Estimation of direct and maternal genetic effects and annotation of potential candidate genes for weight and meat quality traits in a genotyped outdoor dual-purpose cattle breed

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ABSTRACT

With regard to potential applications of genomic selection in small numbered breeds, we evaluated genomic models and focused on potential candidate gene annotations for weight and meat quality traits in the local Rotes Höhenvieh (RHV) breed. Traits included 6,003 birth weights from 370 genotyped cattle with phenotypic records were included in genomic analyses. Model evaluations focused on single- and multiple-trait models with direct and with direct and maternal genetic effects. Genetic relationship matrices were based on pedigree (A-matrix), SNP markers (G-matrix), or both (H-matrix). Genome-wide association studies (GWASs) were carried out using linear mixed models to identify potential candidate genes for the traits of interest. De-regressed proofs (DRP) for direct and maternal genetic components were used as pseudo-phenotypes in the GWAS. Accuracies of direct breeding values were higher from models based on G or on H compared to A. Highest accuracies (> 0.89) were obtained for IMF with multiple-trait models using the G-matrix. Direct heritabilities with maternal genetic effects ranged from 0.62 to 0.66 for BWT, from 0.45 to 0.55 for 200dW, from 0.40 to 0.44 for 365dW, and from 0.48 to 0.75 for IMF. Maternal heritabilities for BWT, 200dW, and 365dW were in a narrow range from 0.21 to 0.24, 0.24 to 0.27, and 0.21 to 0.25, respectively, and from 0.25 to 0.65 for IMF. Direct genetic correlations among body weight traits were positive and favorable, and very similar from different models but showed a stronger variation with 0.31 (A), −0.13 (G), and 0.45 (H) between BWT and IMF. In gene annotations, we identified 6, 3, 1, and 6 potential candidate genes for direct genetic effects on IMF with multiple-trait models using the G-matrix. Direct heritabilities for both traits in the range from 0.40 to 0.50. Even higher heritabilities up to 0.88 for carcass traits were presented (Halli et al., 2020; MacNeil et al., 2010). As the most important finding from a practical breeding perspective, a small number of genotyped RHV cattle enabled accurate breeding values for high heritability IMF.

Key words: dual-purpose cattle, genetic parameters, meat quality, SNP marker, weight

INTRODUCTION

“Rotes Höhenvieh” (RHV) is a dual-purpose medium-sized cattle breed with a uniform red-brown hair color, originated from the Central Uplands of Germany. RHV cattle are mainly kept for quality beef production in low input grazing systems, and selection has focused on adaptation to harsh environments (Halli et al., 2020). In comparison to the mainstream beef cattle breeds, the small RHV population size implies a continuously decreasing selection intensity, with impact on the breed competitiveness. Hence, especially for such local endangered breeds, it is imperative to focus on niche markets, e.g., markets offering special meat products and aiming on meat quality improvements (Biermann et al., 2015). Furthermore, in beef breeds with small population size, it is imperative to apply all available modern technologies such as reproduction techniques or genomic selection to achieve at least moderate genetic gain per year (Pimentel and König, 2012). Incorporation of body weight and meat quality traits into a genetic evaluation scheme requires accurate genetic parameter estimates. Moderate to high direct pedigree-based heritabilities were reported for body weight traits of several beef cattle breeds (Gutiérrez et al., 2007; Regatiere et al., 2012; Caetano et al., 2013), indicating the potential for genetic improvement. The most studied meat quality traits in beef cattle are intramuscular fat content (IMF) and shear force. In their review, Utrera and VanVleck (2004) presented direct heritabilities for both traits in the range from 0.40 to 0.50. Even higher heritabilities up to 0.88 for carcass traits in American Shorthorn cattle were reported by Pariacote et al. (1998). Such moderate to high heritability estimates when modeling pedigree relationships (A-matrix) were confirmed in more recent studies (MacNeil et al., 2010; Mateescu et al., 2015). Using commercially available genetic marker panels (i.e., two markers per panel), significant associations of the...
thyroglobulin-, calpastatin-, and the μ-calpain-marker with meat quality traits were observed for meat quality traits in beef cattle (Van Eenennaam et al., 2007). As shown in deterministic predictions for high heritability traits, training sets comprising 700 to 1,000 animals with genomic marker data and phenotypes enable precise estimates of genomic breeding values (Daetwyler et al., 2008). The very dense 777K SNP chip allowed quite accurate estimates for production traits in beef cattle, even when considering different breeds in the same reference set (Rolff et al., 2010). In a genome-wide association study (GWAS), Lu et al. (2013) used a sample size including 747 crossbred beef cattle and identified 34 SNP markers significantly associated with IMF and meat marbling score.

In addition, especially for weight or weight gain traits in ruminants, a strong maternal genetic component has been identified, even for traits recorded late in life (Mandal et al., 2006). Saatci et al. (1999) and Meyer (1992) indicated biased estimates when neglecting maternal genetic effects in genetic evaluations for sheep and beef cattle, respectively. For weights at different ages recorded in Holstein Friesian calves and heifers, Yin and König (2019) identified a moderate genetic maternal component up to the age of 1 yr. They considered 4,246 animals with genotypes and inferred a large number of SNP markers either contributing to the direct or maternal genetic effects on weights at the age of 3 mo.

The combination of pedigree and genomic information in so-called single-step approaches (e.g., Aguilar et al., 2010) especially offers potential to improve genetic evaluations in small-sized breeds with poorly recorded pedigrees. Single-step methods have been developed for the estimation of genetic parameters and breeding values (Miszatal et al., 2018), as well as for GWAs (Wang et al., 2012). Recently, Shabalina et al. (2021) evaluated genetic parameters from pure genomic, pedigree-based, and single-step approaches considering a small sample size of only 758 genotyped cows with phenotypes for low heritability functional traits. Heritabilities and genetic variances from the single-step approach were in-between the estimates from the pure pedigree and genomic models, and associated with small standard errors.

A further modeling question addresses the application of single-trait genomic (STGM) or multiple-trait genomic models (MTGM), with generally higher accuracies of genetic parameter estimates from MTGM (Jia and Jannink, 2012; Ismael et al., 2017; Srivastava et al., 2019). In beef cattle, body weight and meat quality traits are genetically closely correlated (Gordo et al., 2016), and the benefits from a MTGM over a STGM may be smaller compared to genetic evaluations for low heritability traits (Daetwyler et al., 2012; Guo et al., 2014).

In beef cattle, there is a gap of scientific studies comparing pedigree-based and genomic models, especially for novel meat quality traits from local breeds kept in alternative low input production systems. Furthermore, to the best of our knowledge, no previous GWAS has been conducted to estimate maternal genetic effects on meat quality traits. Consequently, the objectives of this study were to 1) estimate direct and maternal genetic (co)variance components for body weight and IMF traits using pedigree-based, pure genomic, and combined pedigree-genomic models in RHV dual-purpose cattle, 2) compare estimates from single-trait and multiple-trait models with and without maternal genetic effects, and 3) perform GWAS in order to identify genomic regions that are associated with direct and maternal genetic effects on weight traits and on IMF.

