Detection of Quantitative Trait Loci Affecting Leg Conformation Traits in Danish Holstein Cattle

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ABSTRACT

Strong legs and feet give longer herd life of dairy cows. Therefore, many countries include measures of leg and feet conformation traits in their breeding programs, often as early predictors of longevity. Five leg conformation traits were measured on grand-daughters of 19 Danish Holstein sire families with 33 to 105 sons. The traits measured were: rear legs side view, rear legs rear view, hock quality, bone quality and foot angle. A genome scan was performed to detect quantitative trait loci (QTL) based on the 29 autosomes using microsatellite markers. Data were analysed across and within families for QTL effecting leg conformation traits. A regression method and variance component method was used for QTL detection. For the five different leg conformation traits seven chromosome wise significant QTL were detected across families for rear legs side view, 4 for rear legs rear view, 5 for hock quality, 4 for bone quality and one for foot angle.

INTRODUCTION

Mapping of quantitative traits (QTL) is mainly focussing on production traits such as milk yield and milk composition (Bovenhuis and Schrooten, 2002). However, focus in dairy cattle breeding is currently changing to put more weight on non-production or low heritability traits e.g., health traits (Holmberg and Andersson-Eklund, 2003), behavioural traits (Schmutz et al., 2001), functional traits and conformation traits like feet and legs (Schrooten et al., 2000; Kühn et al., 2003). Feet and leg problems in cattle are among of the most common diseases in dairy cattle (Enting et al., 1997) and is the third main reason of involuntary culling (15%) after reproductive problems (26.7%) and udder and mastitis problems (26.5%) (APHS, 1996).

The conformation trait feet and legs are recorded in different sub traits like rear legs rear view, rear legs side view, foot angle, hocks and bone quality. In the Danish recording system these traits are classified on a linear scale from one to nine. The heritability of these traits is in the range of 0.12 to 0.41 (Van Dorp et al., 1998; Perez-Cabal and Alenda, 2002; Hiendleder et al., 2003). In the Danish Holstein population the heritability of these traits are in the range of 0.13 to 0.28 (Pedersen Aamand, 2002). Feet and legs are important traits in determine the lifetime of an animal in the herd. If an animal has bad legs this has a major effect on longevity but not on final profit (Perez-Cabal and Alenda, 2002). In the Danish Holstein the trait feet and legs are positively correlated with udder conformation traits (0.13) and longevity (0.21) (Pedersen Aamand, 2002). Rear leg set has a slightly negative correlation with functional herd life, favouring daughters of bulls that sire progeny with straighter rear legs (Short and Lawlor, 1992). Also, with regard to the health status of the cow, foot and leg traits are important. It has been shown that cows with straighter rear leg set and sharper foot angle were less prone to develop lameness. So far selection for body conformation traits is based on phenotypic and pedigree data only using statistical methods partitioning the phenotype into an additive genetic values and environmental contributions. The trait can be measured late in the life of a cow and the accuracy is low due to the low heritability. Identification of QTL for the different leg

conformation traits could help to select the animals already in an early stage of life with higher accuracy and to focus the selection on specific parts of the legs. In this way it would be easier to breed for leg types, which are less prone to lameness (McDaniel, 1997).
Previous studies have shown that it is possible to detect QTL for feet and leg related traits in Holstein cattle in different countries (Ashwell et al., 1998a,b, 2001; Schrooten et al., 2000; Hiendleder et al., 2003). There are some indications that there are pleiotropic QTL. Hiendleder et al., (2003) detected several QTL chromosomal regions harbouring more than one QTL for feet and leg traits. Information on pleiotropy for QTL would improve MA-BLUP estimates for these traits.
The next step after QTL detection would be detection of the underlying genes of the quantitative traits. This difficult and time consuming however, there are a few examples in cattle showing that it is feasible to detect the underlying genes for milk production e.g., GHR and DGAT1 (Blot et al., 2003; Grisart et al., 2004). So far there are no causal genes detected for feet and leg traits.
To increase the knowledge underlying the genetics of leg conformation traits, several different leg conformation traits were measured in the Danish Holstein cattle population. The aim of the study was to detect QTL across the cattle genome influencing leg related traits.

MATERIALS AND METHODS

Animals

The animal material consists of a grand-daughter design consisting of 19 paternal Danish Holstein sire families with a total 1,373 bulls. The number of sons per grandsire ranged from 33 to 105, with an average family size of 72.3.

