Genetic Parameters and Genome-Wide Association Studies for Body Size Traits of Shuxuan Cattle in China

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Abstract In domestic cattle, the body size traits have important implications in terms of breed characteristics and production performance. Shuxuan cattle is a dual-purpose breed mainly raised in Sichuan province, China, for which we have known less about the genetic parameters and underlying candidate genes in relation to the body size traits. In this study, we obtained the genome-wide single nucleotide polymorphisms (SNPs) using the Illumina Bovine BeadChip in 275 Shuxuan cattle. These SNPs were first used for estimating genetic parameters for the withers height (WH) and diagonal body length (BL). Using the bivariate animal model, the estimates (±standard error) of heritabilities were 0.71 ±0.22 and 0.49 ±0.29 for BL, and their genetic correlation was 0.64 ±0.37. Second, the genome-wide association study (GWAS) was performed. However, these did not result into genome-wide significant SNPs for both WH and BL traits. According to a less stringent suggestive significance, some positional candidate genes were found, and some of them (such as *FAM110B*, *TAS1R2*, *PAX3*, and *FHIT*) were previously reported in literature to be associated with body size traits in cattle. In conclusion, we estimated the genetic parameters in Shuxuan cattle using genomic information for the first time, which are required for implementing the genomic selection programs in the future.

Key words Heritability, Genetic correlation, Genomic evaluation, Genome-wide association study (GWAS)

1 Introduction

Shuxuan cattle is a dual-purpose breed (meat and milk) developed by crossing indigenous Xuanhan cattle with exotic Simmental and Holstein semen[1]. This cattle breed has been mainly raised in Sichuan Province, China, and is still undergoing successive genetic improvement for the economically important traits. In domestic cattle, adult body size is considered as a breed characteristic, such that they could be roughly classified into small, medium and large breeds[2]. Albertí *et al.*[3] systematically compared 15 European cattle breeds and found significant differences in body size measurements and the carcass traits among them. It has been well-known that, however, intra-breed variation in body size is more or less associated with diverse production performances on meat and milk traits. Using 58 265 cattle from 17 populations, a comprehensive meta-analysis revealed that the genetic architecture of stature in cattle is similar to that in humans[4]. Accordingly, body size measurements are hopeful to be further included into breeding program of Shuxuan cattle, whereas their genetic parameters are less known yet in this breed.

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During the past decade, genomic information have been successfully used for the genetic evaluation in cattle and other livestock[5]. The genetic parameters estimated using genomic information would have higher accuracy than that using the traditional pedigree information[6]. Furthermore, genomic information could be used for association analysis, *i. e.*, genome-wide association studies (GWAS), for dissecting the significantly associated markers, genes, and genomic regions[7]. Zhang *et al.*[8] reported the significantly associated single nucleotide polymorphisms (SNPs) with heart girth and hip height in Chinese Holstein cattle using genomic information obtained from the Illumina BeadChip genotyping array. Recently, the genome sequence variants were used for mapping candidate genes significantly associated with body size measurements in Brahman cattle and Yunling cattle[9]. In this study, we simultaneously used Illumina 100 Kb BeadChip array for obtaining genomic information, by which the genetic parameters were estimated for two body size measurements in Shuxuan cattle. Second, GWAS was performed for detecting the underlying candidate genes or genomic regions. These results will be helpful for implementing genomic selection on body size traits of Shuxuan cattle.

2 Materials and methods

2.1 Ethics statement The collection of blood samples, used for the genotyping in this study, was ethically approved by the Institutional Ethics Committee of Sichuan Animal Science Academy.

2.2 Traits and edits Two body measurement traits of withers

height (WH, cm) and diagonal body length (BL, cm) were manually measured and collected for 275 adult multiparous cows raised in one single farm from Xuanhan County, Sichuan province, China. These cows ranged from 39 to 44 months of old when phenotypic data were collected. Regarding raw phenotypic records, the possible outliers were discarded if their values were beyond the population mean ± 3.5 standard deviations (SD). Herein, 272 cows were remained for the following analyses.

