamb data set. The nominal significance level ($p < 0.001$) is indicated by a solid line, and positions of validated SNP are indicated by circles.

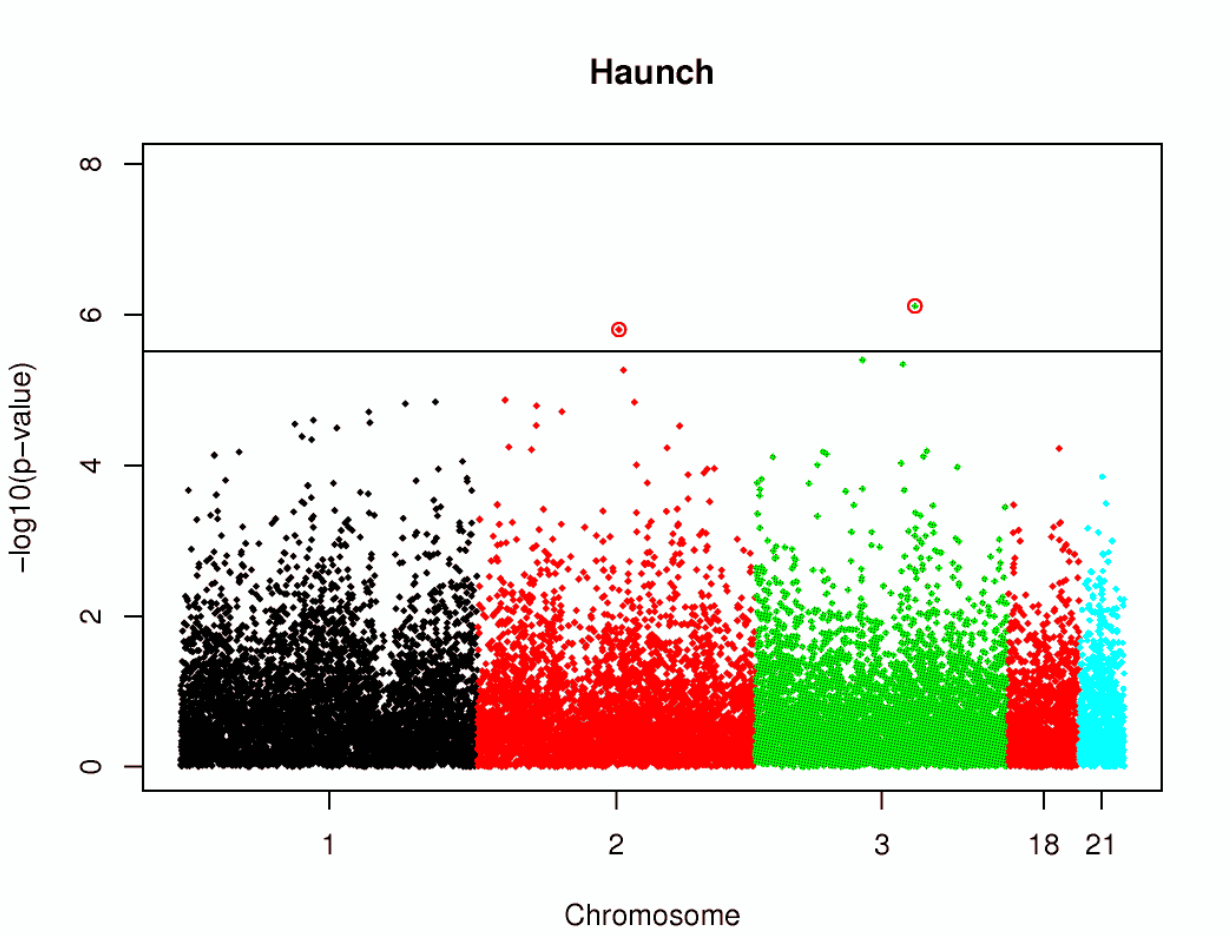

Figure 2 Test statistic profile of SNP effects for haunch in the F1-lamb data set. The nominal significance level ($p < 0.001$) is indicated by a solid line, and positions of validated SNP are indicated by circles.