**MATERIALS AND METHODS**

The research did not involve any direct physical contact to the animals. No experimental studies were conducted for this project. Hence, no additional statement of institutional animal care and use committee is required.

**Animals and Traits**

For weight traits, phenotypic data of 9,184 RHV cattle from 269 herds were provided by ‘Vereinigte Informationssysteme Tierhaltung w. V.’ (VIT) (Verden, Germany), with permission of all RHV breeder societies involved. All herds reflect a pasture-based production system. Data recording for weight traits spanned a period of 20 yr (2000 to 2019) and included birth weight (BWT), 200 d-weight (200dW), and 365 d-weight (365dW).

For intra-muscular fat content (IMF) analyses, a subset including 33 RHV herds provided meat samples from 547 RHV animals from the slaughtering years 2018 to 2020. The meat samples with a thickness of 3.5 cm were taken from the *musculus longissimus dorsi* between the 12th and 13th ribs. All samples were temporarily frozen and stored until analyses in the meat laboratory at Kassel University. IMF was determined by applying near-infrared (NIR) spectroscopy.

Records from herds with less than 10 phenotyped cattle were excluded. All traits were corrected for outliers by excluding values lower or higher the mean ± 3 SD. After data editing, the dataset for weight traits included 6,003 observations for BWT, 5,719 observations for 200dW, 4,594 observations for 365dW, and 547 records for IMF for ongoing genetic-statistical analyses. Means were 36.7 kg (± 5.5 kg) for BWT, 231.4 kg (± 60.4 kg) for 200dW, 342.9 kg (± 74.7 kg) for 365dW, and 2.45 % (± 2.6 %) for IMF. The pedigree dataset included 9,989 animals with 481 sires and 2,910 dams.

**Genomic Data**

The genomic dataset consisted of 777,963 SNP markers from 380 genotyped animals. SNP genotypes quality control was performed using the PLINK software (Purcell et al., 2007). SNPs with a call rate lower than 0.90 (2,581 SNPs), a minor allele frequency lower than 0.05 (146,469 SNPs) and a significant deviation (*P*-value < 10^-6) from Hardy–Weinberg equilibrium (4,939 SNPs) were discarded. Furthermore, 42,670 SNPs located on the sex chromosomes, and 10 cattle due to an individual call rate lower than 0.90, were excluded. Finally, 370 genotyped cattle with 581,304 SNP markers were considered in the ongoing genomic analyses. All of the genotyped animals were phenotyped for weight traits, and a subset of 343 animals had phenotypic records for IMF.

**Genetic-Statistical Models**

The genetic models reflected different genetic relationship matrices. The basic model was a single-trait animal model using the pedigree relationship matrix (A) with direct genetic effects (STPM_d, model 1), which was expanded to a model with direct and maternal genetic effects (STPM_dm, model 2). The STPM_d and STPM_dm were defined as follows:

\[
\text{STPM}_d = \beta_d + \text{Genetic effects} + \text{Error}
\]

\[
\text{STPM}_dm = \beta_d + \beta_m + \text{Genetic effects} + \text{Error}
\]
Genetics of weight and meat quality traits

\[ y = Xb + Z_a \alpha + e \]  

(1)

\[ y = Xb + Z_a \alpha + Z_m \eta + e \]  

(2)

where \( y \) is the observation vector for BWT, 200dW, 365dW or IMF; \( b \) is a vector for fixed effects including herd-year-season, sex, and age at recording as a covariate for 200dW, 365dW, or IMF; \( a \) is a vector for random direct genetic effects; \( m \) is a vector for random maternal genetic effects; and \( e \) is a vector for random residual effects; \( X, Z_a \), and \( Z_m \) are incidence matrices relating the records to the fixed, direct genetic, and maternal genetic effects, respectively.

The (co)variance structure for random effects for the STPM_d was (and correspondingly reduced in STPM_d without maternal genetic effect)

\[
\text{var} \begin{bmatrix} \alpha \\ m \\ e \end{bmatrix} = \begin{bmatrix}
\sigma^2_1 & \ldots & \sigma^2_1 \\
\sigma^2_m & \text{A} & \sigma^2_m \\
0 & 0 & 1\sigma^2_e
\end{bmatrix},
\]

where \( \sigma^2_1, \sigma^2_m, \) and \( \sigma^2_e \) are direct genetic, maternal genetic, and residual variances, respectively; \( \sigma^2_m \) is the covariance between direct and maternal genetic effects; \( \text{A} \) is the numerator relationship matrix among individuals; and \( I \) is an identity matrix for residual effects.

The direct heritability (\( h^2_1 \)), maternal heritability (\( h^2_m \)), and the correlation between direct and maternal genetic effects (\( r_{am} \)) were calculated as follows: \( h^2_1 = \frac{\sigma^2_1}{\sigma^2 + \sigma^2_1} \), \( h^2_m = \frac{\sigma^2_m}{\sigma^2 + \sigma^2_m} \), and \( r_{am} = \frac{\sigma_{am}}{\sqrt{\sigma^2_1 \cdot \sigma^2_m}} \), where \( \sigma^2_1, \sigma^2_m, \) and \( \sigma^2_e \) denote direct genetic, maternal genetic, and phenotypic variances, respectively, and \( \sigma_{am} \) is the direct-maternal genetic covariance. The phenotypic variance was calculated as the sum of the direct genetic variance, the maternal genetic variance, the residual variance, and the covariance between direct and maternal genetic effects.

Multiple-trait pedigree-based models including the four traits simultaneously with only direct genetic effects (MTPM_d, model 3) and with direct and maternal genetic effects (MTPM_dm, model 4) were defined as follows:

\[
y_1 = X_1 \alpha + Z_1 \beta + a_1 + e_1
\]

\[
y_2 = X_2 \alpha + Z_2 \beta + a_2 + e_2
\]

\[
y_3 = X_3 \alpha + Z_3 \beta + a_3 + e_3
\]

\[
y_4 = X_4 \alpha + Z_4 \beta + a_4 + e_4
\]

where subscripts 1 to 4 refer to four traits (i.e., BWT, 200dW, 365dW, and IMF). The (co)variance structure for the MTPM_dm was

\[
\text{var} \begin{bmatrix} \alpha \\ m \\ e \end{bmatrix} = \begin{bmatrix}
\text{A} \sigma^2_1 & \ldots & \text{A} \sigma_{1,m_4} & 0 & \ldots & 0 \\
\ldots & \ldots & \ldots & \ldots & \ldots & \ldots \\
\text{A} \sigma_{m_1,1} & \ldots & \text{A} \sigma_{m_1,m_4} & 0 & \ldots & 0 \\
0 & \ldots & 0 & 0 & \ldots & 0 \\
0 & \ldots & 0 & 0 & \ldots & 0 \\
0 & \ldots & 0 & 0 & \ldots & 0
\end{bmatrix}
\]

where \( \sigma^2_1 \) and \( \sigma^2_m \) are direct and maternal genetic variances, respectively, for trait \( i \) (i.e., \( i = 1 \) to 4); \( \sigma_{1,m} \) is the covariance between the direct genetic effect for trait \( i \) and the maternal genetic effect for trait \( j \) (i.e., \( j = 1 \) to 4); \( \sigma^2_1 \) and \( \sigma_{r,e} \) are residual variances and covariances, respectively; \( \text{A} \) is the numerator relationship matrix among animals; and \( I \) is an identity matrix.