2.3 Genotyping and quality controls Blood samples were collected by veterinarians and stored at −20 ℃. The genomic DNA was extracted using Axy-Prep Genomic DNA Miniprep Kit (Axygen Bioscience, USA). DNA quality was evaluated using the Nanodrop ND-200 spectrophotometer (Themro Scientific), by requiring the concentration of >50 ng/μL. After genome DNA samples were whole-genome amplified and fragmented, they were hybridized on the Illumina 100K Bovine BeadChip (Illumina, San Diego, USA) for 16−24 h at 48 ℃. The nonspecifically hybridized DNA were washed, and the specifically hybridized loci were processed for single-base extension reaction, stained and imaged on an Illumina iScan Reader (Beijing Compass Agritechnology Co., Ltd, Beijing, China).

There were 95 256 raw SNPs, which were subjected to the quality controls (QC) using the Plink software[10]. First, SNPs (N=4 907) located on the sex and unknown chromosomes were removed. Second, the calling ratios were required at least 90% for both the genotyped cattle and SNPs, which discarded 0 animal and 1 484 SNPs. Third, SNPs (N=4 056) were removed if their minor allele frequencies (MAF) were <5% or they significantly deviated from Hardy-Weinberg equilibrium (HWE) with $P < 10^{-8}$. After these QC steps, 84 809 genome-wide autosomal SNPs were finally remained. Linkage disequilibrium (LD) decay within the 10 Mb regions was analyzed using the LD. decay function in sommer R package[11]. The population structure was revealed according to principal components analysis (PCA) using SNPRelate R package[12].

2.4 Estimates of genetic parameters As there was no systematic difference on the herd, age, and gender for this dataset, the variance components were estimated based on the following bivariate animal model:

$$\begin{bmatrix} y_{WH} \\ y_{BL} \end{bmatrix} = \begin{bmatrix} 1 & 0 \\ 0 & 1 \end{bmatrix} \begin{bmatrix} \mu_{WH} \\ \mu_{BL} \end{bmatrix} + \begin{bmatrix} Z_{WH} & 0 \\ 0 & Z_{BL} \end{bmatrix} \begin{bmatrix} a_{WH} \\ a_{BL} \end{bmatrix} + \begin{bmatrix} e_{WH} \\ e_{BL} \end{bmatrix}$$

where y_{WH} and y_{BL} are vectors of body size measurements for *WH* and *BL*, with their population means of μ_{WH} and μ_{BL}, respectively. The a_{WH} and a_{BL} are vectors of additive genetic effects, with their occurrence matrix of Z_{WH} and Z_{BL}. The e_{WH} and e_{BL} are the residual effects. The additive genetic effects and residual effects followed the covariance structures:

$$\begin{bmatrix} a_{WH} \\ a_{BL} \end{bmatrix} \sim N\left(0,\ G \otimes \begin{bmatrix} \sigma^2_{a_{WH}} & \sigma_{a_{WH}a_{BL}} \\ \sigma_{a_{WH}a_{BL}} & \sigma^2_{a_{BL}} \end{bmatrix}\right)$$

and $$\begin{bmatrix} e_{WH} \\ e_{BL} \end{bmatrix} \sim N\left(0,\ I \otimes \begin{bmatrix} \sigma^2_{e_{WH}} & \sigma_{e_{WH}e_{BL}} \\ \sigma_{e_{WH}e_{BL}} & \sigma^2_{e_{BL}} \end{bmatrix}\right)$$

where $\sigma^2_{a_{WH}}$, $\sigma^2_{a_{BL}}$, $\sigma^2_{e_{WH}}$, and $\sigma^2_{e_{BL}}$ are the variances of additive genetic effects and residual effects for *WH* and *BL*, respectively; $\sigma_{a_{WH}a_{BL}}$ and $\sigma_{e_{WH}e_{BL}}$ are the covariance between the two traits. The *I* is an identity matrix; *G* is the relationship matrix that was estimated from genome-wide SNPs (*i.e.*, genomic relationship matrix) according to method of VanRaden[13]. The estimates of variance components were implemented using AI-REML method in BLUPF90 software[14]. The heritabilities (h^2) for each trait and genetic correlations (r_g) between the two traits were calculated using $h^2 = \sigma^2_a/(\sigma^2_a + \sigma^2_e)$ and $r_g = \sigma_{aWHa_{BL}}/\sqrt{\sigma^2_{a_{WH}}\sigma^2_{a_{BL}}}$, respectively.

