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Contribution of All Single Nucleotide Polymorphisms (SNPs) and Minor Allele Frequency Groups to Genetic Variation of Quantitative Traits in Suffolk Sheep

Research Article

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ABSTRACT

Accurate estimation of genetic and non-genetic variance components with pedigree and genomic information is essential for the correct prediction of breeding values. Single nucleotide polymorphisms (SNPs) from Australian Suffolk sheep were used in this research (50K illumine). The characteristics of birth weight, weaning weight, length, and diameter of the wool warp were investigated. To study the relationship between allelic frequency and the amount of additive genetic variance explained. The SNPs were classified into five different groups of rare allelic frequency (MAF). Two statistical models were fitted a separate and joint analysis of each SNPs group statistical analyses were performed with the Bayesian method using the Gibbs sampling technique and the RKHS model (semiparametric method). The amount of genomic heritability estimated by all SNPs in the Bayesian approach were estimated as 0.46, 0.19, 0.75, and 0.48 for the traits of birth weight, weaning weight, length, and wool diameter, respectively. The total heritability estimated for different groups of rare allele frequencies, in the combined analysis were almost similar to the value obtained from all SNPs for all traits. Although the numbers of SNPs in different groups were similar, the amounts of genetic variance explained by MAF groups were different. For the two traits of birth weight and weaning weight, the first group with an allelic frequency of 0.01-0.1 had the highest amount of genomic heritability. The amount of genomic heritability of fibre diameter was variable in five MAF groups. The highest estimated value in the fifth group with rare allele frequency was 0.4-0.5 (about 0.21), and the lowest value was in the third group (0.2-0.3), which was estimated at 0.098. The staple length trait, the genetic variance distribution pattern justified by SNPs, fluctuated between the five MAF groups, and the heritability value varied from zero in the second and fourth groups to about 0.16 in the third group.

KEY WORDS Bayesian method, genomic selection, genomic variance, Suffolk sheep, joint analysis.

INTRODUCTION

Most of the important traits in livestock and agricultural products are quantitative or complex. More improvements in these traits have been made by selecting animals or plants based on their phenotypes and their relatives. In the last decade, the rate of genetic improvement by genomic selection or genomic prediction (GP) has increased (Meuwissen *et al.* 2001). Many quantitative traits are controlled by thousands of variants in the DNA sequence of individual animals and environmental factors. The identification of these causal variants will be useful for genomic

prediction, understanding the physiology and evolution of important traits, and genome editing. However, it is difficult to identify these causal variants because their effects are small and they are in linkage disequilibrium with other DNA variants (Meuwissen *et al*. 2022). Genotyping of single nucleotide markers (SNP) and other dense markers in the genome has made significant genetic progress in livestock breeding programs (Hayes *et al*. 2009). The markers cover the whole genome all the positions of the quantitative traits are covered by the markers and this method has the potential to justify all the genetic variance (Rashedi Dehsahraei *et al*. 2017). In genomic selection, the markers are scattered throughout the genome, so that the entire genetic variance is controlled by the markers. Genomic selection decreases the costs of genetic evaluation and increases genetic improvement by reducing generational distance and increasing the accuracy of selection (Hayes *et al*. 2009). In recent years, many many studies have been conducted using SNP chips to identify genetic variation. In research on Japanese black cattle; by Uemoto *et al*. (2015), heritability was estimated. The studies conducted to obtain the amount of genetic diversity in quantitative traits were carried out as follows: Pimentel *et al*. (2011) studied milk production and composition traits in dairy cows, Jensen *et al*. (2012) studied traits related to production and body fitness in dairy cows; Ogawa *et al*. (2016) Japanese black cow body weight; and Rashedi Dehsahraei *et al*. (2017) quantitative traits in Merino sheep. Segmentation of the allelic spectrum to calculate genetic variability, by Yang *et al*. (2010) for human height, Pimentel *et al*. (2011) for production traits and milk composition in dairy cows and Jensen *et al*. (2012) for traits related to production and fitness organs in dairy cows, Lee *et al*. (2013) for Alzheimer's disease, Abdollahi-Arpanahi *et al*. (2014) for broiler production traits, Ogawa *et al*. (2016) for the body weight of Japanese black cattle; and Rashedi Dehsahraei *et al*. (2017) for traits the body weight of Merino. This study aims to determine the amount of additive genetic variance, resulting from all SNP markers for the traits of birth weight, weaning weight, wool length, and wool diameter in Australian Suffolk sheep, as well as classifying the markers based on rare allele frequency (MAF) and determining the contribution of each group to justify additive genetic variance.