In the multiple-trait analysis, direct genetic correlations between traits were calculated as \( r_{ij} = \frac{\text{A} \sigma_{ij}}{\sqrt{\sigma^2_1 \cdot \sigma^2_j}} \), where \( \sigma_{ij} \) is the direct genetic covariance between traits \( i \) and \( j \); \( \sigma^2_1 \) and \( \sigma^2_j \) are the direct genetic variances for traits \( i \) and \( j \), respectively. Genetic correlations between direct genetic effect for trait \( i \) and maternal genetic effect for trait \( j \) or vice versa, were calculated as \( r_{ij} = \frac{\text{A} \sigma_{ij}}{\sqrt{\sigma^2_1 \cdot \sigma^2_m}} \), where \( \sigma_{ij} \) is the covariance between direct genetic effects for trait \( i \) and maternal genetic effects for traits \( j \); \( \sigma^2_1 \) and \( \sigma^2_m \) are the direct genetic variance for trait \( i \) and the maternal genetic variance for trait \( j \), respectively.

In genomic best linear unbiased predictions (GBLUP), matrix \( A \) was replaced with the genomic relationship matrix (\( G \)). In this regard, single- and multiple-trait genomic models with direct genetic effects (i.e., STGM_d and MTGM_d, respectively), and with both direct and maternal genetic effects (i.e., STGM_dm and MTGM_dm, respectively), were defined. Matrix \( G \) was set up for genotyped animals with \( G = \frac{MM^T}{\sum p^2 x_i x_i} \) as proposed by VanRaden (2008), where \( m \) denotes the number of SNPs, \( p_i \) is the allele frequency at locus \( i \), and \( M \) is a centered matrix of SNP genotypes.

In the single-step GBLUP (ssGBLUP) approach as developed by Aguilar et al. (2010), the combined pedigree-genomic relationship matrix \( H \) was used instead of matrix \( A \). Accordingly, single- and multiple-trait models with matrix \( H \) were fitted (i.e., STHM_d and STHM_dm for single-trait models, and MTHM_d and MTHM_dm for multiple-trait models). The inverse of matrix \( H \) was defined as \( H^{-1} = A^{-1} + \left[ \begin{array}{c}
0 \\
0 \\
0 \\
0
\end{array} \right] - A^{-1} \), where \( G_w = 0.95G + 0.05A_{22} \) and \( A_{22} \) is the submatrix of \( A \) for the genotyped animals. The matrix \( G_w \) was constructed as proposed by VanRaden (2008), in order to render it invertible.

The analyses were conducted using GIBBS2F90 (Misztal et al., 2002). For each analysis, a single chain length of 300,000 samples was generated. After discarding the first 50,000 samples as a burn-in period, posterior means and standard deviations were calculated from every 100th samples. Convergence of the Gibbs chains was checked by visual inspection of the sample trace plots. Furthermore, the lower and upper bounds of the 95% highest posterior density (HPD) were obtained from the derived marginal densities in order to verify convergence of genetic analyses. Attempts to include maternal permanent environmental effects in the multiple-trait analyses implied convergence problems. Therefore, we focused on single- and multiple-trait models without maternal permanent environmental effects.

Model Comparisons

For both single- and multiple-trait models, comparisons considered the three different relationship matrices \( A, G, \) and \( H \). The deviance information criterion (DIC) was used to assess goodness of fit (Spiegelhalter et al., 2002) as \( DIC = D(\theta) + p_D \), where \( D(\theta) \) is the posterior expectation of Bayesian deviance and \( p_D \) is the effective number of model parameters. A smaller DIC indicates model superiority. For random effects, a priori normal distribution was assumed. For covariances, we assumed a scaled inverted chi-square distribution for the
single-trait models and an inverted Wishart distribution for the multiple-trait models.

Additionally, models were evaluated based on the accuracies for direct breeding values (dEBV) and maternal breeding values (mEBV). For each trait, the accuracy of the breeding value of the $i$th genotyped animal ($r_i$) was

$$r_i = \sqrt{1 - \frac{\text{PEV}_i}{\sigma^2_g}},$$

where $\text{PEV}_i$ is the prediction error variance of the breeding value for the $i$th animal, and $\sigma^2_g$ is the direct or maternal genetic variance from the respective model. The prediction error variance for a breeding value was the square of the posterior standard deviation of the respective breeding value. The EBV from the models based on A-matrix were considered as estimates being close to the true breeding value (Daetwyler et al., 2013; Badke et al., 2014). Thus, the deviation of regression coefficients of EBV on GEBV from 1.0 was a further evaluation criterion for the biasness of genomic predictions. In the results, breeding value accuracies and the biasedness of genomic predictions are presented for the genotyped animals with phenotypes.

**Genome-Wide Associations**

De-regressed proofs (DRP) based on pedigree-based EBV are commonly used as pseudo-phenotypes in GWASs (Song et al., 2018; Yin and König, 2019). According to Garrick et al. (2009), the direct or maternal DRP for the $i$th animal was calculated as $\text{DRP}_{i} = \frac{\text{EBV}_{i}}{\sigma^2_g}$, where $\text{EBV}_{i}$ is the pedigree-based direct or maternal breeding value for the $i$th genotyped animal from the MTGM_dm, and $\sigma^2_g$ is the accuracy of the respective breeding value. The GWAS was carried out using the linear mixed model association method as implemented in the GCTA software (Yang et al., 2011). The model 5 was defined as follows:

$$y = \mu + x_i s_i + Z_u + e$$  \hspace{1cm} (5)

where $y$ is the vector of direct or maternal DRP for BWT, 200dW, 365dW, or IMF; $\mu$ is the vector of overall mean effect; $x_i$ is the vector of genotypes coded as 0, 1, or 2; $s_i$ was the effect of the $i$th SNP; $u \sim N(0, \sigma^2_u)$ is the vector of random polygenic effects, with $G$ representing the genomic relationship matrix among animals, and $\sigma^2_u$ is the polygenic variance; $Z$ is an incidence matrix for $u$, and $e$ is the residual random effect.

Manhattan plots for the $-\log10$P-values of the tested SNP for direct and maternal genetic effects were created using the ggplot2 package in R (Wickham, 2009). In order to evaluate the model quality, we calculated the genomic inflation factor (adapted $\lambda$) using the MARTEL software (Garrick et al., 2014), which was defined as

$$\hat{\lambda} = \frac{\text{var}(\hat{\gamma})}{\gamma^2},$$

where $\gamma$ is the genomic inflation factor, and $\hat{\gamma}$ is the estimated genomic inflation factor. The evaluation of $\hat{\lambda}$ indicated superiority of single-step multiple-trait models over single-trait models when considering the maternal genetic effect.