2.5 GWAS and functional investigation The association analysis of SNP was performed for each trait, in which the SNP effect and polygenic effect were simultaneously fitted as mixed linear model as follows:

$$y = 1\mu + sp + za + e.$$

where *p* is the candidate SNP effect tested for significance, *S* is the vector of allele count (*i.e.*, 0, 1, or 2) of this SNP for every cow, and all other parameters were described above. The leaving-one-chromosome-out (LOCO) method, implemented in GCTA software[15], was used for constructing the *G* matrix; in other words, *G* was alternatively computed using all SNPs except those on the chromosome where the candidate SNP is located. The raw *P* values were subjected to multiple testing correction using Bonferroni method[16], and the adjusted $P < 0.05$ was set to be significant. Due to the small sample size of this dataset, the suggestive significance was also set to 10^{-4}.

The genomic regions with 200 Kb both upstream and downstream of the candidate SNPs were subjected to search for the annotated functional genes using biomaRt R package[17]. The ARS-UCD1.2 assembly was used as reference genome. Regarding these candidate genes, functional enrichment analyses were conducted using the DAVID tool[18] in terms of the Gene Ontology (GO) terms and Kyoto Encyclopedia of Genes and Genomes (KEGG) pathways. The default parameters were used for computing *P* values with the threshold of 0.05.

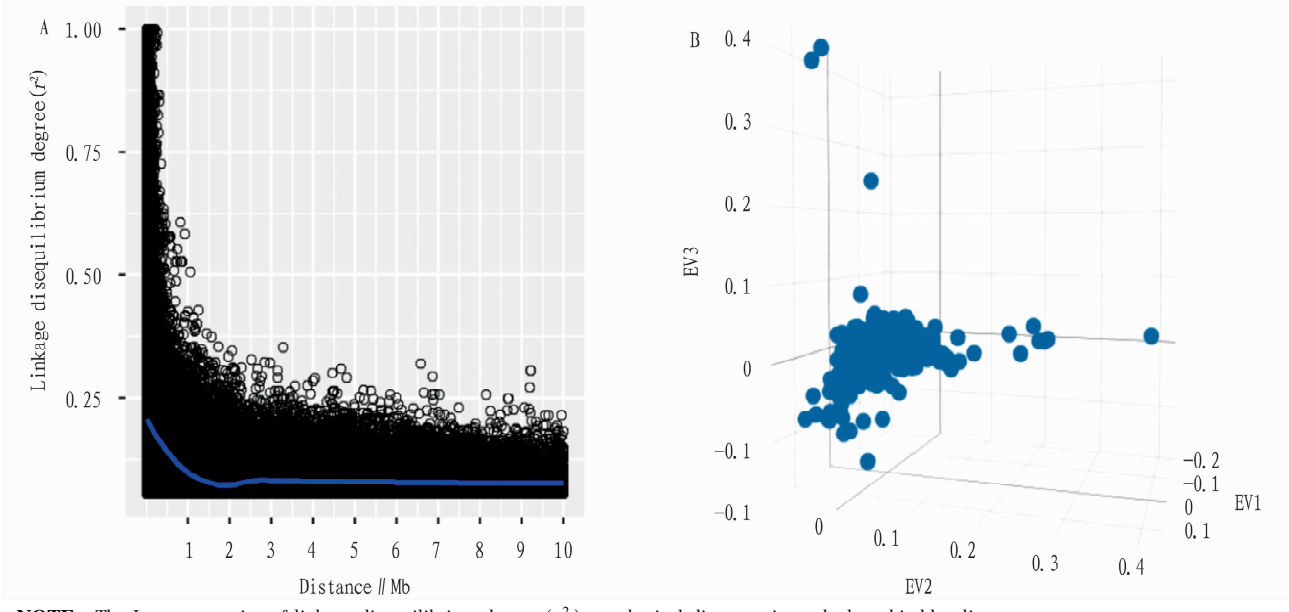
3 Results and analysis

After the QC steps, 84 809 SNPs were remained and distributed through 29 autosomes with average pairwise distances (±SD) of (29.3±27.6) Kb. The LD obviously decreased after the physical distances of SNPs exceed 1 Mb (Fig. 1A); the average r^2 were 0.15±0.14 and 0.08±0.03 for markers at 1 Mb and >1 Mb intervals, respectively. There was no observable population stratification among these cows according to the PCA clustering (Fig. 1B). The descriptive statistics of phenotype and estimates of genetic parameters are shown in Table 1. The Pearson's correlation coefficient of phenotypic measurements was 0.63 between WT and BL, which was comparable to their positive genetic correlation (0.64±0.37) as estimated from genomic information. The higher heritability was observed for WH (0.71±0.22) than that of BL (0.49±0.29), while both of the two traits are highly heritable. However, the relatively high standard errors were present perhaps due to the small sample size in this study.

