A Primary Screen of the Bovine Genome for Quantitative Trait Loci Affecting Carcass and Growth Traits[1,2]

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ABSTRACT: A primary genomic screen for quantitative trait loci (QTL) affecting carcass and growth traits was performed by genotyping 238 microsatellite markers on 185 out of 300 total progeny from a *Bos indicus* × *Bos taurus* sire mated to *Bos taurus* cows. The following traits were analyzed for QTL effects: birth weight (BWT), weaning weight (WW), yearling weight (YW), hot carcass weight (HCW), dressing percentage (DP), fat thickness (FT), marbling score (MAR), longissimus muscle area (LMA), rib bone (RibB), rib fat (RibF), and rib muscle (RibM), and the predicted whole carcass traits, retail product yield (RPYD), fat trim yield (FATYD), bone yield (BOYD), retail product weight (RPWT), fat weight (FATWT), and bone weight (BOWT). Data were analyzed by generating an F-statistic profile computed at 1-cM intervals for each chromosome by the regression of phenotype on the conditional probability of receiving the Brahman allele from the sire. There was compelling evidence for a QTL allele of Brahman origin affecting an increase in RibB and a decrease in DP on chromosome 5 (BTA5). Putative QTL at or just below the threshold for genome-wide significance were as follows: an increase in RPYD and component traits on BTA2 and BTA13, an increase in LMA on BTA14, and an increase in BWT on BTA1. Results provided represent a portion of our efforts to identify and characterize QTL affecting carcass and growth traits.

Key Words: Quantitative Traits, Carcasses, Cattle

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Introduction

Genetic linkage maps in cattle provide the basis for mapping quantitative trait loci (QTL), thus improving our potential to realize genetic selection progress, especially for those traits that are difficult and(or) expensive to measure. Included in this category are carcass and meat quality traits that can vary widely between breeds and biological types (Wheeler et al., 1997). However, methods to assess differences in genetic potential for carcass merit prior to the processing and distribution phase of beef production are not well established. The ability to more accurately predict genetic merit for carcass characteristics early in the life cycle would permit a more direct approach using existing and future germ plasm in integrating production practices with market demands. Selection indices that include QTL with accurately estimated effects on carcass characteristics could reduce the amount of lengthy and costly data collection by providing a means of genetic evaluation early in the life cycle. For populations segregating QTL alleles having major effects, it is conceivable that individuals could be sorted early in the production cycle to match genotypes with production targets. The objectives of the research reported here were to identify chromosomal regions representing QTL influencing carcass and growth traits by genotyping microsatellites on selected backcross progeny from a *Bos indicus* × *Bos taurus* sire.

Materials and Methods

Animals

A Brahman × Hereford bull previously used in the USDA reference population (Bishop et al., 1994) was mated to Hereford, Angus, and F_1 cows from the Germ Plasm Evaluation Cycle IV Project (Cundiff et al., 1998) to produce 300 offspring born in 1994. Breeds of sire for F_1 dams were Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nelore, Piedmontese, or Salers, and breeds of dam for

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F_1 dams were Hereford or Angus. Average age at slaughter was 440 d, with a range of 375 to 497 d.

Cattle were stratified by breed of dam, age, and sex before assigning them to one of four slaughter groups. Slaughter data were obtained at a commercial facility, and the wholesale rib was obtained from the right side of each carcass for dissection into fat, muscle, and bone (Shackelford et al., 1995). Weights of rib fat (**RibF**), rib bone (**RibB**), rib muscle (**RibM**), fat thickness (**FT**), marbling score (**MAR**), and longissimus muscle area (**LMA**) were adjusted to a constant hot carcass weight (**HCW**). Carcass traits predicted from rib dissection data were retail product yield (**RPYD**), fat trim yield (**FATYD**), and bone yield (**BOYD**). Analysis of these traits on either a constant age or HCW basis had little effect on the outcome. Dressing percentage (**DP**), HCW, predicted retail product weight (**RPWT**), fat weight (**FATWT**), and bone weight (**BOWT**) were analyzed on a constant age basis, and the remaining traits were analyzed on a constant HCW basis. The following growth traits were analyzed: birth weight (**BWT**), adjusted weaning weight (**WW**), and adjusted yearling weight (**YW**). Live weights at 28-d intervals from weaning to slaughter were used to calculate individual animal regressions to adjust weaning weight (200 d) and yearling weight (365 d). Traits were preadjusted for the effects of maternal grandsire breed, maternal granddam breed, slaughter group, and sex using data on all 300 progeny prior to selecting extremes for genotyping.