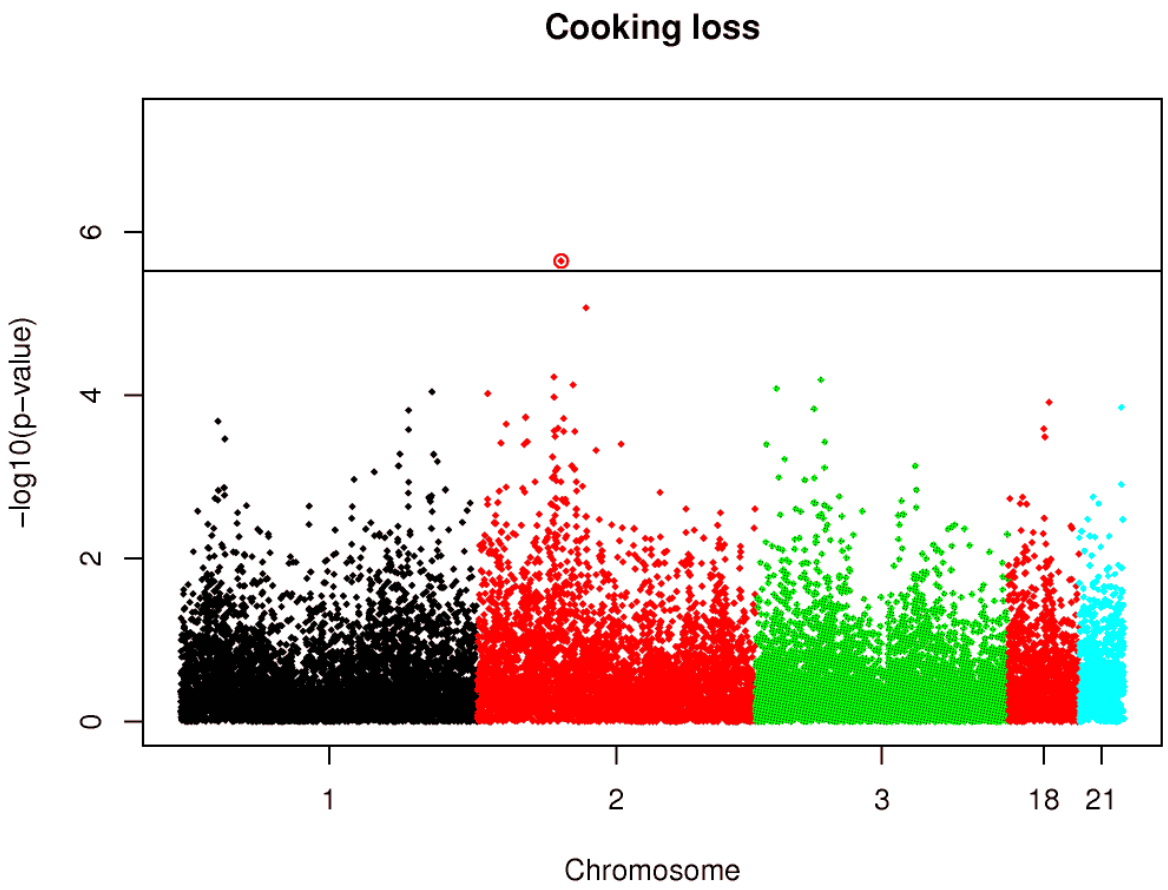

Figure 3 Test statistic profile of SNP effects for cooking loss in the F1-lamb data set. The nominal significance level ($p < 0.001$) is indicated by a solid line, and positions of validated SNP are indicated by circles.

