A Region on Bovine Chromosome 15 Influences Beef Longissimus Tenderness in Steers

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ABSTRACT: A genome scan was conducted using 196 microsatellite DNA markers spanning 29 autosomal bovine chromosomes and Warner-Bratzler shear force collected at d 2 and 14 postmortem on steaks from the longissimus muscle of 294 progeny from one Brahman × Hereford bull mated to *Bos taurus* cows to identify QTL for beef tenderness. One QTL was identified and located 28 cM (95% confidence interval is 17 to 40 cM) from the most centromeric marker on BTA15. The QTL interacted significantly with slaughter group. The difference in shear force of steaks aged 14 d postmortem between progeny with the Brahman paternally inherited allele vs those with Hereford was 1.19 phenotypic standard deviations (explained 26% of phenotypic variance) for one slaughter group and was not significant for three other slaughter groups. Apparently, unknown environmental factors present for three of the four slaughter groups were capable of masking the effect of this QTL. The sensitivity of the QTL effect to environmental factors may complicate utilization of markers for genetic improvement. Future research to elucidate the cause of the QTL × slaughter group interaction may lead to improved strategies for controlling variation in meat tenderness via marker-assisted selection, postmortem processing, or live animal management.

Key Words: Quantitative Traits, Loci, Tenderness, Shear Strength, Cattle, Gene Mapping

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Introduction

Development of interspecies composites exhibiting desirable characteristics of *Bos indicus* and *Bos taurus* cattle without undesirable attributes could be accelerated using marker-assisted selection. Advantages of *Bos indicus* germplasm relative to *Bos taurus* are greater heat tolerance (Carvalho et al., 1995; Hammond et al., 1996), greater resistance to parasites (Fourie and Kok, 1995; Bock et al., 1997) and viral infections (Jimenez et al., 1995; Soeharsono et al., 1995), and improved maternal calving ease (Olson et al., 1993). *Bos indicus* × *Bos taurus* crosses express greater heterosis effects for direct and maternal traits (Peacock et al., 1982) and neonatal survival (Peacock and Koger, 1980) than do crosses within species. Disadvantages of *Bos indicus* germplasm are reduced meat tenderness (Koch et al., 1982; Wheeler et al., 1994), reduced cold tolerance (Josey et al., 1987; Godfrey et al., 1991; Carstens et al., 1997), decreased neonatal survival in temperate climates (Reynolds et al., 1980), delayed puberty (Gregory et al., 1979a; Chenoweth et al., 1996), and decreased paternal calving ease (Gregory et al., 1979b). Identifying QTL for any of these traits would improve our ability to more efficiently use combinations of *Bos taurus* and *Bos indicus* germplasm.

Tough meat is an important problem facing the beef cattle industry (Wheeler et al., 1994), especially for cattle containing *Bos indicus* germplasm. Improving meat tenderness for cattle containing *Bos indicus* germplasm would improve acceptability of beef produced in tropical and subtropical regions that require *Bos indicus* germplasm for adaptability and increase the value of heterosis from *Bos indicus* × *Bos taurus* crosses. The objective of this research was to identify QTL for beef tenderness with differences between *Bos indicus* and *Bos taurus* germplasm.

Materials and Methods

Population and Traits. Slaughter cattle (162 steers and 132 heifers) were produced from mating one Brahman × Hereford sire by artificial insemination to mature (5 to 8 yr of age) Hereford, Angus, and crossbred cows. Sires of the crossbred cows were Hereford, Angus, Shorthorn, Charolais, Gelbvieh, Pinzgauer, Galloway, Longhorn, Nelore, Piedmontese,