The Wellcome Trust Case Control Consortium (2007) reported that the traditional Bonferroni correction based on the total number of SNP tends to produce many false-negative results. Consequently, an adjusted Bonferroni correction was applied to account for multiple testing considering an effective number of 127,730 independent SNP. Accordingly, the genome-wide significance $P$-value threshold was set as 0.05/$n$, where $n$ was the effective number of independent SNP. The effective number of independent SNP was computed using PLINK (Purcell et al., 2007) defining a window size of 50 SNP, a step of 5 SNP and a linkage disequilibrium threshold of 0.5. In addition, a chromosome-wide significance $P$-value threshold was defined as 0.05/$n$, where $n$ was the effective number of independent SNP on the respective chromosome. Chromosome-wide significance thresholds ranged from $6.71 \times 10^{-6}$ for BTA1 to $1.89 \times 10^{-5}$ for BTA25.

A window frame of ±250 kb around each significant SNP (i.e., according to the Bonferroni-corrected thresholds) was considered to annotate potential candidate genes. The significant SNP were mapped to corresponding genes from the Bos taurus ARS-UCD1.2 annotation release 96 assembly from the Ensembl database (http://www.ensembl.org/biomart/martview), using the R package bioMartR (Duranck et al., 2009).

**RESULTS**

**Model Comparison**

The evaluation of DIC indicated superiority of a single-trait model with direct and maternal genetic effects over a respective model ignoring the maternal genetic component (Table 1). Accordingly, DIC decreased by 2.63% for BWT, 0.75% for 200dW, 0.56% for 365dW, and 4.06% for IMF when applying STPM_dm instead of STPM_d. The modeling superiority when taking maternal genetic effects into account was very obvious for the meat quality trait IMF and consideration of SNP marker data. The DIC substantially decreased by 45.39% when using STGM_dm instead of STGM_d and by 21.37% when using STHM_dm instead of STHM_d. Also in single-step multiple-trait analyses (H-matrix), DIC were smaller when including the maternal genetic effect. However, in multiple-trait analyses based on A- or G-matrices, the simpler models ignoring the maternal genetic component indicated slight superiority according to DIC.

Accuracies of dEBV of genotyped cattle with phenotypes from models with only direct genetic effects are presented in Figure 1. For all traits, genomic models (i.e., STGM_d and MTGM_d) displayed the highest accuracies from 0.84 for 365dW to 0.95 for IMF. For body weight traits, a slight increase in dEBV accuracies was observed when using multiple-trait instead of single-trait models. Accuracies of dEBV of genotyped cattle from models with direct and maternal genetic effects are presented in Figure 2A. For body weight traits, dEBV accuracies were very similar when comparing to the accuracies from the respective model without maternal genetic effect as displayed in Figure 1. For IMF, dEBV accuracies were lower when using STHM_dm instead of STHM_d (0.63 ± 0.13 vs. 0.77 ± 0.08, respectively). However, with regard to the multiple-trait modeling, the MTHM_dm revealed a slightly higher accuracy than the MTHM_d (0.75 ± 0.12 vs. 0.73 ± 0.10, respectively). For all traits, the highest accuracies of mEBV were obtained from the MTGM_dm (Figure 2B). Among all models with maternal genetic effects, the accuracy of mEBV was lowest (0.26) for the trait 365dW and when considering the A-matrix in MTPM_dm.

The biasedness of genomic predictions decreased when considering maternal genetic effects (Table 2). The regression coefficients of EBV on GEBV from the STHM_dm were 0.97, 0.97, 1.04, and 0.93 for dEBV of BWT, 200dW, 365dW, and IMF,
respectively. The biasedness increased when using the STGM\_dm instead of the STHM\_dm. With regard to the STGM\_dm, regression coefficients were 0.62, 0.68, 0.66, and 1.24 for dEBV of BWT, 200dW, 365dW, and IMF, respectively. A significant decrease in biasedness was observed for IMF when applying multiple-trait models with the G\(-\)matrix. For instance, for dEBV of IMF, regression coefficients of 1.12 and 1.06 were observed when applying MTGM\_d and MTGM\_dm, respectively.

### Genetic Parameters

The estimated variance components and heritabilities for weight traits and IMF from single- and multiple-trait models with only direct genetic effect are given in Table 3. For all traits, larger additive genetic variances were estimated when applying models with the pure genomic (G) relationship matrix in comparison to the models with pedigree-based (A) and with combined pedigree-genomic (H) matrices. Weight traits displayed moderate heritabilities in the range from 0.29 ± 0.03 (for 365dW; MTPM\_d) to 0.42 ± 0.03 (for 200dW; STGM\_d). Heritabilities for weight traits were quite similar from the models with the pedigree-based relationship matrix (i.e., STPM\_d and MTPM\_d) and the corresponding models with the combined pedigree-genomic relationship matrix (i.e., STHM\_d and MTHM\_d). Due to the increased additive genetic variances, the G\(-\)modeling approach via STGM\_d and MTGM\_d displayed the highest heritabilities. Heritabilities from the STGM\_d were 0.39 ± 0.03 for BWT, 0.42 ± 0.03 for 200dW, and 0.34 ± 0.03 for 365dW. Corresponding estimates from the MTGM\_d were 0.38 ± 0.03 for BWT, 0.41 ± 0.04 for 200dW, and 0.32 ± 0.03 for 365dW. Corresponding estimates from the MTGM\_d were 0.38 ± 0.02 using the MTHM\_d to 0.92 ± 0.05 using the STGM\_d. In comparison to the models with A- and H-matrices, heritability estimates for IMF from the models with G\(-\)matrix (STGM\_d and MTGM\_d) showed significantly lower standard deviations and smaller 95% HPD intervals.

Variance components and genetic parameters for BWT, 200dW, 365dW, and IMF estimated from single- and

### Table 1. Deviance information criterion (DIC) for birth weight (BWT), 200 d-weight (200dW), 365 d-weight (365dW), and intra-muscular fat content (IMF)

| Model\(^1\) | Trait | BWT | 200dW | 365dW | IMF |
|--------------|-------|------|-------|-------|-----|
| STPM\_d      |       | 33550.22 | 55997.89 | 48460.38 | 1764.71 |
| STPM\_dm     |       | 32668.94 | 55579.83 | 48188.37 | 1693.14 |
| STGM\_d      |       | 33546.25 | 55939.54 | 48455.03 | 1295.16 |
| STGM\_dm     |       | 32756.95 | 55386.76 | 48141.21 | 707.25 |
| STHM\_d      |       | 33532.48 | 55988.20 | 48450.43 | 2143.64 |
| STHM\_dm     |       | 32637.26 | 55555.44 | 48167.01 | 1685.45 |
| MTPM\_d      |       | 102071.62 |       | | |
| MTPM\_dm     |       | 180085.57 |       | | |
| MTGM\_d      |       | 39480.21 |       | | |
| MTGM\_dm     |       | 95307.52 |       | | |
| MTHM\_d      |       | 196621.48 |       | | |
| MTHM\_dm     |       | 105188.21 |       | | |