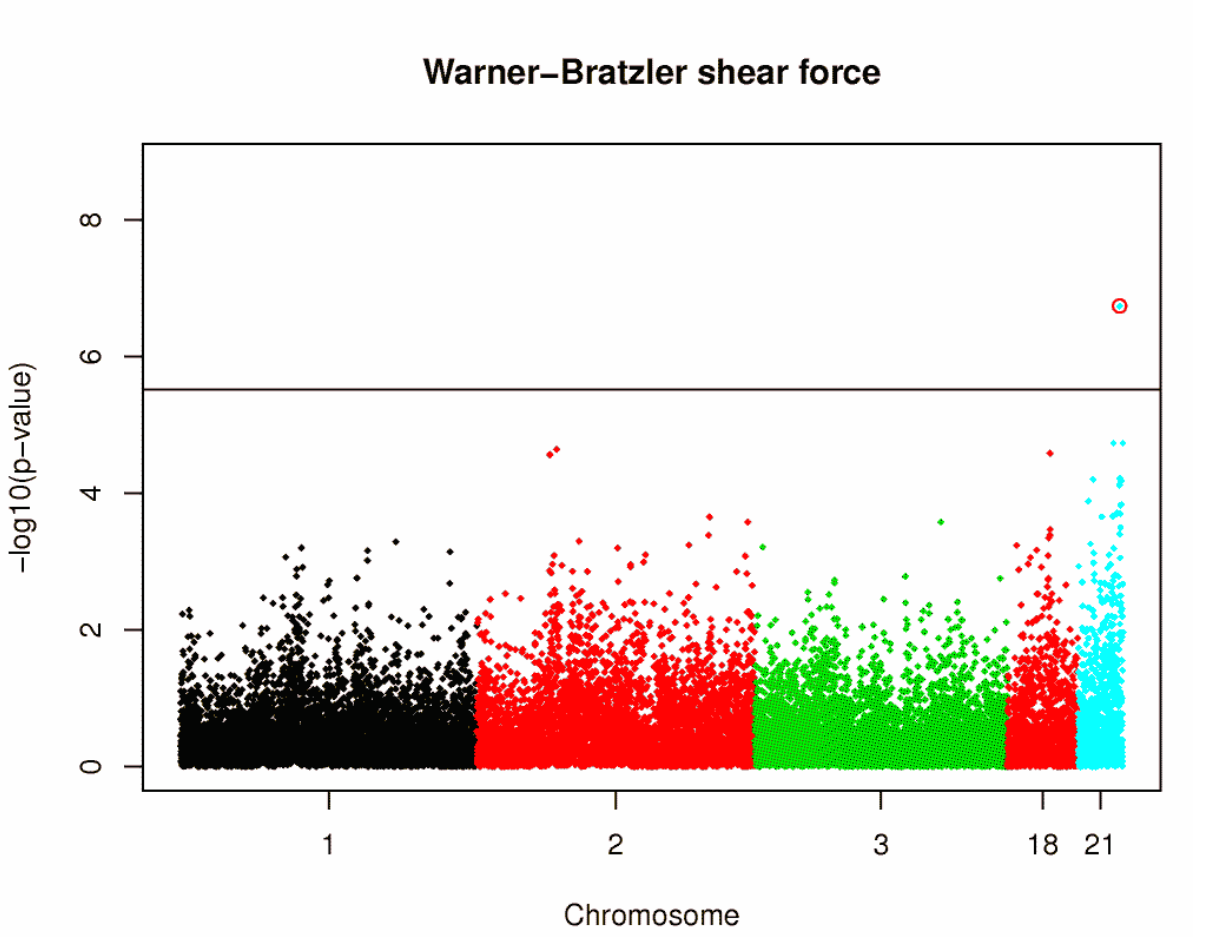

Figure 4 Test statistic profile of SNP effects for Warner-Bratzler shear force in the F1-lamb data set. The nominal significance level ($p < 0.001$) is indicated by a solid line, and positions of validated SNP are indicated by circles.