MATERIALS AND METHODS

Phenotypic data

The data used in this study included phenotypic records from 680 Suffolk sheep, which included 380 males and three hundred females from 3 sires (Half-sib family). All animals were born at Falkiner Memorial Field Station in Australia. The traits studied were birth weight (BW), weaning weight (WW), fibre diameter (FD), and staple length (SL). The descriptive statistics of traits studied are shown in Table 1.

Table 1 Descriptive statistics of traits studied

Trait (unit)	n	Mean	SD	Min	Max
Birth weight (kg)	300	4.35	1.05	1.26	7.45
Weaning weight (kg)	630	18.50	4.15	7.35	31.28
Fibre diameter (µm)	285	23.47	2.78	17.39	30.63
Staple length (mm)	285	81.56	12.17	46.25	124.75

Genotypic data

In this study, 48599 SNP markers from the Illumina 50k Ovine Bead chip were used after removing sexual chromosomes and unmapped SNPs. SNPs that departed from Hardy–Weinberg equilibrium ($P<10^{-6}$) based on a Chi-square test, SNPs that had a minor allele frequency (MAF) <0.01, or a missing rate >0.05 were excluded from the analysis. After quality control, 43821 markers remained for analysis. The quality control of SNPs was done with the PLINK program (Purcell *et al*. 2007). Table 2 shows the characteristics of the marker panel.

Table 2 Characteristics of marker panel used

Total number of SNPs	**48599**
SNPs with MAF < 0.01	196
SNPs not in Hardy–Weinberg equilibrium ($P<10^{-6}$)	4582
SNPs with missing rates > 0.05	0
SNPs used	43821
Individuals with genotype missing rate > 0.05	0
Mean distance (Kbp)	55.188
Maximum distance (Kbp)	1180.886
Minimum distance (Kbp)	4.548

SNPs: single nucleotide polymorphisms.

Genomic variation captured by SNP markers

To study the relationship between allele frequency and the amount of additive genetic variance explained by markers, SNPs were classified into five groups of MAF (0.01-0.1, 0.1-0.2, 0.2-0.3, 0.3-0.4, and 0.4-0.5). In this classification, the number of SNPs were 10578 for first group, 8092 for second group, 8822 for third group, 8096 for fourth group and 8233 for fifth group. To explore the genomic variance of the five MAF bins, five additive parametric kernels were constructed. To estimate the proportion of additive genetic variation by each group of MAFs, analyses were performed in two different scenarios, (1): fitting additive kernels (G) for each MAF-bin (i.e. five models were fitted, and one additive genetic variance component was considered in each analysis) or fitting (G matrix) for all SNPs without distinction of MAF-bin (2): fitting five additive kernels jointly (G1+G2+…+G5), with each kernel linked to one class of MAF. This model allowed the inference of five separate additive genetic variance components, each one assigned to special MAF groups. All additive kernels were parametric and kernel matrices were constructed based on

VanRaden's model (VanRaden, 2008). The amount of variation captured by all SNPs together or each MAF group separately or jointly was estimated using linear mixed models. These models are explained in the following.

Separate analysis with additive kernels (G)

We fitted models by considering the relationship matrix (kernel) within each of the five MAF groups. The following model was used for data analysis (denoted as model 1):

$y_i = \mu + g(x_i) + e_i$ (1)

Where:
y_i: observations of sheep i (BW, WW, FD, and SL).
μ: intercept.
g (xi): linear function of SNP genotypes xi.
ei: model residual for sheep i, (Corrections were made for fixed effects of year of birth, sex, birth type before analysis).

In this model, the genetic signals (g) were represented by Gα, G is an n × n kernel matrix indexed by the observed SNP covariates such that G ~ XXT, X is an SNP genotype matrix.

Here, X matrix is centered and standardized to form G matrix, then divided by the number of SNPs, as proposed by VanRaden (2008) and Yang *et al*. (2010), and α is the vector of the Reproducing Kernel Hilbert Spaces (RKHS) regression coefficients that are estimated as the solution that minimizes:

$l(\alpha|\lambda) = (y-G\alpha)' (y-G\alpha) + \lambda\alpha' G\alpha$

Where:
α~N (0, G-1σ^2g), σ^2g: additive variance captured by SNPs.
λ: regularization factor.
g: Gα, is equal to the number of individuals, i.e. 300, 630, 285 or 285 individuals for BW, WW, FD, and SL, respectively. The matrix form of model 1 is:

$y = 1\mu + G\alpha + e$ (2)

Where:
1: vector of ones.
e: vector of the residual of the models with e~ N(0, Iσ^2e), where σ^2e is the variance of the residual.