Genomic Screen

A primary genomic screen was conducted using 238 microsatellite markers (Kappes et al., 1997; http://sol.marc.usda.gov/cattle). Ninety-four of the 300 progeny were selected to be those with the highest RPYD and lowest FT or the lowest RPYD and highest FT. A second group of 93 animals out of the 206 remaining progeny were selected for extremes in Warner-Bratzler shear force (Keele et al., 1999). Genotypic data for two animals excluded the sire as a parent; thus, 185 progeny were included in the final analysis. Procedures for DNA isolation, PCR amplification, and genotyping strategies have been described (Kappes et al., 1997).

Statistical Analysis

An F-statistic profile was obtained by regression of phenotypes on the conditional probability of receiving the Brahman allele from the sire computed at 1-cM intervals (Knott et al., 1996). An F-statistic peak was considered significant if it exceeded a threshold value corresponding to .05 expected false-positives per genomic screen and suggestive when 1 false-positive was expected per genomic screen (Lander and Kruglyak, 1995). The significant (.05) F-statistic threshold (T) was 17.23, and the suggestive (1.0) threshold was 10.17. These thresholds were obtained by iteratively finding the value of T (±.01) that satisfied

$$(c + 2\rho g \nu_1 T)\int_T^{\infty} \text{Prob}_F(x,\nu_1,\nu_2)dx = E(n_{FP}),$$

where c is the number of autosomes (29), ρ (1) is inversely related to the serial covariance between F-statistics corresponding to linked loci as a result of linkage disequilibrium, g is genomic length (27.75 morgans), $\text{Prob}_F(x,\nu_1,\nu_2)$ is the probability density function for a central F distribution with ν_1 (1) numerator df and ν_2 (183) denominator df, and $E(n_{FP})$ is the targeted expected number of false-positives for a genome screen (.05 for significant or 1 for suggestive). That is, for $E(n_{FP})$ = .05 one false-positive with an F-statistic at the threshold (T) value of 17.23 or greater would be expected from 20 whole genome scans.

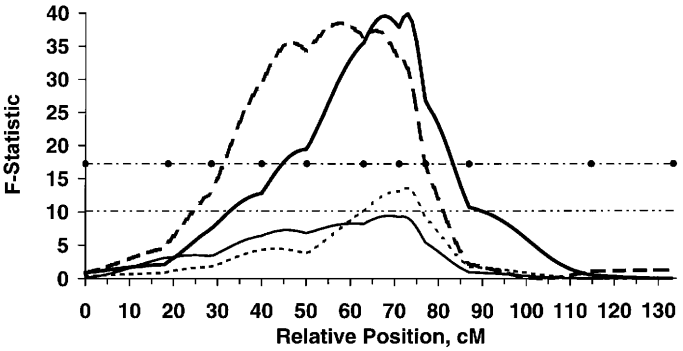

Figure 1. F-statistic profile for BTA5. The F-statistic is plotted against the relative position in centimorgans (cM). The profiles are for Rib B (—), DP (— — —), Rib F (– – –) and BWT (—). The upper horizontal line represents a significance level of $E(n_{PF})$ = .05 and the lower represents a significant level of $E(n_{PF})$ = 1. Beginning at the centromeric end, the dots on the upper horizontal line indicate the relative position of the markers, which were BMS1095, BP1, RM103, BMC1009, BL37, BR2936, CSSM022, RM029, BMS1248, BMS597, and BM8126.