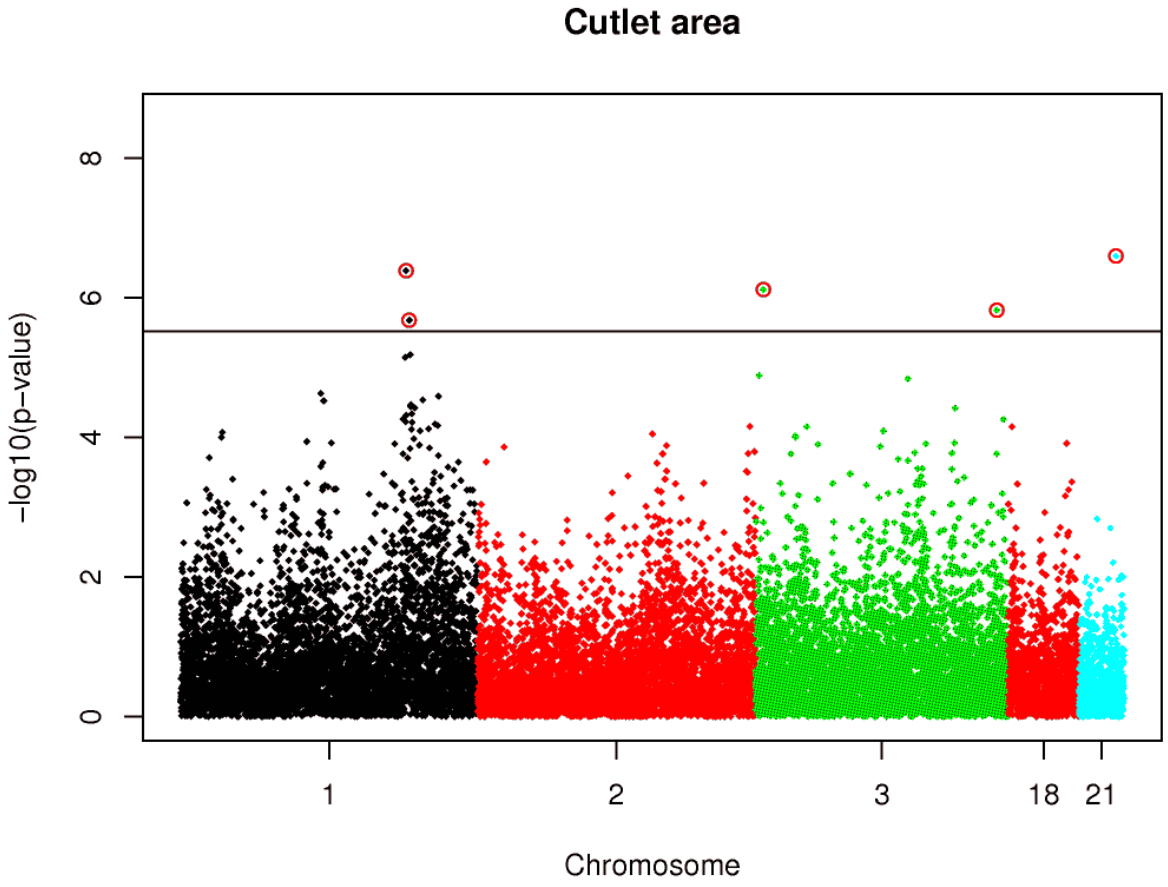

Figure 5 Test statistic profile of SNP effects for cutlet area in the F1-lamb data set. The nominal significance level ($p < 0.001$) is indicated by a solid line, and positions of validated SNP are indicated by circles.

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GENERAL DISCUSSION

The current dissertation contains three parts. In the first chapter, growth curves and feed conversion were investigated. In the second chapter, the concentration of three branched chain fatty acids in lamb meat and fat, and relation to changes in sensory analysis were examined. In the last part, chapters three to five, analyses of the genetic background, genetic parameters, and a chromosome-wide association study using imputed SNP panels were conducted. All experiments were performed with Merinoland (ML) sheep and five crossbreds of meat type sire breeds and ML ewes.

Data

The datasets for all analyses performed, were rather small. For all trials it would have been desirable to use a larger sample size and especially more rams per sire breed to better distinguish between sire and sire breed effects and to represent the variation within sire breeds in a larger extend.

Growth descriptors

Growth curves in this trial compared with the trait average daily body weight gain (ADG) showed the same crosses being superior. ADG, an important economic trait for meat production (Al-Mamun et al., 2014) is used in many sheep breeding programs to describe growth. It is easier to measure and handle than growth curve parameters. For practical reasons daily gain can be recommended to use, despite if altering the shape of a growth curve is attractive as summarized by (Fitzhugh, 1976), e.g. to lower mature weight while maintaining the growth rate is a very interesting method to reach early slaughter weight while lowering the maintenance costs for the parental stock.

