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Association analysis for udder index and milking speed with imputed whole-genome sequence variants in Nordic Holstein cattle

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ABSTRACT

Genome-wide association testing facilitates the identification of genetic variants associated with complex traits. Mapping genes that promote genetic resistance to mastitis could reduce the cost of antibiotic use and enhance animal welfare and milk production by improving outcomes of breeding for udder health. Using imputed whole-genome sequence variants, we carried out association studies for 2 traits related to udder health, udder index, and milking speed in Nordic Holstein cattle. A total of 4,921 bulls genotyped with the BovineSNP50 BeadChip array were imputed to high-density genotypes (Illumina BovineHD BeadChip, Illumina, San Diego, CA) and, subsequently, to whole-genome sequence variants. An association analysis was carried out using a linear mixed model. Phenotypes used in the association analyses were deregressed breeding values. Multitrait meta-analysis was carried out for these 2 traits. We identified 10 and 8 chromosomes harboring markers that were significantly associated with udder index and milking speed, respectively. Strongest association signals were observed on chromosome 20 for udder index and chromosome 19 for milking speed. Multitrait meta-analysis identified 13 chromosomes harboring associated markers for the combination of udder index and milking speed. The associated region on chromosome 20 overlapped with earlier reported quantitative trait loci for similar traits in other cattle populations. Moreover, this region was located close to the *FYB* gene, which is involved in platelet activation and controls IL-2 expression. *FYB* is a strong candidate gene for udder health and worthy of further investigation.

Key words: udder conformation, milking speed, genome-wide association study

INTRODUCTION

Animal welfare and production costs have spurred interest in breeding for improved functional traits (Boettcher, 2005). A cow's milking ability is defined by the milking speed, average milk flow rate, maximum milk flow rate, and total milking time. Milking ability influences the working time required for milking and is genetically correlated with mastitis incidence. Heritability values for milking ability traits are medium to high, with values of 0.42 for average milk flow, 0.56 for maximum milk flow, and 0.38 for milking time in German Holsteins (Gade et al., 2007). Genetic correlations of these 3 traits with SCS were 0.35, 0.38, and 0.24, respectively (Gade et al., 2007). Higher milk flow and shorter milking time were associated with increased susceptibility to mastitis. Sewalem et al. (2011) reported a heritability of 0.14 for milking speed in Canadian Holstein. The genetic correlation between milking speed and SCS was 0.25 (0.41 and 0.25 for first and second lactations, respectively; Boettcher et al., 1998). Taken together, these results support an association between faster milking and higher SCS.

Mastitis could lead to udder injury, longer milking time, incomplete udder draining, and increased SCS, whereas complete draining will help to prevent clinical mastitis (Rupp and Boichard, 2003). Udder conformation (teat placement, length of fore udder, and udder depth) has an effect on mammary gland health and has been used as an indicator trait to enhance selection for mastitis resistance by inclusion in a selection index (Lund et al., 1994; Carlstrom et al., 2013). Due to low heritability and lack of data, however, selection for udder health traits is generally more difficult than for production traits in dairy cattle.

The SNP marker panels are routinely used for genomic prediction in dairy cattle and have almost doubled the rate of genetic gain (Hayes et al., 2013). Faster genetic gain in low heritability traits can be achieved through genomic selection augmented by QTL information (Boichard et al., 2016). Weights can be defined

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for individual SNP based on their known associations with phenotypes of interest. This process could increase the accuracy of genomic prediction (Brøndum et al., 2015; van den Berg et al., 2016). Due to the availability of SNP arrays, genome-wide association studies identifying associations between common genetic variants with phenotypic differences in a trait have been extensively used in dairy cattle (Sahana et al., 2014). Recent QTL mapping studies have identified QTL associated with mammary gland-related phenotypes in several cattle populations (Cole et al., 2011; Kadri et al., 2015; Pausch et al., 2016). The QTL for milking speed, udder morphometric, mastitis traits, and milk yield traits were mapped by Gray et al. (2012).