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or Salers. Dams of the crossbred cows were Hereford or Angus. Birth dates ranged from March 14 to May 11, 1994. After weaning at approximately 200 d of age, cattle were fed a corn and corn silage-based diet. Energy density of the finishing diet was gradually increased to 3.12 Mcal of ME/kg of DM for the last 144 d prior to slaughter. Cattle were stratified by breed composition of dam and age within sex before assignment to slaughter date. All crossbreed types were represented within each slaughter group. Slaughter dates were May 15 and June 26 for steers and June 12 and July 24, 1995, for heifers; however, steers outnumbered heifers by 30, so 15 steers were killed with heifers to equalize numbers per slaughter date. Cattle were transported from the research center to a commercial plant (ca. 1-h transit time) where they were slaughtered. The wholesale rib was obtained from the right side of each carcass and transported (2°C) to the U.S. Meat Animal Research Center. Vacuum-packaged steaks (2.54 cm thick) were frozen (−20°C) after 2 or 14 d postmortem. Subsequently, steaks were thawed (24 h at 5°C) and broiled to an internal temperature of 70°C. Cooked steaks were chilled (24 h at 4°C) before removal of six cores (1.27 cm diameter) per steak for measurement of Warner-Bratzler shear force (**WBS**). Each core was sheared once using a universal testing machine equipped with a Warner-Bratzler attachment. The WBS value used in subsequent analyses was the average of the values determined from the six cores. This procedure is consistent with guidelines established by the American Meat Science Association (AMSA, 1995).

Genetic Markers. One hundred ninety-six microsatellite markers were selected from Kappes et al. (1997; http://www.marc.usda.gov/cattle) to be roughly evenly distributed across all 29 autosomes. Extraction of DNA, PCR protocols, and genotype scoring methods are the same as described previously (Bishop et al., 1994; Kappes et al., 1997). In addition to chromosomal position, criteria for selection of markers were heterozygosity in the Brahman × Hereford bull and ease of scoring. The Brahman × Hereford bull used in this study was the sire to part of the USDA cattle reference population (Kappes et al., 1997). Genotypic data for the sire were available prior to initiation of the current project, and this made it possible to select markers with the highest information content.

Multistep Genotyping Process. Ninety-four cattle were selected to be extreme for WBS2 and WBS14 (47 tender and 47 tough). Two wells devoted to the Brahman × Hereford sire for reference filled a 96-well microtiter plate. Selection of extremes was based on WBS2 and WBS14 adjusted for slaughter group, age, and maternal grandsire breed. Markers from all 29 autosomes were genotyped across the 94 animals to serve as a primary screen. Following the primary screen, a secondary screen was conducted in which the 200 calves with intermediate WBS and all dams were genotyped for markers on chromosomes showing promising peaks in F-values. This process greatly reduces the amount of genotyping required to identify QTL for a single trait or group of closely related traits while sacrificing only a trivial amount of power (Lander and Botstein, 1989).

Statistical Analysis. A scatterplot of WBS2 by WBS14 (Figure 1) revealed a funnel-shaped pattern with a high density of points associated with low values for both traits and wide scatter or low density of points associated with high values for both traits. This data pattern is a classical indication of an association between the mean and standard deviation or variance; hence, we applied a log transformation to WBS2 and WBS14 prior to statistical analysis to standardize the variance. Quantitative trait loci were identified by a peak in the F-statistic profile obtained from regression of WBS2 and WBS14 on the probability of receiving the Brahman allele (Knott et al., 1996) computed at 1-cM intervals across autosomes. The fixed effects of slaughter group, age, and maternal grandsire breed were preadjusted for (adjustments estimated from the full data set) the primary screen and adjusted simultaneously for the secondary screen. In addition, interactions between QTL and slaughter group were routinely tested. If a QTL × slaughter group interaction was found, different QTL effects for each slaughter group were estimated. Multiple QTL models were not tested.

An F-statistic peak was considered significant if it exceeded a threshold corresponding to an expected number of false-positives per genome scan (**ENFP**) of .05 and suggestive if ENFP = 1 (Lander and Kruglyak, 1995). Significant (ENFP = .05) and suggestive (ENFP = 1) F-statistic thresholds were 18.2 and 10.5 for the primary screen (94 extreme progeny) and 20.2 and 13.3 for the full data set. These threshold values were obtained by iteratively finding the value of T (± .01) that satisfied

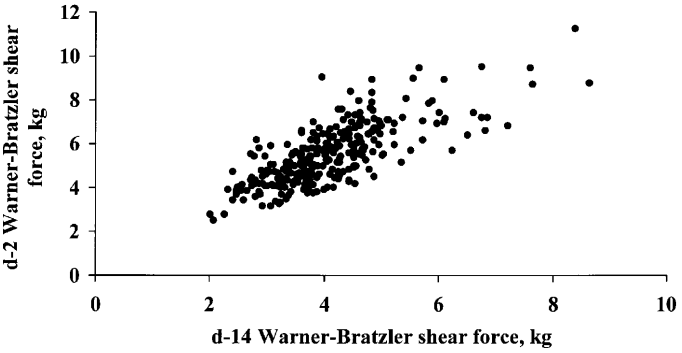

Figure 1. Warner-Bratzler shear force measured 14 d after slaughter (WBS14) plotted by shear force measured 2 d postmortem (WBS2).