Branched chain fatty acids (BCFA)

The results of the trial showed branched chain fatty acids being unproblematic in lamb meat of the tested crosses under the realized conditions, which are typical for intense fattening systems. The analysis of BCFA is rather expensive and time consuming and so is the sensory

analysis. Together with the lack of correlation between BCFA concentrations in meat and fat to the sensory abnormality of meat detected in the sensory analysis of Henseler (2013), makes BCFA concentration currently rather uninteresting for implementation in breeding programs.

Specific problems in sheep breeding

For the present dissertation project a F1 crossbreeding scheme was used, because it is a common approach for producing fattening lambs and is common for ML ewes in Germany. Differences between the crossbreds and purebred ML became obvious in all experiments of the present study. Crossbreeding in sheep has several advantages, e.g. it benefits from heterosis and breed complementarity (Nitter, 2003). On the other hand, crossbreeding entails some management challenges like replacement management of the purebred ewes. Independently from producing crossbreds or purebreds, in practice few sires are shared amongst flocks or even flocks of different owners. This has two main reasons. First, artificial insemination and other reproduction methods are very rarely used, and second, natural-service and sharing of rams results in a complex of hygiene problems. However, not sharing sires results in disadvantages in estimating breeding values: progeny testing takes place only in one environment and therefore compatibility with other flocks is not given (Reinhardt, 2008; Ruten et al., 2013).

Another general problem in sheep breeding are the low inputs and investments in sheep production. This is mainly because sheep production systems are predominantly pastoral based and extensive in nature, and sheep breeding programs have a relatively flat structure (van der Werf et al., 2010). Furthermore, beside wool and meat production, landscape preservation became an important source of income: nowadays, for many sheep farmers more than 50% of income are grants (Blücher, 2014). For landscape preservation it is of lower relevance, whether high quality sheep (in terms of breeding value) are used or not. As a result, these sheep owners do not focus on creating or maintaining a high quality flock regarding meat traits, but more likely to select for management and robustness traits. This might be even more the case because landscape preservation pastures usually do not provide high quality

roughage concerning energy and protein content. The nutrition level also was found to interact with muscling characteristic due to mutation in the *myostatin* gene (Haynes et al., 2015) and seems to influence also weight traits by restricting the lamb`s ability of exploiting its genetic potential (Hegarty et al., 2006). Hence, there is a need to observe and later on implement traits with respect to this extensive production in sheep. It might be of interest to focus on traits, which are less environmental sensitive e.g. eye muscle depth (Hegarty et al., 2006), because of the wide scope of environments in sheep production. The challenge will be to set up a breeding program to enhance meat traits, giving the possibility also to do research and collect data for traits relevant in future, e.g. management, robustness, growth curve or new meat or meat quality (MQ) traits. Nevertheless, this should be done while coping with limited financial resources. Currently, it seems unlikely that sheep breeders or sheep breeding associations in Germany can afford a sufficient investment in a breeding program setup without direct or indirect government-support. A cooperation between the Landesschafzuchtverbände as already existing to develop and maintain estimation of BLUP EBVs (Vit, 2015) for a variety of breeds common in Germany e.g. Ile de France, ML, BHM, Suffolk, Texel (Landwirtschaftskammer Niedersachsen, 2014) should be further encouraged. Such a cooperation between the Landesschafzuchtverbände, breeding associations with activity mainly on the level of federal states within Germany and affiliated under the umbrella organization “Verein deutscher Landessschafzuchtverbände e.V.” (VDL), is essential because of the genetic exchange occurred in the past and the profit of larger datasets and therefore higher accuracies of EBVs.

Implementation in breeding programs

There are several requirements concerning a breeding program for a Merinoland-based lamb production. The program should be profitable in terms of financial and genetic merit. Additionally it should have a certain flexibility to respond rapidly to changes in breeding objectives (Hayes et al., 2013). One possibility might be setup of a nucleus breeding program. These programs are characterized by the main breeding work is being done in small nucleus

populations, mainly via purebred methods (William & Simianer, 2011). Nucleus flocks contain superior individuals compared to the whole population and are usually under special observation and conditions, e.g. use of breeding methods, extensive recording etc. Males bred in the nucleus flock often are raised as future natural-service rams under the same environmental and sanitary conditions, therefore their genetic evaluation, on the basis of individual performance, is more accurate (Danchin-Burge et al., 2010). The use of a nucleus is interesting because only relatively few individuals need to be tested (which lowers testing and maintenance cost) and also EBVs for females can be calculated with accuracies close to young males (Banks, 1997), which is of special interest because some traits can be measured solely on the basis of one gender.