Results

Data obtained from a genomic screen of progeny (185 of the 300 progeny) from a Brahman × Hereford F_1 sire provided genome-wide significant evidence for a QTL on BTA5; the Brahman allele was responsible for increasing RibB and decreasing DP relative to the Hereford allele (Figure 1). Significant increases in BOYD (F = 36.5) and BOWT (F = 28.8) were also detected (not shown). There was suggestive evidence

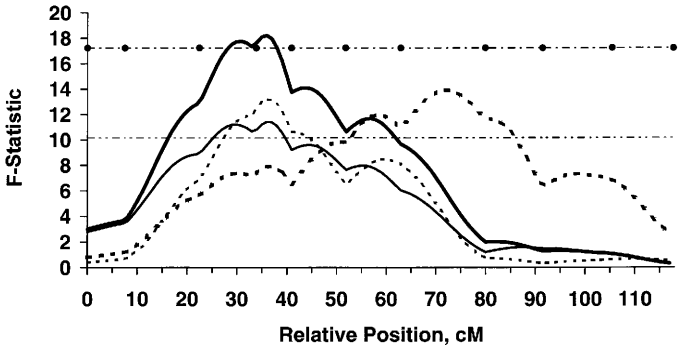

Figure 2. F-statistic profile for BTA2. The F-statistic is plotted against the relative position in centimorgans (cM). The profiles are for RPYD (—), RibM (—), MAR (– – –), and FT (— — —). The upper horizontal line represents a significance level of $E(n_{PF})$ = .05 and the lower represents a significant level of $E(n_{PF})$ = 1. Beginning at the centromeric end the dots on the upper horizontal line indicate the relative position of the markers, which were PROC, ILSTS026, TEXAN-2, URB042, BMS803, BM356, BMS353, TGLA226, BMS829, BMS2519, and IDVGA-2.

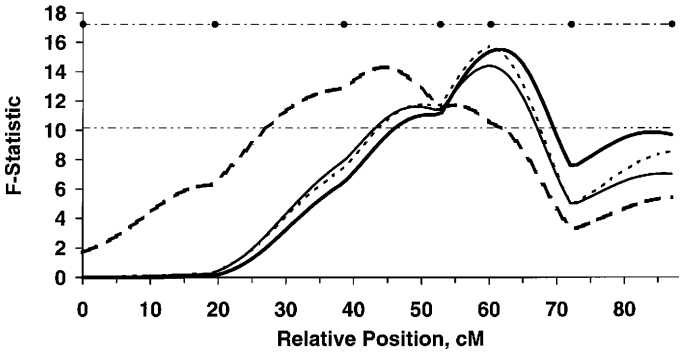

Figure 3. F-statistic profile for BTA13. The F-statistic is plotted against the relative position in centimorgans (CM). The profiles are for RPYD (—), RibM (—), RibF (– – –), and DP (— — —). The upper horizontal line represents a significance level of $E(n_{PF})$ = .05 and the lower represents a significant level $E(n_{PF})$ = 1. Beginning at the centromeric end the dots on the upper horizontal line indicate the relative position of the markers, which were TGLA23, BMC1222, BM720, BM9248, BMS1676, INRA196, and BM6548.

for this Brahman allele decreasing RibF and increasing BWT compared with the Hereford allele (not shown). There was also suggestive evidence for an effect on MAR (F = 10.2) and FATYD (F = 13.6).