Farmers in Denmark, Finland, and Sweden frequently use equipment that automatically measures milk yield and milking duration on every test day or during every milking. These high-quality data are collected for use in management and could be used to improve the genetic evaluation for milking ability traits. In this study, we performed association analyses for udder index and milking speed with imputed whole-genome sequence (WGS) variants in Nordic Holsteins. Subsequent multitrait meta-analyses were used to verify whether detected QTL were simultaneously associated with both traits. Finally, we compared the association results in the present study with previously reported association results for mastitis resistance in the literature.

MATERIALS AND METHODS

Animals and Phenotypes

Bulls from Nordic Holstein cattle with deregressed estimated breeding values (DRP) for udder index and milking speed were used in the analyses. Higher breeding values indicate better udder conformation and higher milking speed. The udder index describes the genetic potential for udder conformation and is a linear combination of subindices for fore udder attachment, rear udder height, rear udder width, udder cleft/support, udder depth, teat length, teat thickness, teat placement (front), teat placement (back), and udder balance. For breeding value predictions, the Nordic Cattle Genetic Evaluation (www.nordicebv.info) traditionally has used farmers' recordings of subjective scores of milking speed of individual cows compared with their herd mates. Since August 2014, breeding values for milking speed have been based on both farmers' scores and automatic measurements of milking speed from automatic milking systems and conventional milking parlors (<http://www.nordicebv.info/wp-content/uploads/2015/04/Improved-breeding-value-for-milkability.pdf>). For details on the recording

Table 1. Descriptive statistics of deregressed estimated breeding value (DRP) and reliability of udder index and milking speed in Nordic Holstein cattle

Summary	Udder index		Milking speed	
	DRP	Reliability	DRP	Reliability
Number	4,921	4,921	4,832	4,832
Mean	94.45	0.77	97.32	0.77
SD	14.39	0.08	15.33	0.13
Minimum	54.80	0.40	55.70	0.33
Maximum	133.50	0.99	138.80	0.99

of phenotypes and breeding value estimates, see www.nordicebv.info. The DRP were derived from Interbull genetic evaluations on the Nordic scale based on the EBV and effective daughter contributions (Fikse and Banos, 2001). Descriptive statistics of DRP and reliabilities for these 2 indices are listed in Table 1. Histograms of DRP and their reliabilities for the 2 indices are presented in Figures 1 and 2. The correlations between Nordic total merit index and udder index and milking speed are 0.17 and 0.02, respectively (http://www.nordicebv.info/wp-content/uploads/2017/03/NAV-routine-genetic-evaluation-122016_FINAL.pdf). The correlation between the DRP of udder index and milking speed for the bulls used in the analysis was 0.13.

SNP Genotypes and Imputation to WGS Level

The association study was carried out by using imputed WGS data, as previously described by Iso-Touru et al. (2016) and Wu et al. (2016). All 4,921 bulls were genotyped with the Illumina BovineSNP50 BeadChip (54k) ver. 1 or 2 (Illumina, San Diego, CA). The 54k genotypes were imputed to WGS variants by using a 2-step approach. First, all animals were imputed to the high-density (HD) level by using a multibreed reference of 3,383 animals (1,222 Holsteins, 1,326 Nordic Red Dairy Cattle, and 835 Danish Jerseys), which had been genotyped with the Illumina BovineHD BeadChip. Subsequently, these imputed HD genotypes were imputed to the WGS level by using a multibreed reference of 1,228 animals from *Run4* of the 1,000 Bull Genomes Project (1,148 cattle, including 288 individuals from the global Holstein-Friesian population, 56 Nordic Red Dairy Cattle, 61 Jerseys, and 743 cattle from other breeds; Daetwyler et al., 2014) and additional data from Aarhus University (80 individuals, including 23 Holsteins, 30 Nordic Red Dairy Cattle, and 27 Danish Jerseys).

Different variant calling pipelines were used for the 1000 Bull Genome Project data and the in-house Nordic data at Aarhus University. The WGS data at Aarhus

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