Table 1 Descriptive statistics of phenotype and genetic parameters

Traits	Phenotype		Genetic parameters (±standard error)			
	Mean	*SD*	*a*	*e*	h^2	r_g
WH	272	120.7	50.55±17.16	19.35±17.16	0.71±0.22	0.64±0.37
BL	272	134.6	110.56±66.15	109.73±61.00	0.49±0.29	

NOTE WH = Withers height, BL = Diagonal body length, *SD* = standard deviation, *a* = variances of additive genetic effects, *e* = variances of residual effects, h^2 = heritability, r_g = genetic correlations between the two traits.



NOTE The Loess regression of linkage disequilibrium degree (r^2) on physical distances is marked as this blue line.

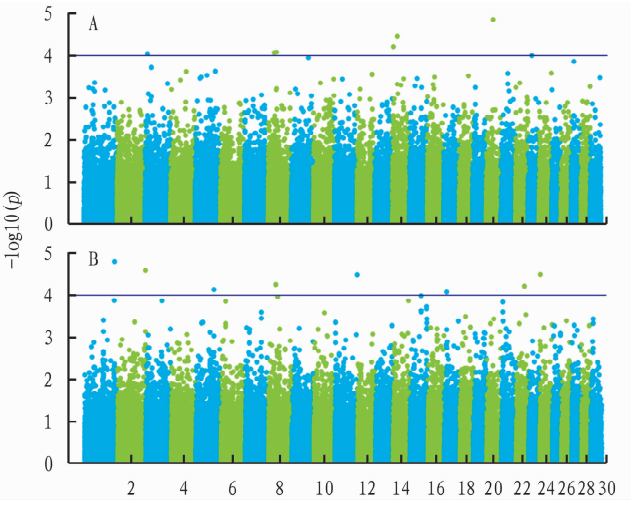
Fig. 1 Linkage disequilibrium decay (A) of SNPs and principal component analysis-based clustering of samples (B)

We did not detect genome-wide significant SNPs for both WH and BL traits, with the lowest -log10 (*P*) of 4.85 and 4.79 (Fig. 2). Therefore, we alternatively set a more relaxed suggestive significance with $P < 10^{-4}$ and found six and eight candidate SNPs for WH and BL, respectively (Table 2). For WH, the six candidate SNPs were located on BTA3, BTA8, BTA14, and BTA20, around which there were 12 candidate genes with an interval of 400 Kb in length. For BL, the eight candidate SNPs were located on different chromosomes, and seven of them could be related with 31 genes. Furthermore, no functional term, including GO term and KEGG pathway, was significantly enriched regarding this candidate gene dataset.

Table 2 Candidate genomic regions and genes of association analysis

Traits	Regions	Candidate genes
WH	BTA3: 10713673-11113673	*OR10AA1*, *OR10AA1C*, *OR6N2*, *OR6N1*, *OR6K6*, *OR6K5*, *OR6K4*, *OR6K2*, *SPTA1*, *OR10Z1*
	BTA8: 30869589-31269589	*MPDZ*
	BTA8: 42845977-43245977	None
	BTA14: 5464211-5864211	None
	BTA14: 23972762-24372762	*FAM110B*
	BTA20: 34282907-34682907	None
BL	BTA1: 144198713-144598713	*ICOSLG*, *DNMT3L*, *AIRE*, *PFKL*, *CFAP410*, *TRPM2*, *LRRC3*, *TSPEAR*, *KRTAP10-8*, *KRTAP12-2*
	BTA2: 133736568-134136568	*IFFO2*, *ALDH4A1*, *TAS1R2*, *PAX*
	BTA5: 85742731-86142731	*SOX5*
	BTA8: 35618482-36018482	None
	BTA11: 105529430-105929430	*OLFM1*, *PPP1R26*, *PIERCE1*, *MRPS2*, *LCN10*, *LCN15*, *LCN8*, *TMEM141*, *CCDC183*, *RABL6*
	BTA17: 10449976-10849976	*PRMT9*, *TMEM184C*, *EDNRA*
	BTA22: 40492320-40892320	*FHIT*
	BTA24: 3291395-3691395	*TSHZ1*, *PTGR3*

NOTE WH = Withers height, BL = Diagonal body length.