There was evidence for four QTL affecting the proportion of fat and muscle in the wholesale rib cut. A significant positive effect (Brahman-Hereford) on RPYD, a predicted or composite trait, was detected on BTA2 (Figure 2). Component traits of RPYD significant at the suggestive level were an increase in muscling (RibM) and a decrease in MAR. Also, at the suggestive level, LMA was increased and RibF, FATYD, and FATWT were decreased. Fat thickness was also implicated; however, in this initial genomic screen, the maximum F-statistic peak was shifted relative to the peak for RPYD and RibM. Support for a QTL on BTA13 with similar effects is just below the significance threshold for several traits (Figure 3). This QTL seems to decrease (Brahman relative to Hereford) DP (F = 14.2) and RibF while RibM and RPYD were increased. Other traits above the suggestive threshold were a decrease in FT, FATYD, and FATWT and an increase in RibB and BOYD. Unlike the putative QTL on BTA2, there was no indication of MAR being affected by a QTL on BTA13.

Additional putative QTL with effects at or above the suggestive threshold were detected on BTA18 and BTA26 (Table 1). The effect of a Brahman allele on BTA18 was an increase in RibF resulting in a decrease in RPYD. The effect of a Brahman allele on BTA26 was an increase in rib muscling (RibM, LMA) and decrease in fat (RibF and FATYD).

A suggestive F-statistic peak (F = 17) at approximately 19 cM on BTA14 indicated a Brahman allele for a larger LMA compared with the Hereford allele (Table 1). Other than a minor suggestion of an effect on FT (F = 9.37), there was only minor support (F < 6) for any of the other carcass or wholesale rib measurements being affected by a QTL on BTA14. Although the effect on LMA was at the significance threshold, a specific effect on LMA without more definitive effects on related traits (e.g., RibM) reduced our confidence in this QTL. Likewise, kidney, pelvic, and heart fat (**KPH**) was increased by a putative QTL on BTA11, but no other measurements of fat seemed to be influenced.

Shown in Figure 4 is suggestive evidence for a QTL on BTA1; the Brahman allele increasing birth weight relative to the Hereford allele. Although evidence for a growth-related QTL was not compelling, it was supported by effects at or near the suggestive threshold on the correlated traits YW, WW, and HCW.

Discussion

A primary genomic screen with markers at 10- to 20-cM intervals on animals selected to represent the extreme values for a phenotype (selective genotyping) is an approach for obtaining the approximate map location of QTL with a reduced amount of genotyping (Lander and Botstein, 1989). However, using data from extreme animals for a selected trait results in estimated QTL effects that are biased upward in absolute value. Further, apparent QTL effects on traits correlated to various degrees with the selected trait will be biased upward to various degrees and can lead to erroneous interpretations. In contrast,

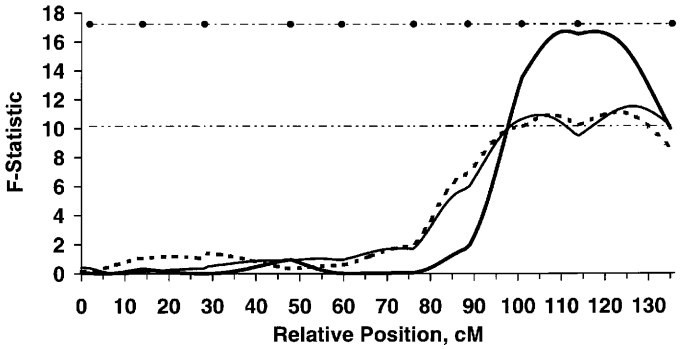

Figure 4. F-statistic profile for BTA1. The F-statistic is plotted against the relative position in centimorgans (cM). The profiles are for BWT (—), WW (— — —), and YW (—). The upper horizontal line represents a significance level of $E(n_{PF})$ = .05 and the lower represents a significant level of $E(n_{PF})$ = 1. Beginning at the centromeric end the dots on the upper horizontal line indicate the relative position of the markers, which were TGLA49, BMS2321, ILSTS104, BMS948, ILSTS083, BMS8246, BMS119, BMS1789, UWCA46, and BMS4014.

selective genotyping has no effect on the F distribution under the null hypothesis. This is because selective genotyping affects the mean square for QTL and error by the same proportional increase (1 + the product of selection intensity and the truncation point); hence, the bias cancels in the F statistic. The basis for these conclusions follows.