\(^1\)ST\(\ast\)M\_d and ST\(\ast\)M\_dm denote single-trait models, and MT\(\ast\)M\_d and MT\(\ast\)M\_dm denote multiple-trait models with only direct (d) and with direct and maternal genetic (dm) effects, where \(\ast\) refers to the pedigree-based (A), genomic (G), or combined pedigree-genomic (H) relationship matrix.
Table 4. Multiple-trait models with direct and maternal genetic effects are presented in Table 4. For all traits, generally higher direct heritabilities were estimated when fitting the maternal genetic effect in comparison to the respective models ignoring the maternal component. The direct heritabilities for weight traits from the different models with maternal genetic effects were similar and ranged from 0.62 to 0.64 for BWT, from 0.45 to 0.55 for 200dW, and from 0.40 to 0.44 for 365dW. Again, highest heritabilities (0.48 to 0.76) were estimated for IMF, but values were generally lower than from models ignoring the maternal genetic component. Maternal heritabilities for BWT, 200dW, and 365dW from the different models with maternal genetic effects were in a narrow range from 0.21 to 0.24, 0.24 to 0.27, and 0.21 to 0.25, respectively (Table 4). However, for IMF, a wider range of maternal heritabilities was estimated from 0.25 (STGM_dm) to 0.65 (MTPM_dm). For IMF, the 95% HPD intervals for direct and maternal genetic variances overlapped when applying single-trait models with A- and H-matrices.

**Direct Genetic and Maternal Genetic Correlations**

Genetic covariances and genetic correlations among BWT, 200dW, 365dW, and IMF from the multiple-trait models with maternal genetic effects and considering the different genetic
relationship matrices are displayed in Table 5. Estimates were quite similar from the different modeling approaches. The direct genetic correlations among the body weight traits BWT, 200dW, and 365dW were throughout positive and favorable. In this regard, the lowest direct genetic correlations were estimated between BWT and 365dW (0.16, 0.13, and 0.12 from the MTPM_dm, MTGM_dm, and MTHM_dm, respectively). The highest direct genetic correlations were estimated between 200dW and 365dW (0.57, 0.61, and 0.63 from the MTPM_dm, MTGM_dm, and MTHM_dm, respectively). Slightly antagonistic direct genetic relationships were identified between IMF with 200dW and 365dW. The genetic correlations between IMF and 200dW were −0.23, −0.15, and −0.02, and between IMF and 356dW 0.12, 0.01, and 0.05 from the MTPM_dm, MTGM_dm, and MTHM_dm, respectively.

Low- to moderate-maternal genetic correlations were estimated among the different traits (Table 5). The highest correlations were $0.55 \pm 0.07 \text{ (MTHM_dm)}$ between 200dW and 365dW, and $0.45 \pm 0.08 \text{ (MTPM_dm)}$ between 200dW and IMF. The lowest maternal genetic correlations of $0.08 \pm 0.11$, $-0.09 \pm 0.15$, and $-0.22 \pm 0.17$ were estimated between 365dW and IMF using MTPM_dm, MTGM_dm, and MTHM_dm, respectively.

Within the same traits, quite strong negative direct-maternal genetic correlations were estimated, ranging from $-0.77$ to $-0.82$ for BWT, from $-0.63$ to $-0.68$ for 200dW, from $-0.71$ to $-0.72$ for 365dW, and from $-0.18$ to $-0.49$ for IMF (Table 5). Posterior SD were largest in all analyses including IMF.

### Genome-Wide Associations

Manhattan plots from the GWAS for direct and maternal genetic effects on BWT, 200dW, 365dW, and IMF are given in Figure 3. The genomic inflation factors for additive genetic effects ranged from 0.99 for BWT to 1.01 for 200-dW. For maternal genetic effects, the genomic inflation factors ranged from 0.98 for BWT to 1.00 for 200-dW. One SNP (rs137226468) on BTA2 surpassed the genome-wide significance threshold ($P = 3.91 \times 10^{-7}$), which was associated with the direct genetic effect on IMF only. According to the chromosome-wide significance threshold, 5, 7, 2, and 7 SNP were significantly associated with direct genetic effects on BWT, 200dW, 365dW, and IMF, respectively. For the same significance threshold, 10, 8, 7, and 13 significant SNP were significantly associated with maternal genetic effects on BWT, 200dW, 365dW, and IMF, respectively.
For the direct genetic effect on BWT, we identified six potential candidate genes. Two of these genes (ENSBTAG000000048983 and FBXW7) are located on BTA17 (Table 6). Three genes (NOL10, ODC1, and SMG6) and one gene (FRK) were also annotated as potential candidate genes for 200dW and for 365-dW, respectively. Six potential candidate genes (ENSBTAG000000052399, VWC2L, BMP7, TME11232D, UBE2Q2, and CHRN8) were annotated for the direct genetic effects on IMF. Regarding maternal genetic effects on BWT, four potential candidate genes (SHROOM3) on BTA6, ZNF609 on BTA10, and PECA1 and TEE2 on BTA19) were identified. The ZNF609 gene included the largest number of significant SNP (seven SNP), located within or in close distance. Two genes (TMMEM82 and SEC11A) and four genes (GRHL2, FGA, FGB, and CTNNA3) were inferred as potential candidate genes for the maternal genetic effect of 365-dW and on IMF, respectively.

**DISCUSSION**

**Direct Heritabilities for Weight and Meat Quality Traits**

In the present study, direct heritabilities for weight traits ranged from 0.41 to 0.66 when applying the enhanced models considering the direct and the maternal genetic effect. For IMF, heritabilities ranged from 0.48 to 0.76. Generally, already published heritabilities for weight and meat quality traits as well as the corresponding variance components display a broad range of estimates (Marshall, 1994; Utrera and Van Vleck, 2004). Possible explanations address breed particularities, applied statistical methods and considered respective model effects, the number of phenotypic records, pedigreed inconsistencies as well as specific slaughtering effects for meat quality traits (Utrera and Van Vleck, 2004). Reported heritabilities for BWT were 0.22 (Müllenhoff, 2008), 0.23 (Brandt et al., 2010), 0.32 (Chud et al., 2014), and 0.61 (Mackinnon et al., 1991). Heritabilities for weaning weight were 0.12 (Brandt et al., 2010), 0.18 to 0.21 (Jeyaruban et al., 2009), 0.20 (Mackinnon et al., 1991), 0.20 to 0.23 (Meyer, 1995), 0.21 (Santana et al., 2013), and 0.26 to 0.28 (Williams et al., 2012). Heritabilities for yearling weight were 0.26 to 0.29 (Jeyaruban et al., 2009), 0.25 (Mackinnon et al., 1991), 0.28 to 0.31 (Meyer, 1995), 0.29 (Zuin et al., 2012), and 0.38 to 0.64 (Guidolin et al., 2012). Heritabilities for IMF in cattle were 0.27 (Torres-Vázquez and Spangler, 2016), 0.31 (MacNeil et al., 2010), 0.38 (Soroka et al., 2011), 0.47 to 0.52 (Crews et al., 2003), and 0.93 (Shackelford et al., 1994). For marbling score, which is genetically highly correlated with IMF (Devitt and Wilton, 2001; MacNeil et al., 2010), Srivastava et al. (2019) estimated a heritability of 0.35 and
0.38 in Korean Hanwoo cattle from a single-trait pedigree-based model and a multiple-trait pedigree-based model, respectively. Hence, heritabilities for weight traits and IMF in the dual-purpose RHV population reflect the range of estimates as published for different commercial beef cattle breeds.