NOTE The blue lines show the suggestive significance.

Fig. 2 Manhattan plots for withers height (A) and diagonal body length (B) traits

4 Discussion and conclusions

4.1 Discussion In domestic cattle, body size and conformation measurements have the important implications on both breed characteristics and production performances[2,19]. To better prepare breeding programs for genetically selecting the optimum body size, it is necessary to estimate the related genetic parameters and explore the underlying candidate genes. Using pedigree information, Frizzas *et al.* [20] estimated heritability (0.25 – 0.42) and genetic correlations (varied from weak negative to strong positive correlations) for body weight and scrotal circumference at 12 and 18 months of age in male Nellore cattle. In Bali cattle, the heritability estimates of 0.41 ± 0.08 and 0.39 ± 0.08 were obtained for the withers height and body length, respectively; and the genetic correlation between withers height and body length was 0.05[21]. In this study, we obtained higher heritabilities and genetic correlations for the two traits, which would reflect the breed differences and different genetic relationship measurements were included. In comparison with traditional pedigree records, use of genomic information for calculating genetic relationship could provide higher accuracy on estimates of genetic parameters[6]. For the linear body measurement traits, the inclusion of partially genotyped animals could improve the accuracy of genomic evaluation in Hanwoo beef cattle[22].

In addition to estimates of genetic parameters, previous GWAS have been performed for exploring underlying candidate genes for body size traits in cattle. Raza *et al.* [23] reviewed previous GWAS and summarized the candidate genes significantly associated with growth, carcass, and meat quality in beef cattle. For the heart girth and hip height at 6, 12, 18, and 24 months of age in Chinese Holstein cattle, dozens of candidate genes were suggested and some of them were known as highly related to development and skeletal and muscular growth[8]. In Simmental beef cattle, 21 genes were promising candidate genes being significantly associated with body height, body length, hip height, heart size, abdominal size, and cannon bone size. Chen *et al.* [9] conducted GWAS for 15 body size traits for Brahman cattle and Yunling cattle using the autosomal SNPs derived from whole-genome sequences, and found some biologically meaningful genes. However, we did not obtain genome-wide significant SNP for the two traits of body height and body length in this study. This result would be partially explained by the relatively small sample size included in this study.

Although no genome-wide significant SNP was detected in this study, some biologically meaningful genes were revealed according to the literature investigation. Among them, *FAM110B* (family with sequence similarity 110 member B), which is a protein-coding gene located on BTA14 and involved in increasing cell number and cell size, was reported to be associated with carcass and growth traits in Hanwoo[24]. Also, *FAM110B* was previously reported to be associated with carcass weight in the Hanwoo cattle[25]. *TAS1R2* (taste 1 receptor member 2), located on BTA2 and is responsible to sensor the taste, was previously reported to be significantly associated with body height of Qinchuan cattle[26]. In rabbits, *TAS1R1* was also suggest to be one of the candidate genes affecting growth performance and dressing percentage in rabbits[27]. The associations of SNP and haplotype analysis for paired box 3 (*PAX3*) gene were reported with growth traits in Chinese cattle[28]. The fragile histidine triad diadenosine triphosphatase (*FHIT*) gene was suggested to be candidate gene associated with cattle productive traits in Xinjiang brown cattle[29]. These literature evidence could support that the found genomic regions and candidate genes would be associated with body size traits in Shuxuan cattle.

4.2 Conclusions In this study, we used genomic information for estimating the heritability and genetic correlations for both body height and body length traits in Shuxuan cattle. These SNPs were further subjected to association analysis, by which some known candidate genes were revealed to be significantly associated with body size traits in cattle. The results would be helpful for implementing genomic evaluation for this cattle breed.

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