Markers and Maps

Markers were chosen from previous published maps (Barendse et al. 1997) and from the website of the Meat Animal Research Center (http://sol.marc.usda.gov/). All autosomes [*Bos taurus* chromosomes (**BTA**) 1-29] were covered in a whole genome scan. The genome was screened using 327 micro-satellite markers with an average marker content of 7.97 cM. Marker genotypes were determined on an automated sequence analyser (ABI, Perkin Elmer). The map was created using Cri-MAP version 2.4 (Green et al., 1990) and the Haldane map function. The calculated map distances were used in the QTL analysis.

Phenotypic Data

Daughters of bulls were scored for their leg conformation on location by trained inspectors. The five leg conformation traits scored were: Rear legs side view; Rear legs rear view; Hock quality; Bone quality; and Foot angle. These traits were subjectively scored on a linear scale from 1 to 9, divided into nine classes where 1 and 9 nine represented biological extremes. Estimated breeding values (EBV) for leg conformation traits of sons were calculated using a single trait Best Linear Unbiased Prediction (BLUP) animal model. These EBV's were used in the QTL analysis.

QTL Analysis

The data was analysed with a multipoint regression approach for across and within family analysis, the variance component method was used to validate QTL found across families and for characterization of QTL when more then one QTL was detected on the same chromosome.
Regression analysis. Population allele frequencies at the markers were estimated using an EM-algorithm. Allele frequencies were subsequently assumed known without error. Phase in the sires was determined based on offspring marker types. Subsequently this phase was assumed known without error. Segregation probabilities at each map position were calculated using information from all markers on the chromosome simultaneously using Haldane's mapping function (Haldane,

1919). Phenotypes were regressed onto the segregation probabilities. Significance thresholds were calculated using permutation tests (Churchil and Doerge, 1994).

Variance component analysis. Single trait single QTL analysis. Each trait was analysed separately using linkage analysis. The full model can be expressed as:

$$\mathbf{y} = \mathbf{X}\beta + \mathbf{Zu} + \mathbf{Wq} + \mathbf{e}, \quad (1)$$

where **y** is a vector of n observations, **X** is a known design matrix, **β** is a vector of unknown fixed effects, which is in this case only the mean, **Z** is a matrix relating to individuals, **u** is a vector of additive polygenic effects, **W** is a known matrix relating each individual record to its unknown additive QTL effect, **q** is a vector of unknown additive QTL effects of individuals and **e** is a vector of residuals. The random variables **u**, **q** and **e** are assumed to be multivariate normally distributed and mutually independent (Lund et al., 2003).

IBD matrix. First the gametic relationship matrix (Fernando and Grossman, 1989) was calculated and then using the linear relationship between the gametic relationship matrix and the IBD matrix, the IBD matrix was designed (George et al., 2000). The covariance structure among the random QTL allelic effect of all animals in de the pedigree, are described in the gametic relationship matrix. The information of the transmission of linked markers is used to calculate the IBD probabilities at the position of a putative QTL position (Sørensen et al., 2003).

Significance level. Significance thresholds were calculated using a quick method to compute approximate threshold levels that control the genome-wise type I error (Piepho, 2001). A significance level of 5% chromosome wise was considered to be significant.

RESULTS

The analysis across all 19 families detected 21 QTL. The identified QTL are seven for rear legs side view, five for rear legs rear view, four for hock quality, four for bone quality and one for foot angle (Table 1). The QTL are spread across 17 different chromosomes of which four chromosomes (1, 11, 15 and 27) affecting two different traits. The QTL were detected on chromosomes with different marker densities indicating that marker density did not hamper QTL detection in this study. The QTL explained 5.1% up to 19.1% of the total genetic variance.

The regression analysis and the variance component analysis revealed the same QTL as being significant for the across family analysis. This indicates that using the quick method to compute the approximate threshold (Piepho, 2001) is a good method to reveal the significance thresholds compared to the permutation test (Churchill and Doerge, 1994).

The regression method was used for a within family analysis to find the segregating families. The number of segregating families per trait per chromosome was in the range from 1 to 7 (Table 1). In case there are two QTL segregating on one chromosome (BTA1, BTA11, BTA15, and BTA27) not the same sires are segregating for the QTL. Only on BTA27, where one QTL is segregating for bone quality and one for hock quality, these QTL have one segregating sire in common.