In comparison to the models with only direct genetic effects, the models with both direct and maternal genetic effects implied higher heritabilities as direct-maternal genetic effects explained a large percentage of the phenotypic variation. For BWT, 200-d weight (200dW), and intra-muscular fat content (IMF) traits estimated via multiple-trait models with direct and maternal genetic effects reflect the uncertainty of the heritabilities estimates, which might be related to the limited number of phenotypic records. Heritabilities for IMF from single and multiple trait models with the same relationship matrices were very similar. For instance, direct heritabilities for IMF from both models with the same relationship matrices were very similar. However, for IMF, we estimated larger direct heritabilities and smaller 95% HPD intervals when using models with different relationship matrices. The quite high IMF heritability and genetic variance for IMF in the local RHV dual purpose cattle population suggest the uncertainty of the heritabilities estimates, which might be related to the limited number of phenotypic records. Heritabilities for IMF from single and multiple trait models with the same relationship matrices were very similar. For instance, direct heritabilities for IMF from both models with the same relationship matrices were very similar.

The inclusion of the maternal genetic effect into genetic evaluation models is imperative; otherwise, the direct heritability will be overestimated (Meyer, 1992). Recently, even from an extended time-lagged and across-generation perspective in dairy cattle, consideration of maternal genetic effects improved the statistical modeling quality (Kipp et al., 2021). For BWT, weaning weight, and yearling weight in beef cattle, the maternal effects explained a large percentage of the phenotypic variation (Waldrum et al., 1993). Accordingly, in our study, maternal

### Table 5. Genetic covariances (above the diagonal) and genetic correlations (below the diagonal) among birth weight (BWT), 200-d weight (200dW), 365-d weight (365dW), and intra-muscular fat content (IMF) traits estimated via multiple-trait models with direct and maternal genetic effects

| Model Effect | Trait | d | m |
|--------------|-------|---|---|
|              |       | BWT | 200dW | 365dW | IMF | BWT | 200dW | 365dW | IMF |
| d            | BWT   | 23.27 (6.78) | 19.76 (8.82) | 2.16 (0.30) | -6.32 (0.59) | -2.61 (6.15) | -3.19 (7.72) | -1.61 (0.44) |
| 200dW | 0.27 (0.07) | 475.77 (87.07) | -10.61 (3.09) | -3.17 (3.88) | -281.10 (47.72) | -150.88 (68.30) | -23.64 (3.60) |
| 365dW | 0.16 (0.07) | 0.57 (0.06) | 7.85 (3.19) | -11.56 (5.99) | -154.33 (76.06) | -635.45 (114.18) | 4.84 (5.59) |
| IMF       | 0.31 (0.05) | -0.23 (0.06) | 0.12 (0.05) | -2.81 (0.30) | 5.26 (2.35) | -9.33 (2.59) | -2.14 (0.25) |
| m            | BWT   | -0.82 (0.02) | -0.06 (0.07) | -0.16 (0.08) | -0.67 (0.06) | 7.37 (3.88) | 13.41 (5.09) | 1.84 (0.28) |
| 200dW | -0.04 (0.09) | -0.63 (0.05) | -0.25 (0.11) | 0.15 (0.06) | 0.19 (0.09) | 237.09 (58.22) | 18.61 (3.43) |
| 365dW | -0.04 (0.08) | -0.24 (0.10) | -0.72 (0.06) | -0.19 (0.06) | 0.24 (0.09) | 0.50 (0.08) | 4.54 (6.45) |
| IMF       | -0.20 (0.06) | -0.43 (0.06) | 0.06 (0.07) | -0.49 (0.05) | 0.38 (0.07) | 0.45 (0.08) | 0.08 (0.11) |
| d            | BWT   | 24.99 (7.76) | 15.80 (9.38) | -1.31 (0.81) | -5.79 (0.70) | -1.39 (5.56) | 8.17 (7.58) | 0.87 (1.07) |
| 200dW | 0.26 (0.07) | 372.62 (90.63) | 12.01 (9.80) | -5.41 (6.00) | -361.42 (58.24) | -206.33 (63.07) | -1.05 (7.82) |
| 365dW | 0.13 (0.08) | 0.61 (0.07) | 1.12 (7.99) | -2.65 (7.10) | -196.35 (62.73) | -608.76 (99.54) | -1.73 (12.87) |
| IMF       | -0.13 (0.09) | -0.15 (0.12) | 0.01 (0.09) | 0.42 (0.66) | -23.89 (5.85) | -32.53 (7.03) | -0.90 (0.98) |
| MTPM dm    | BWT   | -0.77 (0.04) | -0.10 (0.10) | -0.04 (0.09) | -0.07 (0.11) | 6.44 (3.98) | 5.39 (4.80) | 0.20 (0.61) |
| 200dW | -0.02 (0.08) | -0.68 (0.04) | -0.29 (0.08) | -0.46 (0.09) | 0.16 (0.09) | 246.42 (54.11) | 7.07 (4.67) |
| 365dW | 0.10 (0.08) | -0.31 (0.08) | -0.71 (0.05) | -0.48 (0.08) | 0.10 (0.08) | 0.52 (0.09) | 3.72 (6.20) |
| IMF       | 0.15 (0.18) | -0.03 (0.17) | -0.28 (0.22) | -0.18 (0.09) | 0.05 (0.17) | 0.21 (0.13) | -0.09 (0.15) |
| d            | BWT   | 17.96 (7.06) | 13.52 (9.33) | 3.14 (0.52) | -5.69 (0.69) | 0.59 (5.22) | 7.04 (8.74) | -0.34 (1.16) |
| 200dW | 0.20 (0.07) | 512.02 (85.72) | -1.10 (5.26) | -1.61 (4.66) | -285.18 (60.83) | -144.01 (61.71) | -2.77 (6.73) |
| 365dW | 0.12 (0.08) | 0.63 (0.05) | 3.45 (4.75) | -3.25 (6.89) | -178.70 (54.32) | -560.56 (84.91) | 17.94 (10.01) |
| IMF       | 0.45 (0.06) | -0.02 (0.10) | 0.05 (0.07) | -1.71 (0.39) | -18.13 (3.44) | -24.19 (4.50) | -1.05 (0.66) |
| MTHM dm    | BWT   | -0.78 (0.04) | -0.03 (0.08) | -0.05 (0.10) | -0.41 (0.08) | 4.70 (3.75) | 2.99 (5.72) | 0.55 (0.600) |
| 200dW | 0.01 (0.08) | -0.63 (0.06) | -0.30 (0.07) | -0.50 (0.07) | 0.12 (0.10) | 236.27 (47.06) | 8.49 (4.82) |
| 365dW | 0.08 (0.10) | -0.24 (0.10) | -0.72 (0.04) | -0.50 (0.07) | 0.06 (0.11) | 0.35 (0.07) | -9.60 (7.55) |
| IMF       | -0.05 (0.18) | -0.06 (0.14) | 0.31 (0.16) | -0.29 (0.17) | 0.15 (0.15) | 0.26 (0.13) | -0.22 (0.17) |

Posterior SD of estimates are given in brackets.