The variance structure was as follows:

$V = G\sigma^2g + I\sigma^2e$
$V = Z'GZ + R$

The predicted genetic values in a testing set (ĝt,test) were:

$\hat{G}t,test = Gt,test,train\ G^{-1}t,train\ \hat{g}t,train$ (3)

Where:
Gtest, train: rectangular matrix of genomic relationships between testing and training individuals, which represents a subset of the total G constructed from all individuals in the training and testing sets.
Gtrain: genomic relationship between individuals in the training set.
ĝtrain: vector of predicted genetic signals of individuals in the training set.

Joint analysis of five additive kernels (G1+G2+· · ·+G5)

In the joint analysis of the five classes of MAFs, the linear model can be represented as:

$y = 1\mu + t=1hGt\alpha t + e$ (4)

y: vector of observations.
1: vector of ones.
μ: intercept.
h: 5 is the number classes of MAF.
αt~ (0, Gt-1σ2gt) with t= 1, 2, . . ., 5: regression vector in RKHS for MAF-bin t.
Gt: matrix of additive genomic relationships for the tth MAF-bin.
σ2gt: variance that is captured by SNPs in the tth MAF-bin.
e ~ N(0, I σ^2gt): vector from residuals of model, where σ^2e is the variance of residual, and I is an identity matrix.

Therefore, the joint density of the five random vectors and the residual term is:

pe, g1,…,gt|σe2, σg12,…,σgt2= N(e|0, Iσe2)t= 1hN(gt|0, Gtσgt2)

The marginal distribution of the data in the model has an expected value of 1 μ and the variance-covariance matrix is:

$V=t=1hGt\sigma gt2+I\sigma e2$
$V=Z'GZ + IS^2e$

Where:
G: var-covar matrix of random effects.
GS^2g: prediction of the genetic value obtained with SNPs in MAF t for individuals in the testing set was as follows:

$\hat{g}_{t,test} = G_{t, test,train} G^{-1}_{t,train} \hat{g}_{t,train}$ (5)

Where notations are as in (1), except that t indicates the G matrix of tth MAF-bins.

Bayesian analysis implementation

Variance components were estimated using the RKHS regression as implemented in the BGLR package (Pérez and de los Campos, 2013). The Bayesian approach was conducted using Gibbs sampling. A Markov Chain Monte Carlo (MCMC) with 100000 samples was run for each fitted model and the first 10000 samples were discarded as burn-in and thinned at a rate of 5. Convergence diagnostics and statistical and graphical analysis of Gibbs sampling were checked by visual inspection of trace plots of some parameters (i.e. variance components).

RESULTS AND DISCUSSION

The first two levels of the MDS test showed the presence of three subpopulations in the studied herd (Figure 1).

Several types of research showed that by performing the multidimensional measurement test, the members of the same family are together in the same cluster (Gu *et al*. 2011; Sun *et al*. 2013; Emrani *et al*. 2017). In this research, the first two levels of the multidimensional measurement test showed that the people of a step family are placed inside a cluster. To estimate the components of genomic variance, the first three levels of the multidimensional measurement test were included as auxiliary variables in the model.

Variance components for wool and growth traits using the RKHS model with univariate analysis in Suffolk sheep are shown in Table 3. The values of genomic variance obtained in this research were estimated as 0.74, 4.41, 2.50, and 55.95 for the traits of birth weight, weaning weight, fibre diameter, and staple length, respectively. The genomic heritability estimated in this study is 0.46 ± 0.16 for birth weight, 0.19 ± 0.11 for weaning weight, 0.75 ± 0.05 for fibre diameter, and 0.48 ± 0.06 for staple length (SL). The heritabilities estimated for Suffolk sheep in this study, for birth weight and weaning weight traits, were almost equal of the estimates reported for these traits in Rashedi Dehsahraei *et al*. (2017). Using a 50K marker panel of Suffolk sheep, these researchers reported a genomic heritability of 0.45 for birth weight and 9.19 for weaning weight. Genomic heritability in Border sheep for production traits (body weight and wool) reported by Taheri Yeganeh *et al*. (2022), was different from the values estimated in this study. These researchers reported a genomic heritability value of 0.58 for birth weight, 0.47 for weaning weight, 0.59 for wool yarn diameter, and 0.20 for wool yarn length in Border sheep.