Table 1. QTL peaks for carcass traits with F-statistic values at the suggestive level of significance[a]

Chromosome and trait	Relative position	F-statistic	Brahman-Hereford allele effect[b]
18			
RibF	84	11.89	–
FATYD	84	11.89	–
RPYD	84	11.44	+
26			
RibF	6	10.61	+
FATYD	6	10.61	–
RPYD	5	10.27	–
LMA	18	10.36	–
RibM	8	11.60	–
14			
LMA	19	17.01	–
11			
KPH	90	12.79	–
7			
BWT	2	10.33	–

[a]F-statistic values between 10.17 (P = 1) and 17.23 (P = .05) are considered to be suggestive evidence for a QTL. A total of 17 traits were evaluated.

[b]Phenotypic effect of inheriting Brahman alleles vs Hereford alleles.

Suppose we had based our analysis on 94 animals selected to be extreme for a single trait (shear force or retail product yield), the expected value of the estimate biased by selection (a_{s94}) expressed as a function of the true effect (a) is

$$a_{s94} = \frac{2\left[e^{-\frac{(2t-a)^2}{8}} - e^{-\frac{(2t+a)^2}{8}}\right]}{p\sqrt{2\pi}} + a.$$

The true QTL effect (a) is the difference between cattle inheriting the Brahman allele from their sire minus those inheriting Hereford (SD units). The absolute value of the lower and upper truncation points ($-t$, t) is chosen to satisfy

$$\int_{t-\frac{a}{2}}^{\infty} f(x)dx + \int_{t+\frac{a}{2}}^{\infty} f(x)dx = p$$

$f(x)$ is the standard normal probability density function and p ($.31 = \frac{94}{300}$) is the proportion of animals selected to be genotyped.

Loci with the greatest statistical evidence were those affecting RibB and DP (BTA5), BWT (BTA1), RPYD (BTA2 and BTA13), DP (BTA13), and LMA (BTA14). The putative QTL on BTA2 and BTA13 for increased muscling and decreased fat in the wholesale rib require additional genetic and phenotypic measurement for confirmation. Based on the current analysis, RPYD is affected by the locus on BTA2, and the component traits used to predict RPYD are significant only at the suggestive level; this is also the case for the putative QTL on BTA13. The QTL on BTA2 mapped at approximately 35 cM from the beginning of the linkage group; thus, it is unrelated to the double muscling, *mh*, locus, which is at 4 cM (Smith et al., 1997; Casas et al., 1998). The QTL on BTA2 and BTA13 generally affected the same traits in the same direction. With additional data, it will be important to determine whether these QTL and those on BTA18 and BTA26 (Table 1) act independently or additively.

Based on data from three F_1 Brahman × Charolais sires, Davis et al. (1998) reported five QTL that increased birth weight. Only one of the five map locations was shared between two of the three sires and none of the QTL mapped to BTA1, as does the putative QTL we are reporting (Figure 4). We did however, observe a peak just below the suggestive (F = 9.4) threshold for an increase in birth weight on BTA5 in the same region as that reported by Davis et al. (1998). Collectively, these results point to the need to characterize QTL allelic variation in several breeds and breed crosses before marker-assisted selection can be effectively implemented on a widespread basis.

On BTA5 we observed compelling evidence for a QTL that increased the amount of bone in a wholesale rib and decreased DP for progeny inheriting the Brahman allele compared with the Hereford allele (Figure 1). The QTL on BTA13 that influences the proportion of rib fat and lean also seems to confer a decreased dressing percentage without any apparent affect on bone, as was observed for the QTL on BTA5 (Figure 3). In experiments comparing carcass traits between several sire breed groups, Brahman crosses tended to have a slightly higher DP than other breeds (Koch et al., 1982). A comparison of breed group means from Cycles III and IV of the Beef Germ Plasm Evaluation Project (Koch et al., 1982; Wheeler et al., 1996, 1997) indicated that there is a weak negative genetic correlation between DP and BOYD. Like many carcass traits measured as ratios, DP is influenced by many variables such as preslaughter handling, stage of maturity, degree of fatness, and muscle to bone ratio. It will require carefully controlled studies to determine which independent variable(s) are influenced by a QTL affecting DP. However, the lack of mechanistic information does not preclude the useful application of QTL with general effects.