DISCUSSION

The study of QTL is an important method to determine which chromosome regions and genes are involved in quantitative traits in farm animals. In the present study, 21 QTL were detected distributed across 17 different chromosomes for five different leg traits. These traits are genetically correlated to lameness in dairy cattle (van Dorp et al., 1998). The QTL found in this study can be of interest to select for specific part of the legs in an early stage in life of the animal and thereby improve the health status of the cow.

Table 2 shows QTL for leg conformation traits previous reported on US Holstein cattle (Ashwell et al., 1998a,b, Ashwell et al., 2001), Dutch Holstein cattle (Schrooten et al., 2000), German Holstein cattle (Hiendleder et al., 2003) and in three French dairy cattle breeds, French Holstein, Normande, and Montbéliarde (Boichard et al., 2003). Comparing those results to the present study one can see that eight new chromosomes show a QTL, which were not previously reported, while nine chromosomes positive for a QTL were already detected in the previous studies. For the trait foot angle we only detected one QTL on BTA8, which has not been reported before. In contrast QTL for foot angle were more abundant in both the German Holstein population (five QTL detected on BTA5, BTA6, BTA17, BTA21, and BTA23) (Hiendleder et al., 2003) and the US Holstein population (six QTL detected on BTA9, BTA12, BTA16, BTA17, BTA22, and BTA23) (Ashwell et al., 1998ab, Ashwell et al., 2001). Even though many QTL were identified in both German Holstein and US Holstein, none seemed to overlap. Only on BTA17 both studies identified a QTL, but the most significant markers were more then 50 cM apart.

BTA14 was previously reported to harbour a QTL for rear leg side view (Ashwell et al., 1998b) near marker BM6425. This marker is approximately 50 cM apart from the marker interval RM011-BM4630, in which a QTL was detected for rear leg side view in our study. Within family analysis of the Danish Holstein population did not show any significant QTL near marker BM6425, therefore it is not likely that these QTL are caused by variation of the same genes. The chromosomes BTA7, BTA11, and BTA21 were reported earlier to harbour QTL related to leg traits, but not for the trait rear legs side view, in addition our study revealed three chromosomes which have not been reported earlier for leg related traits.

For the trait rear legs rear view four chromosomes were detected in the Danish Holstein population. Of which three have not been reported earlier (BTA1, BTA28, BTA29), while BTA13 was previously reported to harbour a QTL for rear leg set rear view (Hiendleder et al., 2003). It is difficult to compare the location of the QTL between the German Holstein population and the Danish Holstein population, because the markers used in both populations are not all the same. However, based on the map provided by Thomsen et al., (2000) the approximate distance between MILSTS077 and AGLA232 is 70 cM in the German Holstein population. In addition, marker BM720 has been used in both populations and confirmed the distance between these markers, therefore it is not likely that these QTL are the same.

The QTL detected for hock quality were located four different chromosomes (BTA11, BTA12, BTA15, and BTA27). Hiendleder et al., (2003) reported three chromosomes (BTA11, BTA23 and BTA21). The distance between the marker on BTA11 close to the position mentioned by Hiendleder et al., (2003) is about 50 cM apart from the marker bracket in which the QTL is detected in our study. The other QTL detected in our study (BTA12, BTA15, and BTA27) were not reported before to contain QTL for hock quality, however, BTA12 and BTA27 QTL are reported previously for leg related traits (Ashwell et al., 1998b, 2001).

The QTL identified for the trait bone quality on BTA15, BTA17, BTA26, and BTA27 have not been reported before. Interestingly the QTL on BTA27 for bone quality is in the same marker bracket as the QTL for hock quality.

The molecular information obtained in this study opens the possibility to select for leg conformation traits in an early stage of life of the cow. Which help to improve the health status of the Danish Holstein population.