Banks (1997) demonstrated the value of a nucleus breeding program for Poll Dorsets (42 sires and 500 ewes), after three years providing seven of the Australian Top 10 national sires. As a result, the value and the genetic gains can be assumed high and achievable in relatively short time. Therefore, a nucleus breeding program should be considered especially for ML, the numerous most important sheep breed in Germany. However, financing such a program may be problematic in terms of finding a balance between investment and benefit as well as finding an optimum flock size: large enough to involve sufficient variation but not oversized to restrict maintenance costs.

Another approach with greater potential for making genetic change is genomic selection (GS) (Schaeffer, 2006). Marker assisted selection (MAS) and GS are DNA-based selection schemes, where the selection decision is based not only on traditional methods using pedigree and/or phenotype alone but also genotype information (Hayes et al., 2013). Both methods use markers in linkage disequilibrium (LD) with quantitative trait loci (QTL) of the aimed trait to enhance accuracy of BLUP EBV. MAS utilize only few markers, which were identified in previous gene mapping studies and having in ideal a relatively large effect. However, in real data sets the identified genetic markers with an influence on trait variation explain collectively only a small proportion of the traits, a phenomenon that is called the ‘missing heritability’ in

human genetics. In contrast, for GS, which was developed by Meuwissen et al. (2001), many and dense markers are used, covering the whole genome and potentially explaining all the genetic variance of a quantitative trait. Meanwhile there is a commercial dense SNP panel also available for sheep e.g. the OvineSNP50 BeadChip (Illumina, San Diego, CA, USA). To implement GS into a breeding program there exist several indispensable requirements. First of all, a reference, also called discovery set, and a validation or test set is needed (Meuwissen et al., 2001; van der Werf et al., 2014). The reference needs to be built of SNP-chip genotyped individuals with phenotypes of desired traits and/or with EBV of (high) accuracy. From this reference set, the genomic predictors are estimated. In addition, a further set of individuals is necessary for validation and to assess the accuracy of the genomic predictors. After validation, the genomic predictors can be used to calculate GEBVs for candidates and selection decisions can be made. GS is of special interest for traits that are difficult or expensive to measure such as fertility or future traits e.g. methane emission (Hayes et al., 2013). Also for carcass or MQ traits, where records are only derived from relatives because of invasive or destructive approaches (Daetwyler et al., 2012; Knight et al., 2014), or traits expressed late in life like longevity traits (Lee et al., 2015), GS is of interest, because of selection decisions can be made already for young candidates. Concerning MAS and use of a very low density marker panel (as in chapter five), this density seems not sufficient, most likely because of a high effective population size, and therefore, less favorable LD. In populations with large effective population size, and hence, small variance of true relationship, a large number of markers is necessary (Goddard et al., 2010) to receive acceptable accuracies. In general, the higher the genetic variety of a population, the larger the reference set and the more dense the marker panel needs to be assigned. To estimate the effective population size, either genotypic data or population parameters can be used. The effective population size is rather high (>100) in many sheep breeds (e.g. Baloche et al. (2014); Danchin-Burge et al. (2010); Kijas et al. (2009); Zhao et al. (2014)). The dataset used for the present experiments is of special interest. This is because utilization of a crossbred training set for GS can increase the crossbred performance compared to two purebred or combined reference populations (Esfandyari et al., 2015). These