Many studies using genome-wide SNP data have shown that a large proportion of heritability for quantitative traits can be explained by common SNPs. For example, Yang *et al*. (2010) showed in their study for human height that 45% of the variation could be explained by fitting all SNPs simultaneously. Lee *et al*. (2012) noted that a significant proportion of overall variation for common human diseases is accounted for by common SNPs. For example, in their study, the estimated genomic heritability was 0.24 for Alzheimer's disease, 0.26 for endometriosis, and 0.30 for MS. Rashedi Dehsahraei *et al*. (2018) estimated the amount of genomic variance for Merino sheep using the Bayesian method and the RKHS model for birth weight of 0.45 and weaning weight of 5.27. These researchers obtained the genomic heritability value of 0.58 for birth weight and 0.46 for weaning weight. In research for wool yarn diameter and wool yarn length of Australian Merino sheep, genomic heritability values using the Bayesian method were reported as 0.72 and 0.47, respectively (Rashedi Dehsahraei *et al*. 2017).

In a model using the SNP panel, 50K, 32% of the total additive genetic variance was for fertility trait (Ogawa *et al*. 2016) and approximately 80% for milk production traits (Haile-Mariam *et al*. 2013), captured by SNPs in dairy cattle. The amount of the explained variance and estimated heritability depends on factors such as the number of markers, the amount of linkage disequilibrium (LD) between markers and causal mutations as a result of recombination at the population level, the amount of LD between markers and genes at the family level as a result of family structure in the population, and it depends on action of the gene.

Genomic variance components associated with different MAF groups: To consider the contribution of markers in different allelic spectra in justifying genetic variance, five different MAF groups were defined for the studied traits. Figure 2 shows the amount of genomic heritability for the traits of birth weight, weaning weight, diameter, and length of wool in separate and combined analyses, for five different rare allele frequency groups. In combined analysis, the total heritability estimated for different rare allele frequency groups was almost similar to the value obtained from all SNPs, for all traits.

Although the number of SNPs in different groups were similar, the amount of genetic variance explained by MAF groups were different. In the combined analysis, the genomic heritability of birth weight at the allelic frequency threshold of MAF > 0.01 ranged from 0 to about 0.33 in five MAF groups. The highest estimated value in the first group with allelic frequency was 0.01-0.1.

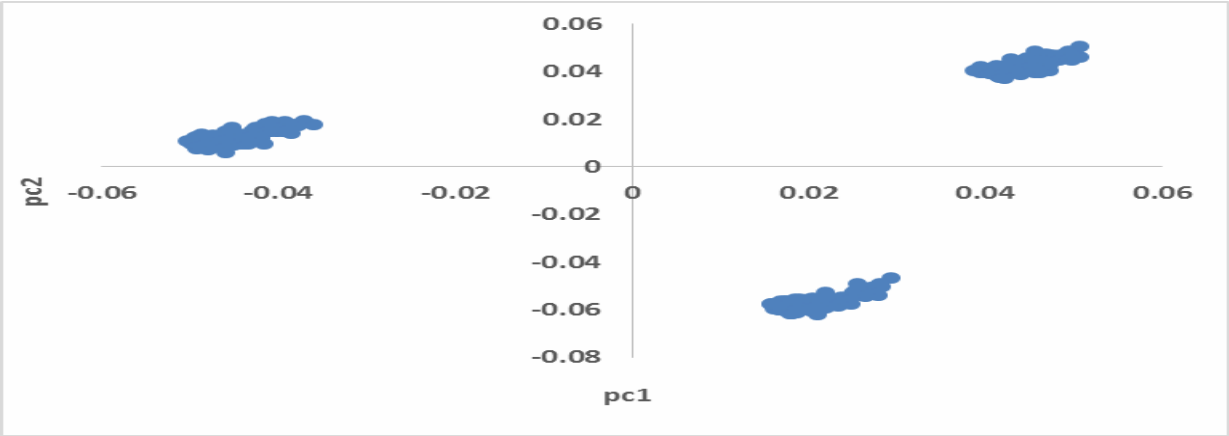

Figure 1 Determining the population structure by multidimensional measurement test (MDS) for genotyped sheep