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Table 1. Overview QTL obtained in the single trait analysis across families

Trait	Chr.[1]	Pos.[2] (cM)	Marker bracket	% of total σ^2_g	% of total σ^2	Likelihood Ratio[3]	Nr. sires[4]
Rear legs side view	BTA1	36.2	BMS4017-BMS4000	6.5	7.0	6.0	1
	BTA2	88.0	BMS1866-BMS1987	7.2	7.9	7.0	2
	BTA3	110.0	BM7225-BM2924	10.2	10.6	13.9	7
	BTA7	104.0	OARAE129-ILSTS006	8.1	8.9	7.8	5
	BTA11	8.0	BM716-BMS2569	5.9	6.2	7.3	2
	BTA14	30.0	RM011-BM302	6.5	6.8	6.9	4
	BTA21	44.0	INRA103-BMS2815	5.8	6.3	6.0	3
Rear legs rear view	BTA1	72.2	BMS4008-BM8246	8.0	7.7	6.5	1
	BTA13	76.0	BL1071-AGLA232	5.8	5.3	6.8	3
	BTA16	8.0	TGLA245-HUJ614	5.8	6.3	7.6	3
	BTA28	50.0	BMS1714-BMC2208	11.1	10.6	7.8	4
	BTA29	0.1	BM4602-BMS1857	5.6	5.5	9.0	7
Hock quality	BTA11	30.0	INRA177-2-RM096	5.3	3.8	6.0	2
	BTA12	98.0	BMS975-BMS1316	5.1	3.8	6.3	2
	BTA15	78.0	BMS2076-BMS820	7.0	4.9	7.6	2
	BTA27	62.0	HUJI13-BM203	7.3	5.0	10.4	4
Bone quality	BTA15	78.0	BMS2076-BMS820	7.5	5.5	6.8	2
	BTA17	32.0	CSSM9-OARFCB48	5.3	4.6	6.3	2
	BTA26	52.0	BMS882-BM804	6.7	5.7	6.7	3
	BTA27	62.0	HUJI13-BM203	4.9	4.6	6.0	2
Foot angle	BTA8	92.0	MCM64-CSSM047	19.1	17.4	5.6	3

[1]Chr. = Chromosome

[2]Pos. = Position on the chromosome in centiMorgan (cM)

[3]All QTL given exceed the 5% chromosome wide threshold determined via the Piepho-method (Piepho, 2001).

[4]Number of segregating sires in the population was determined using the regression method. Each sire family exceed the 5% chromosome wise threshold determined by the permutation test.

Table 3. Results from studies on detection of QTL for leg conformation traits

Chr.[1]	Trait	Marker/Marker Bracket	Position[2]	Study[3]
BTA5	Foot angle	Lysmic-ETH10	72	F/G
BTA6	Foot angle	FBN14	88	F/G
	Rear leg set	BP7	85	D
BTA7	Feet and leg score	BM2707		B
BTA9	Heel depth	BM2504	32	E
	Foot angle	BM4204		A
	Feet and legs	BM4204		A
BTA11	Hocks	INRA032	61	F/G
	Rear leg set rear view	INRA032	61	F/G
BTA12	Foot angle	BM6404		C
	Feet and leg composite	BM6404		C
	Rear legs rear view	BM6404		C
BTA13	Hocks	MILSTS077	53	F/G
	Rear leg set rear view	MILSTS077	54	F/G
BTA14	Rear leg side view	BM6425		B
BTA16	Feet and legs CI	BM719		B
	Rear leg side view	BM719		B
	Foot angle	BM719		B
BTA17	Foot angle	RM156-BMS2220	5	F/G
	Foot angle	BM8125		B
	Rear leg view	BM8125		B
BTA18	Heel depth	ILSTS002	74	E
BTA19	Rear leg set	BM17132	76	D
BTA21	Foot angle	BM8115-HEL5	6	F/G
	Hocks	HEL5	12	F/G
	Rear leg set rear view	HEL5	12	F/G
BTA22	Foot angle	BM3628		A
	Feet and leg score	BM3628		A
	Feet and legs CI	BM3628		A
BTA23	Foot angle	KIEL_E7-BM1443	84	F/G
	Foot angle	BM1905		A
	Rear legs rear view	CYP21		A
BTA24	Rear leg set	AGLA269	17	D
	Foot diagonal	AGLA269	17	D
	Feet and legs	CSSM31-AGLA269	15	D
BTA27	Feet and legs CI	BM3507		B
	Rear leg side view	BM3507		B

[1]Chr. = Chromosome

[2]Position = Position on the marker map used in the study in which the QTL was detected

[3]A = Ashwell et al. 1998a, B = Ashwell et al. 1998b, C = Ashwell et al. 2001, D = Schrooten et al. 2000, E = Boichard et al. 2003, F = Hiendleder et al. 2003, G = Thomsen et al. 2000.