$$(c + 2\rho g\nu_1 T)\int_T^{\infty} Prob_F(x,\nu_1,\nu_2)\,dx = \frac{ENFP}{n_{\text{tests}}}, \quad [1]$$

where c is the number of autosomes (29), g is genomic length (27.75 morgans), ρ (1) is one-half of the derivative of the autocorrelation function of F-statistics with respect to the distance separating linked loci (morgans) evaluated at zero distance, $Prob_F(x,\nu_1,\nu_2)$ is the probability density function for a central F distribution with ν_1 (1) numerator df and ν_2 denominator df, and n_{tests} is the number of tests. Dividing ENFP by n_{tests} is a Bonferroni correction that accounts for the expected increased incidence of false-positives due to multiple testing (e.g., testing a different QTL effect for each slaughter group in the secondary screen). The number of tests and ν_2 were 1 and 92 for the primary screen (94 extreme animals) and 4 and 242 for the secondary screen (full data set). The F-statistic peaks that exceed a threshold corresponding to the usual type I error rate of 5% will be identified as nominally significant even though ENFP = 19. Hence, in order from most stringent to least, thresholds are ENFP = .05 (significant) followed by ENFP = 1 (suggestive) and then ENFP = 19 (nominally significant, P = .05).

The 95% confidence interval for QTL was obtained by excluding regions of the chromosome with F-statistic values falling below the 5 percentile of the F distribution under the alternative hypothesis (assuming that the effects obtained at the maximum F are true). The 5 percentile was obtained from a noncentral F distribution with ν_1 = 1, ν_2 = 242, and noncentrality parameter equal to ν_1 × maximum F. The validity of this approach depends strongly on uniform genomic coverage that is approximately true if the interval between informative flanking markers is 10 cM or less.

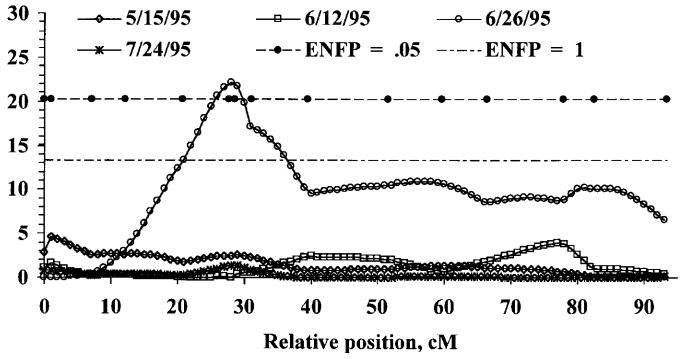

Figure 2. F-statistic profile for BTA15 and Warner-Bratzler shear force measured on d 14. Slaughter dates were May 15 (5/15/95), June 12 (6/12/95), June 26 (6/26/95), and July 24, 1995 (7/24/95). Horizontal dashed lines represent F-statistic thresholds corresponding to expected number of false-positive peaks (ENFP) of .05 and 1. Indicated by filled circles are the relative positions (cM) of markers on BTA15 that were, in order from centromere to telomere: MGTG13B, BR3510, BMS1004, ADCY2, JAB8, HEL1, BMS1782, INRA50, HBB, Z27076, POTCHA, ILSTS027, BL1095, BMS686, and BMS429.

Simulation Study. Power was approximated by simulating 100,000 realizations of a half-sib population containing 300 progeny. The simulation was repeated for a range of QTL effects. Differences between offspring receiving alternative sire alleles were .4, .5, .6, .7, or .8 SD. The marker used to compute F statistics was located 0 cM from the QTL. The F-statistics for QTL were calculated using either the full data set or the 94 most extreme (47 high and 47 low) progeny (selective genotyping). The only fixed effect in the analysis was the mean for either the full data set or selective genotyping. The F-statistic thresholds corresponding to expected numbers of false positives of .05, 1, 2, and 3 were 16.896, 10.02, 8.396, and 7.429 for the full data set and 18.204, 10.543, 8.782, and 7.745 for selective genotyping. Thresholds were based on Lander and Kruglyak (1995).