Table 3 Genomic variance components[1] for body weight and wool traits with univariate analysis using the Reproducing Kernel Hilbert Spaces (RKHS) method by all set of single nucleotide polymorphisms (SNPs) together in Suffolk sheep

Trait (unit)	σ^2_g (SE)	σ^2_e (SE)	σ^2_p (SE)	h^2_m (SE)
Birth weight (kg)	0.74 (0.34)	0.88 (0.24)	1.62 (0.05)	0.46 (0.16)
Weaning weight (kg)	4.41 (2.39)	19.18 (2.15)	23.59 (0.45)	0.19 (0.11)
Fibre diameter (µm)	2.50 (0.30)	0.85 (0.20)	3.35 (0.21)	0.75 (0.05)
Staple length (mm)	55.95 (14.07)	61.82 (9.55)	117.77 (6.61)	0.48 (0.06

σ^2_g: genomic variance; σ^2_e: residual variance; σ^2_p: phenotypic variance and h^2_m: direct genomic heritability.

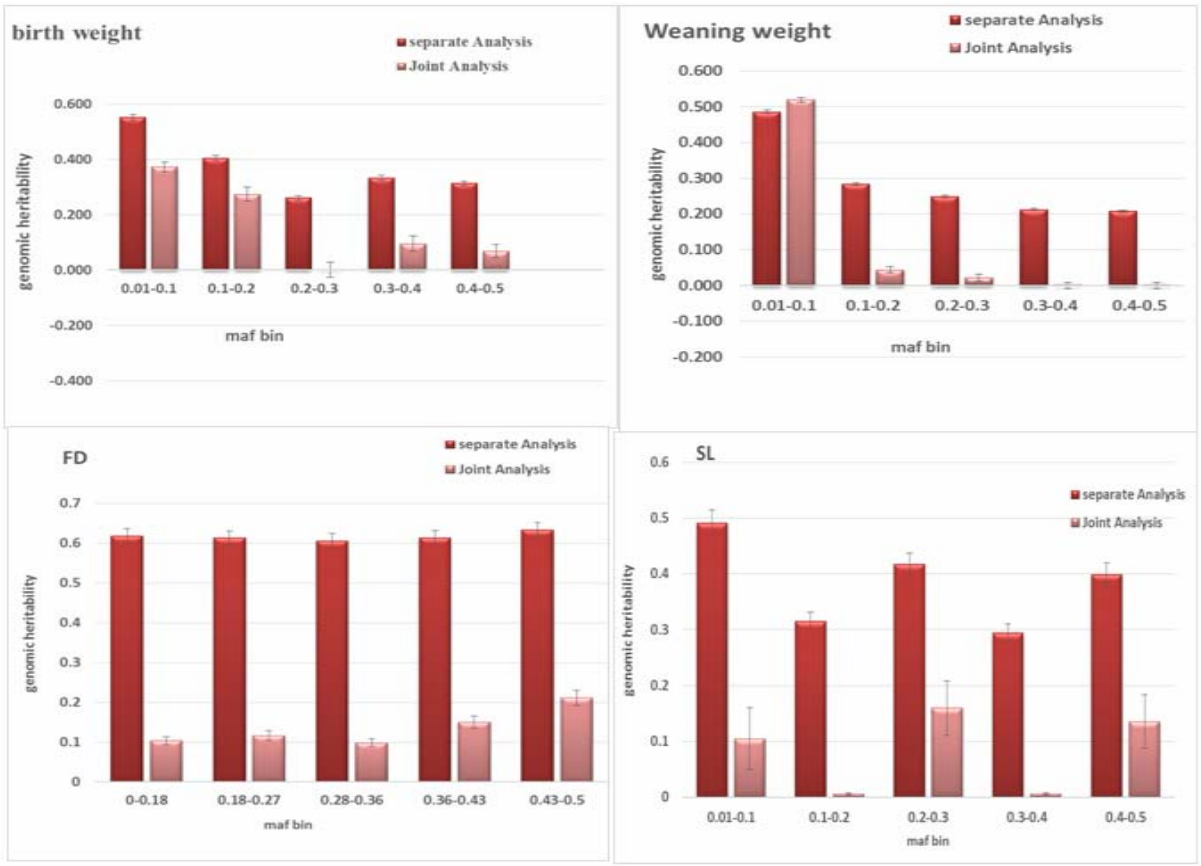

Figure 2 Contribution to genetic variance of single nucleotide polymorphisms (SNPs) partitioned into five bins of minor allele frequency MAF for birth weight (BW), weaning weight (WW), Fibre diameter (FD) and Staple length (SL)
The number of SNPs included in each MAF bin is as follows: 0.01-0.1, n= 10578; 0.1-0.2, n= 8092; 0.2-0.3, n= 8822; 0.3-0.4, n= 8096; 0.4-0.5, n= 8233
The whiskers represent 95% asymptotic confidence intervals