1 MTPM dm denotes multiple trait models with direct and maternal genetic effect, where * refers to pedigree-based (A), genomic (G), or combined pedigree-genomic (H) relationship matrices.

2 d and m denotes estimates for direct and maternal genetic effects, respectively.
heritabilities were quite high in the range from 0.21 to 0.24 for BWT, from 0.24 to 0.27 for 200dW, and from 0.21 to 0.25 for 365dW. These estimates for the maternal genetic component in dual-purpose RHV cattle correspond with maternal heritabilities for BWT, weaning weight, and yearling weight in specialized beef cattle breeds as reported by Brandt et al. (2010), Eler et al. (1995), Meyer (1992), Meyer (1994), Robinson (1996), and Tosh et al. (1999). Nevertheless, the maternal genetic impact especially for trait recorded late in life was larger in the RHV outdoor population than in the commercial beef breeds. Accordingly, in the RHV breed, cows and their offspring are raised on pasture without feeding supplements. Hence, the dam’s milk is the most important energy supply for offspring of all ages and explains the respective strong maternal genetic component. Dam milk quality may also affect meat quality traits recorded in offspring, explaining the quite high maternal heritabilities for IMF in the range from 0.29 to 0.65 in the present study. In Duroc pigs with a breeding focus on meat quality and which are predominantly used in low input systems, Hoque et al. (2008) estimated maternal heritabilities between 0.13 and 0.15 for IMF. In contrast, for meat quality traits of beef cattle kept in feedlots, the maternal heritability was close to zero, e.g., 0.03 for rib eye area (Abdel-Aziz et al., 2005) and 0.03 for marbling score in Japanese Black cattle (Shimada et al., 1998).

Correlations Between Direct and Maternal Genetic Effects for Weight and Meat Quality Traits
Correlations between the direct genetic effect and the maternal genetic effect for weight traits in the RHV breed, estimated via multiple-trait models, were unfavorable and ranged between −0.77 and −0.82 for BWT, between −0.63 and −0.68 for 200dW, and between −0.71 and −0.72 for 365dW. Similarly, pronounced negative direct-maternal correlations for BWT were reported by Müllenhoff (2008) and by Eler et al. (1995). Contrarily, Brandt et al. (2010), Meyer et al. (1992), Müllenhoff (2008), and Tosh et al. (1999) reported positive direct-maternal correlations for BWT in the range from 0.04 to 0.32. For weight or weight gain traits recorded later in life, direct-maternal correlations as estimated in commercial beef cattle displayed a huge variation, i.e., from −0.57 to 0.16 for weaning weight in the study by Müllenhoff (2008) and in the range from −0.13 to −0.32 in the study by Eler et al. (1995). For yearling weight, the direct-maternal correlations were −0.48 to 0.49 (Meyer et al., 1992), −0.22 (Swalve, 1993), and −0.17 (Eler et al., 1995).

The correlations between the direct and the maternal genetic effects for IMF in the present study from the different models ranged from −0.18 to −0.49. Accordingly, regarding meat quality in beef cattle, Johnson et al. (2002) reported antagonistic relationships between direct and maternal genetic effects for rib eye area with a correlation estimate of −0.67. As stated by Lee (2001), a clear biological explanation for the antagonistic relationships between maternal and direct genetic effects for meat quality traits is not available. Nevertheless, regarding conservation programs in local small sized populations, a negative covariance between direct and maternal genetic effects might favorably contribute to genetic variation.

Figure 3. Manhattan plots for direct and maternal effects on birth weight (A), 200 d-weight (B), 365 d-weight (C), and intra-muscular fat content (D). The red line displays the genome-wide significance threshold according to the adjusted Bonferroni correction. The red and the blue dots represent significant SNP according to the genome-wide and the chromosome-wide significance thresholds, respectively. The genome-wide significance threshold was $3.91 \times 10^{-7}$ and the chromosome-wide significance thresholds ranged from $6.71 \times 10^{-6}$ for BTA1 to $1.89 \times 10^{-5}$ for BTA25.
## Genetic Correlations Among Weight and Meat Quality Traits

Genetic correlations between the direct genetic effect among BWT and weight traits from later ages (200dW and 365dW) from all multiple-trait models were throughout positive. Genetic correlations between measurements within a closer time interval (i.e., between BWT and 200dW) were slightly higher than between BWT and 365dW. Different gene activities for different body weight traits recorded at birth and recorded more than 1 yr later have been reported by Yin and König (2019) in cattle and by Aikins-Wilson et al. (2021) in pigs. In beef cattle, Brandt et al. (2010) and Eler et al. (1995) reported a genetic correlation between BWT and weaning weight of 0.20 and of 0.23, respectively, reflecting our estimate between BWT and 200dW. Higher genetic correlations between these two traits were estimated by Chud et al. (2014) with 0.36, Mackinnon et al. (1991) with 0.57, and by Tosh et al. (1999) with 0.73.

In the present study, we found differing genetic correlations between IMF and BWT, depending on the considered relationship matrix. The correlation was 0.31 on the basis of the A-matrix (MTPM_dm) and 0.45 on the basis of the H-matrix (MTHM_dm), but close to zero with −0.13 when modeling the pure genomic G-matrix (MTGM_dm). We assume that the small number of genotyped animals explains the similarities of estimates from A- and H-matrices, but differing results with higher accuracies of breeding values (Figure 1) from the G-matrix. Such aspects were outlined by Shabalina et al. (2021) in the context of genetic evaluations in an organic dairy cattle production system, including a very small number of genotyped cows from organic herds.

In the present study, genetic correlations between IMF and 200dW were of antagonistic nature (−0.02 to −0.23), but slightly positive between IMF and 365dW (0.01 to 0.12). However, when taking the posterior SD into account, all correlations were very close to zero, and reflecting estimates from the literature between weight at later ages and meat quality and carcass traits in cattle. For example, a genetic correlation of 0.04 between 210-d weight and back fat thickness, and of −0.09 between 210-d weight and rump fat, was reported by Zuin et al. (2012). Similar genetic correlations of −0.10 and