Results and Discussion

Genome Scan. From a genome scan using 196 markers genotyped across 94 animals that were extreme for both 2- and 14-d Warner-Bratzler shear force, five chromosomes (BTA3, 4, 15, 19, and 21) were selected for secondary screening (genotype additional animals and markers) based on having the highest peaks in F statistic profiles compared to other chromosomes. Following the primary genome scan, only one of these peaks (BTA15) achieved a suggestive level of significance (ENFP < 1), and the other four peaks (BTA3, 4, 19, and 21) were nominally significant (P < .05). Following genotyping dams and intermediate progeny and correcting errors, only the peak on BTA15 was high enough to achieve a genome-wide level of significance (ENFP ≤ .05; Figure 2; Lander and Kruglyak, 1995), and the other four peaks were only nominally significant. Nominally significant peaks are not compelling enough to identify as QTL because in a genome scan covering 29 chromosomes and 2,775 cM, we would expect to observe 19 nominally significant peaks by chance alone (95% confidence interval = 11 to 27 peaks) even if no real QTL exist. Though not high enough to exceed background levels, these nominally significant peaks might indicate real QTL; hence, it is probably worthwhile in additional studies to genotype markers from these chromosomes using additional progeny and(or) families in an attempt to accumulate more definitive evidence.

Relative Position and Confidence Interval for QTL. A significant (ENFP < .05) QTL for Warner-Bratzler

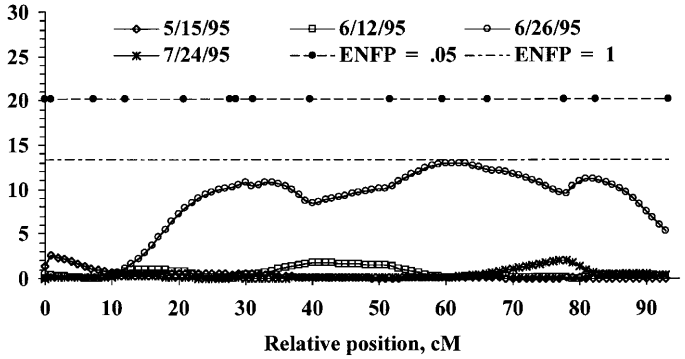

Figure 3. F-statistic profile for BTA15 and Warner-Bratzler shear force measured on d 2. Slaughter dates were May 15 (5/15/95), June 12 (6/12/95), June 26 (6/26/95), and July 24, 1995 (7/24/95). Horizontal dashed lines represent F-statistic thresholds corresponding to expected number of false-positive peaks (ENFP) of .05 and 1. Indicated by filled circles are the relative positions (cM) of markers that were, in order from centromere to telomere: MGTG13B, BR3510, BMS1004, ADCY2, JAB8, HEL1, BMS1782, INRA50, HBB, Z27076, POTCHA, ILSTS027, BL1095, BMS686, and BMS429.

shear force measured on d 14 postmortem was identified on BTA15, with its most likely position indicated by a peak F-statistic of 22.2 at 28 cM from the most centromeric marker (MGTG13B; Figure 2) for cattle slaughtered on June 26, 1995. For the other slaughter groups (May 15, June 12, and July 24, 1995) there were no significant QTL effects (Figure 2). Markers most closely flanking the peak were HEL1 (27.7 cM) and BMS1782 (28.6 cM). The 95% confidence interval extends from 17 (between ADCY2 and JAB8) to 40 (HBB) cM telomeric of MGTG13B. The boundaries of the 95% confidence interval were close to markers. The small F-values that truncate the 95% confidence interval were *not* the result of excessive distance to the nearest marker. Hence, the presence of marker intervals > 10 cM on BTA15 does not bias the confidence interval estimation. Smaller F-statistic peaks for WBS14 that did not achieve suggestive levels of significance were observed near 60 and 80 cM (Figure 2). For WBS2, F-statistic peaks occurred in the same general regions on BTA15 as for WBS14, but peaks were of lesser magnitude and, in fact, did not achieve suggestive levels of significance (Figure 3). The highest F-statistic peak for WBS2 approached a suggestive level of significance near 60 cM.