authors further demonstrated an improvement in genomic prediction by tracing the line origin of alleles in crossbreds, if they are not very close related. The high cost of genotyping relative to the individual value of the animal (even using low-density chips and imputation) imposes a significant cost/benefit challenge in sheep, and one which makes optimization of use of genomic prediction likely to be quite different from that in dairy cattle (Baloche et al., 2014). On the other hand, the genotyping costs have rapidly decreased. In addition, in cattle, low-density chips are alternative tools that reduce genotyping costs per animal (Dassonneville et al., 2012; García-Ruiz et al., 2015), allowing the genotyping of more individuals (Dassonneville et al., 2012), or increasing the data available for a reference population. GS up to-date is not commonly used in sheep breeding. Currently to our knowledge only in Australia and New Zealand, breeding programs are running including GS for meat-type sheep. In both countries a combination of GS and a nucleus flock was developed. In contrast to Australia, where also several breeds were investigated, in New Zealand a multi-breed approach was set up (Auvray et al., 2011). In Australia the so-called INF (information nucleus flock) was established and used as a basic for the reference population, while for validation selected rams with EBVs of high accuracy were used (Fogarty et al., 2007; Swan, 2012). Even though breeders in New Zealand work with a multi-breed approach, and via the utilization of very dense marker panels or even whole-genome sequence, prediction equations across breeds are conceivable (de Roos et al., 2009), according to Hayes et al. (2013) and van der Werf et al. (2014) this technique currently cannot be recommended. According to the authors, this is presumably because of differences in LD across sheep breeds, which made a pooling of reference populations and genomic prediction across breeds largely unsuccessful to-date.

The basic for a setup of the reference and the validation set could be started to build right by now. This can be done by collecting DNA samples of individuals with EBVs, candidates getting EBVs in future, and phenotyped individuals to provide data when starting GS. A large reference set is desired because it provides more accurate estimations of the genomic predictor, especially when the effective population size is large or heritabilities low (Goddard & Hayes, 2009; Meuwissen et al., 2001). The most important questions about reference sets (according

to van der Werf et al. (2014)) are the selection of optimal animals for it and its minimum size. The size of the reference set directly affects costs and the accuracy of genomic predictions (van der Werf et al., 2014), but also depends on the kind of approach, which means structure of the chosen population, marker density of the panel and the characteristic of the aimed traits. On the other hand, imputed data should provide most of the mentioned advantages of high density panels (or whole-genome sequence; Hayes et al., 2012), and, therefore, are an interesting cost-effective alternative when the low density SNP panel is of sufficient density. Finally yet importantly, it is fundamental that the sheep breeders and consumers accept new breeding approaches. Possibly the recent invention of BLUP already provides a basis for new inventions in breeding and will enhance acceptance and support of the breeders, while consumers need to be convinced by the products. Nevertheless, an information campaign and early involvement of the breeders will be required.

Future research

It was revealed that further research is necessary to clarify influences of age, ripening and storage on BCFA. Other influencing substances like e.g. scatole and its possible interactions to BCFA should be tested. The sensory testing not only of meat, but also of fat and both in combination might reveal some new insights. In the future, controlling of these traits may become important to include into sheep breeding programs.

For future research it will be of interest to enlarge the phenotypic dataset for ML with records of traits important under extensive conditions. In the long-term, the setup of a nucleus flock and/or GS will be of high interest, especially for implementing hard-to-measure traits. One potentially interesting trait-“package” would be growth descriptors to alter the shape of growth curves as already mentioned above, to maintain or increase high growth rates in youth, but reaching the (lowered) mature weight to decrease maintenance costs of the flock, especially during the non-pasture time of year. Furthermore, enlarging the genotype dataset with more individuals and with a higher density of genotypes will provide several possibilities. The most important ones are the delivering of more accurate results regarding heritability and

correlations estimation between traits as well as datasets to undertake GWAS and GS. GS possibly can raise accuracies of breeding values and genetic gain especially in hard-to-measure traits. Regarding to financial limitations the possibilities of imputation from a low density panel should be considered.

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AFFIDAVIT

Pursuant to Sec. 8(2) of the University of Hohenheim`s doctoral degree regulations for Dr. sc. agr.

1. I, Katja Schiller hereby declare that I have independently completed the doctoral thesis submitted on the topic *Phenotypic and genetic analysis of meat production traits in German Merinoland purebred and crossbred lambs.*

2. I only used the sources and aisd documented and only made use of permissible assistance by third parties. In particular, I properly documented any contents, which I used – either by directly quoting or paraphrasing – from other works.

3. I did not accept any assistance from a commercial doctoral agency or consulting firm.

4. I am aware of the meaning of this affidavit and the criminal penalities of an incorrect or incomplete affidavit. I hereby confirm the correctness of the above declaration. I hereby affirm in lieu of oath that I have, to the best of my knowledge, declared nothing but the truth and have not omitted any information.

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