For weaning weight at this threshold, the amount of genomic heritability ranged from 0 to 0.16. The allelic frequency group of 0.01-0.1 accounted for the highest amount of genomic variance. For the two traits of birth weight and weaning weight, the first group with an allelic frequency of 0.01-0.1 had the highest amount of genomic heritability. The third rare allele frequency group had the lowest genomic heritability value for birth weight, 0.2-0.3. For the weaning weight of the fourth and fifth groups, they estimated the lowest amount of genomic heritability.

The estimates obtained from five different MAF groups were different from each other in separate and combined analyses for two attributes of diameter and yarn length. In a separate analysis, the variances for each group were skewed due to (LD). For both traits, the values estimated in separate analyzes were higher than the values obtained in the joint analysis for all groups. In the separate analysis of different MAF groups, the amount of genomic variance obtained for different groups was somewhat similar. In the combined analysis, there was a high variation between the genetic variance identified by different subgroups.

The total estimated heritability in the combined analysis was similar to the value obtained from all SNPs, for both traits, but in the separate analysis, the total heritability in five different rare allele frequency groups was much higher than the value obtained from all SNPs. The amount of genomic heritability of fibre diameter was variable in five MAF groups. The highest estimated value in the fifth group with rare allele frequency was 0.4-0.5 (about 0.21), and the lowest value was in the third group (0.2-0.3), which was estimated at 0.098. The staple length trait, the genetic variance distribution pattern justified by SNPs, fluctuated between the five MAF groups, and the heritability value varied from zero in the second and fourth groups to about 0.16 in the third group. Since selection takes place in livestock populations, the distribution of genetic variance varies according to allelic frequency. Abdollahi-Arpanahi *et al*. (2014) reported in a study on broiler chickens that 75% of the genomic variance for body weight and breast muscle traits was explained by markers with a frequency of less than 0.2. Results on the amount of genomic heritability in human populations have also been reported. In a study of schizophrenia patients, about 70% of the total variance related to common SNPs was explained with MAF < 0.1 (Lee *et al*. 2012). Rashedi Dehsahraei *et al*. (2017), in a study on Australian Merino sheep, reported that about 80% of the genetic variance of birth weight and about 86% of the genetic variance of weaning weight was explained by common SNPs with MAF < 0.18.

In research conducted by Rashedi Dehsahraei *et al*. (2017) for Merino sheep wool traits, results similar to those reported in this research showed different frequency groups of rare alleles. For the length of the wool warp, the heritability value varied from zero in the second and fourth groups to about 0.15 in the third group. For wool warp diameter, the highest heritability value was estimated in group five with an allelic frequency of 0.43-0.5. The lowest heritability value was calculated in the third group of combined allele frequencies. As suggested by Lee *et al*. (2013), a large, ideal sample size and better coverage of low-frequency variants are needed to obtain stronger and more reliable inferences.

In this study, for quantitative traits in Suffolk sheep, we tried to partition the additive genetic variances captured by genome-wide SNP markers into two different components, based on the information on their MAFs. Results indicated that the whole additive genetic variance captured by all available SNPs could be separately estimated as the two components. Using SNPs in different MAF ranges might explain different parts of the additive genetic variance for the quantitative traits.

The results could have provided some information on the genetic architecture for the quantitative traits in Suffolk sheep, although its validity may be limited, mainly due to the sample size and the use of simpler statistical models in this study. There will be other sources to characterize each of SNP markers (e.g., genome position information, gene function information and so on), and then these could give a chance to analyze with a different way to partition all available SNPs.

CONCLUSION

Our results showed that a significant part of the genetic variance can be explained by the common variants of body weight and wool traits in Suffolk sheep. All MAF groups contribute to additive genetic variance regardless of the studied trait. When grouping the markers, it was found that the contribution of different groups of SNPs with rare allele frequency in explaining the genetic variance for the four examined traits was different, and in general, a significant part of the genetic variance was explained by SNPs with MAF > 0.20.

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