The QTL that seems to affect bone and dressing percentage, BTA5, or dressing percentage alone, BTA13, share map positions with genes involved in the GH-IGF endocrine axis. Growth hormone receptor maps at approximately 65 cM on BTA13 (Barendse et al., 1994), and IGF-I maps at 73 cM on BTA5 (Kappes et al., 1997). It is premature to suggest these as candidate genes; however, it is interesting to consider the well-known effect that this endocrine axis has on visceral organ and skeletal development (Cohick and Clemmons, 1993). Also, this region of BTA5 seems to be syntenic to a region of mouse chromosome 10, where a deletion acting as a recessive allele, *hg*, resulting in an accelerated postweaning growth rate, has been mapped (Horvat and Medrano, 1995, 1996). The available data on the components of growth do not, however, suggest a differential effect on the growth of any tissue or organ system in these mice (Famula et al., 1988), and deletion of a region containing *hg* did not include IGF-I (Horvat and Medrano, 1995).

The power of a primary genomic screen, such as we are reporting, is not sufficient to ensure definitive identification of all segregating QTL. This is predicated on the number of animals tested and reliability of the F-statistic, which is influenced by marker informativeness, especially when markers are at 10- to 20-cM intervals. A secondary screen involving additional animals and markers is required to verify QTL indicated by suggestive F-statistic peaks. For some traits we observed suggestive peaks on up to six chromosomes, which requires a substantial amount of genotyping for verification. Because in practice many putative QTL based on results from primary genomic screens will not be characterized in a timely manner, it is prudent to make public the results of primary genomic screens in order to provide a means of comparing preliminary data from different experiments and laboratories.

Genetic linkage maps for cattle were developed to < 5 cM average coverage in approximately 5 yr. Equally rapid use of these maps to detect and characterize QTL having modest (> .5 SD) effects will be hampered by the lack of suitable families of sufficient numbers with accurate phenotypic data and the amount of genotyping required. Verifying the segregation of a QTL and establishing the phase of marker/QTL alleles in a sufficient number of sires to accurately sample a breed or population is a formidable task. The difficulty in establishing linkage disequilibrium between marker alleles and QTL alleles is dependent on the map density and informativeness of bovine microsatellites as well as the frequency of segregation of QTL alleles. Therefore, use of QTL based on a very small sample size of genetic material, such as we are reporting here, will, in many cases, await identification of additional microsatellites or nonmicrosatellite polymorphisms in close proximity to the causal gene so that the effects and phases of QTL can be estimated in a reasonably large number of small families. Even with a limited sampling it should be possible to gain insight into important considerations such as interactions between QTL and unusual patterns of inheritance. Ultimately, a realistic target is to use QTL alleles for carcass traits as a tool to better match production end-points to finishing programs. Being better able to meet demand for the high-quality middle meats without putting excess fat on feeders with diminished potential for high quality grades would increase the overall efficiency of beef production.

Implications

Quantitative trait loci for carcass and growth traits can be identified using the bovine genetic linkage map. In a *Bos taurus* × *Bos indicus* backcross design, progeny inheriting the *Bos indicus* marker allele on Chromosome 5 had a significantly lower dressing percentage and higher proportion of bone in the wholesale rib cut compared to those inheriting the *Bos taurus* allele. Analysis of additional families and breeds is required to determine the effect and frequency of alleles influencing these traits. This QTL and several other putative QTL affecting carcass traits will provide a portion of the data needed to successfully incorporate marker-assisted selection into beef breeding programs.

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