QTL Effects. The effect of the QTL located at 28 cM on BTA15 varied among slaughter groups. Results are presented by slaughter group. Means on the observed scale for cattle inheriting different sire alleles is a function of the mean, the effect, and the variance on the log scale. The largest and most significant effect occurred for cattle slaughtered June 26. For this slaughter group, the mean, QTL effect (Brahman minus Hereford), and standard deviation were 1.375, .256 (maximum F = 22.2; ENFP = .02), and .216 for the natural log of WBS14. On the observed scale, mean WBS14 was 4.6 kg ($e^{1.375 + .256/2 + .0466/2}$) for calves inheriting the Brahman allele and 3.46 kg ($e^{1.375 - .256/2 + .0466/2}$) for Hereford. The effect was 1.04 kg, 1.19 SD or 29% ($e^{.256} - 1$). The QTL accounted for 26% of the phenotypic variance within this slaughter group.

The next largest effect on WBS14 occurred on May 15, was less than half as large as the June 26 result, and was not significant (.089 on a log scale; maximum F = 2.5; ENFP = 77). Even though the effect on May 15 was smaller than the June 26 result, it was consistent in sign. A common thread between these two slaughter groups is that they were both composed entirely of steers. The pooled effect was .173 (maximum F = 19.04; ENFP = .04) on the log scale. Least squares means (pooled across the two steer slaughter groups) were 4.41 kg ($e^{1.375 + .173/2 + .0466/2}$) for cattle inheriting the Brahman allele and 3.71 kg ($e^{1.375 - .173/2 + .0466/2}$) for Hereford. The effect was .7 kg, .8 SD, and 19%.

For cattle slaughtered on June 12 and July 24 (mostly heifers), the QTL effects on WBS14 were small, insignificant, and slightly negative (Brahman minus Hereford). We hesitate to ascribe these interactions between QTL and slaughter group to an interaction of QTL × sex because sex is highly confounded with slaughter group, and steers and heifers were managed separately (e.g., different pens, implants, implant schedules, and diets).

QTL genotypic effects on WBS2 for BTA15 were similar in sign but of lesser magnitude compared to results reported for WBS14 (data not shown).

Positional Candidate Genes. The 95% confidence interval containing the QTL is flanked by two genes with human homologues located on different chromosomes, adenylate cyclase 2 at relative position 12.1 cM (ADCY2; HSA5p15.3–p15.1; Stengel et al., 1992) and hemoglobin beta at 39.6 cM (HBB; HSA11p15.4; Lin et al., 1985; Figure 2). This lack of synteny coupled with the fact that HSA11 has homologues on BTA29 interspersing homology with BTA15 indicates that the current coarseness of the human-bovine comparative map may complicate the identification of positional candidate genes.

Genomic Coverage. All targeted QTL (effects ≥ .4 SD) that are heterozygous in the sire have probably not been detected. Missed QTL might be the result of low power, incomplete coverage (i.e., long marker intervals), and poor marker information content. The powers for detecting (ENFP ≤ .05) QTL with effects of .4, .5, .6, .7, and .8 SD were .16, .40, .69, .89, and .98 (Table 1). The probability of undetected QTL (ENFP > 3) was .37, .14, .03, .005, and .0004 for QTL with effects of .4, .5, .6, .7, and .8 SD. Undetected QTL with effects ≥ .6 SD that are near informative markers

Table 1. Power[a] of detecting quantitative trait loci (QTL) from a single half-sib family with 300 progeny and either genotyping all progeny or the 94 most extreme progeny