### Table 6. Potential candidate genes related to the identified single-nucleotide polymorphisms (SNP) associated with direct (d) and maternal (m) genetic effects on birth weight (BWT), 200-d weight (200dW), 365-d weight (365dW), and intra-muscular fat content (IMF) traits

| Trait | Effect | BTA | Gene name | Gene position | No. of significant SNP within/close to gene | Most significant SNP |
|-------|--------|-----|-----------|---------------|------------------------------------------|----------------------|
|       |        |     |           |               |                                          | rs number | Position | in gene | P-value |
| BWT   | d      | 6   | HS3T1     | 106504062-106540229 | 0/2 | rs136251364 | 106314217 | No | 4.50E-06 |
|       |       | 15  | BBOX1     | 57758972-57839046  | 0/1 | rs137689845 | 57781671  | Yes | 7.08E-06 |
|       |       | 17  | ENSBTAG00000048983 | 5007893-5022532  | 0/0 | rs109750506 | 5131401  | No | 5.88E-06 |
|       |       | 17  | FBXW7     | 5256463-5351434    | 0/0 | rs109750506 | 5131401  | No | 5.88E-06 |
|       |       | 23  | TUBB2A    | 50525012-50528874  | 0/0 | rs109760348 | 50501825 | No | 1.43E-05 |
|       |       | 23  | TUBB2B    | 50489737-50494257  | 0/0 | rs109760348 | 50501825 | No | 1.43E-05 |
|       | m     | 6   | SHROOM3   | 91317426-91647743  | 0/0 | rs110666415 | 91494841 | Yes | 2.27E-06 |
|       |       | 10  | ZNF609    | 45385273-45582446  | 0/0 | rs135585847 | 45410963 | Yes | 5.94E-06 |
|       |       | 19  | PECAM1    | 48541625-48619840  | 0/0 | rs41919301  | 48557862 | Yes | 4.96E-06 |
|       |       | 19  | TEX2      | 48368410-48482779  | 0/0 | rs41919273  | 48538199 | Yes | 4.69E-06 |
| 200dW | d      | 11  | NOL10     | 86971480-87061426  | 0/0 | rs110941186 | 87050463 | No | 2.69E-06 |
|       |       | 11  | ODC1      | 87197374-87204771  | 0/0 | rs110941186 | 87050463 | No | 2.69E-06 |
|       |       | 19  | SMG6      | 23080151-23280691  | 0/0 | rs41904211  | 23107053 | Yes | 9.76E-06 |
| 365dW | d      | 9   | FRK       | 34593961-34691721  | 0/0 | rs43339651  | 34929448 | No | 7.08E-06 |
|       | m     | 11  | TMEM182   | 7459624-7509293    | 0/0 | rs43661127  | 76951353 | No | 7.48E-06 |
|       |       | 21  | SEC11A    | 22328984-22362069  | 0/0 | rs134746982 | 22359151 | Yes | 7.37E-07 |
| IMF   | d      | 2   | ENSBTAG0000052399 | 10183664-102121963 | 0/0 | rs137226468 | 102157462 | No | 1.54E-07 |
|       |       | 2   | VWC2L     | 102407028-102619802 | 0/0 | rs137226468 | 102157462 | No | 1.54E-07 |
|       |       | 13  | BMP7      | 5888962-58975046   | 0/0 | rs108949054 | 59075952 | No | 1.07E-05 |
|       |       | 17  | TMEM132D  | 47426664-48084896  | 0/0 | rs109093435 | 47665130 | Yes | 1.29E-06 |
|       |       | 21  | UBE2Q2    | 31126645-31188035  | 0/0 | rs42815709  | 31132302 | Yes | 9.87E-06 |
|       | m     | 14  | GRHL2     | 62721044-62888891  | 0/0 | rs136368193 | 62727223 | Yes | 4.01E-06 |
|       |       | 17  | FGA       | 2859932-2868867    | 0/0 | rs134206866 | 2888493 | No | 1.25E-06 |
|       |       | 17  | FGB       | 2894488-2932611    | 0/0 | rs136514361 | 2895691 | Yes | 1.25E-06 |
|       |       | 28  | CTNNA3    | 22282909-24121400  | 0/0 | rs136938446 | 22852412 | Yes | 7.61E-06 |

1BTA, *Bos taurus* chromosome.
2Number of SNP that reached the Bonferroni-corrected genome-wide (in bold) or chromosome-wide significance threshold.

(Maniatis, et al., 2013). Hence, especially in the RHV outdoor system, it may be the challenge to improve the economically important meat quality trait IMF without neglecting the also very important maternal abilities.
stratification. Many of the potential candidate genes detected in the present study support previous reports for the same or correlated traits in beef cattle populations. The gene HS3ST1 (a potential candidate gene for direct genetic effects on BWT) and the genes ZNF609, PECAM1, and TEX2 genes (potential candidate genes for maternal genetic effects on BWT) were associated with carcass and body weight traits in beef cattle (Kim, et al., 2011; Naserkheil et al., 2020; Bruscadin et al., 2021). In a selection signature segment on BTA10, Boitard et al. (2021) also detected ZNF609 as a candidate gene for carcass traits in a beef cattle population. SMG6, a potential candidate gene for the maternal genetic effect on 200dW, was significantly associated with rib eye area in beef cattle (Wang et al., 2020). The results from the present study support the associations reported by Wang et al. (2020), because Caetano et al. (2013) estimated a moderate positive correlation between rib eye area and weight gain from 210 to 365 d. For 365-dW, the FRK and TMEM182 genes were identified for direct and maternal genetic effects, respectively. FRK is a protein coding gene which is associated with feed efficiency and feed intake in beef cattle (Sherman et al., 2010; Higgins et al., 2018). The TMEM182 gene is known to be involved in the development of muscle tissues (Wu et al., 2008; Freeborn et al., 2020).

For direct genetic effects on IMF, the most significant SNP (rs137226468) is located in close distance to the ENSBTAG0000052399 and VWC2L genes on BTA2. ENSBTAG0000052399 is a protein coding gene, but the function of this gene is unknown. VWC2L and BMP7, another potential candidate gene for direct genetic effects on IMF, are reported as candidate genes for feed efficiency in pigs (Wang et al., 2015) and in beef cattle (Zhang et al., 2020). The VWC2L gene regulates the osteoclast activation and matrix mineralization (Ohyama, et al., 2012), and the BMP7 gene is a lipid-related candidate gene. In several studies conducted in beef cattle (Srikanth et al., 2020; Wang et al., 2020; Zhang et al., 2020), BMP7 was also found to be associated with carcass traits (e.g., backfat thickness, rib eye area, lean meat yield, and carcass marbling score) and average daily gain.

The estimated genetic parameters for weight traits and IMF in the local RHV dual-purpose cattle population kept in outdoor production systems indicate trait improvement possibilities via breeding approaches. Especially for the meat quality trait IMF, quite high heritabilities were estimated. Especially from the background that meat quality traits do not play a role in breeding goals for commercial beef cattle breeds in Germany, we strongly suggest to develop an RHV breeding goal including IMF. Probably due to the intensive calf–cow relationship in the outdoor suckler system, we identified a quite strong maternal genetic component on weight traits at different ages as well as on IMF. Hence, it may be imperative to apply models with maternal genetic effects in genetic evaluations. Furthermore, we suggest to focus on RHV cattle genotyping, especially when aiming on breeding goal traits with high heritabilities. In this regard, a comparatively small number including less than 1,000 genotyped animals implied reliable genetic parameter estimates with acceptable standard errors. Furthermore, on the basis of the G-matrix, we identified breeding values with highest accuracies.

Conflict of Interest Statement
None declared.
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