Effect (SD) and expected number of false-positives for full data set	Expected number of false-positives for selective genotyping					
	≤ .05	.05 to 1	1 to 2	2 to 3	> 3	Total
.4						
≤ .05	.1426	.1081	.0086	.0022	.0016	.2630
.05 to 1	.0203	.1712	.0648	.0342	.0631	.3536
1 to 2	.0002	.0159	.0161	.0126	.0507	.0954
2 to 3	.0000	.0048	.0062	.0064	.0377	.0551
> 3	.0000	.0037	.0068	.0097	.2127	.2329
Total	.1631	.3037	.1026	.0649	.3657	—
.5						
≤ .05	.3846	.1813	.0118	.0032	.0023	.5833
.05 to 1	.0203	.1493	.0511	.0262	.0441	.2911
1 to 2	.0000	.0077	.0081	.0065	.0248	.0471
2 to 3	.0000	.0020	.0028	.0027	.0146	.0221
> 3	.0000	.0012	.0022	.0029	.0501	.0564
Total	.4049	.3414	.0760	.0416	.1360	—
.6						
≤ .05	.6836	.1602	.0093	.0024	.0017	.8571
.05 to 1	.0097	.0649	.0204	.0097	.0157	.1204
1 to 2	.0000	.0018	.0020	.0016	.0054	.0108
2 to 3	.0000	.0003	.0006	.0004	.0030	.0043
> 3	.0000	.0002	.0004	.0004	.0065	.0075
Total	.6933	.2273	.0327	.0145	.0323	—
.7						
≤ .05	.8898	.0781	.0034	.0007	.0005	.9726
.05 to 1	.0024	.0142	.0039	.0017	.0030	.0252
1 to 2	.0000	.0002	.0002	.0001	.0007	.0013
2 to 3	.0000	.0000	.0000	.0000	.0002	.0003
> 3	.0000	.0000	.0000	.0000	.0005	.0005
Total	.8923	.0925	.0077	.0027	.0049	—
.8						
≤ .05	.9758	.0206	.0007	.0001	.0001	.9973
.05 to 1	.0002	.0015	.0005	.0002	.0003	.0026
1 to 2	.0000	.0000	.0000	.0000	.0000	.0000
2 to 3	.0000	.0000	.0000	.0000	.0000	.0000
> 3	.0000	.0000	.0000	.0000	.0000	.0000
Total	.9760	.0222	.0012	.0003	.0004	—

[a]Power was approximated by simulating 100,000 replications of a half-sib population containing 300 progeny. Differences between offspring receiving alternative sire QTL alleles were .4, .5, .6, .7 or .8 SD. The F-statistic thresholds corresponding to expected numbers of false-positives of .05, 1, 2, and 3 were 16.896, 10.02, 8.396, and 7.429 for the full data set and 18.204, 10.543, 8.782, and 7.745 for selective genotyping. Thresholds were based on Lander and Kruglyak (1995).

are unlikely, whereas the likelihood of undetected QTL with smaller effects is relatively high. Selective genotyping did not compromise the detection of QTL because the joint probability of success (ENFP ≤ .05) for the full data set and failure (ENFP > 3) for selective genotyping was low: .0016, .0023, .0017, .0005, and .0001 for QTL with effect of .4, .5, .6, .7, and .8 SD, respectively (Table 1). All peaks with ENFP ≤ 3 were studied further by genotyping progeny with intermediate phenotypes. Collectively, these results indicate that selective genotyping is an effective prescreening procedure.

Long intervals between flanking markers represent blind spots in genomic coverage that potentially hide QTL. For example, on average, only 66 of the 94 cattle would be informative for identifying a QTL located in the middle of a 30-cM interval (30% lost from ambiguous crossovers). Even though genomic coverage was extensive, it was not complete. The average interval between flanking markers or between apparent chromosomal ends (ends of linkage groups, Kappes et al., 1997) and extreme markers was 13.2 cM, with 35% ≤ 10 cM, 86% ≤ 20 cM, and 96% ≤ 30 cM. The eight (4%) intervals greater than 30 cM were 53.6 cM on chromosome 16, 46.8 cM on 10, 41.7 cM on 19, 38.6 cM on 13, 36.7 cM on 3, 36.2 cM on 12, 33.3 cM on 12, and 32.4 cM on 6.

Genomic coverage can be further compromised by markers with low information content resulting from low heterozygosity, a small number of alleles, or an uninformative distribution of alleles. Even though the sire was heterozygous for all markers used, 1/4-Brahman calves with the same heterozygous genotype as the sire were ambiguous when dams were not genotyped (markers in genomic regions not selected for secondary screen). However, for markers in which the sire's Brahman allele was rare in the dam population, we were able to use the frequency of the sire's Brahman allele relative to the sum of the frequencies of the sire's alleles in the cow population (P_b) to compute the probability that the calf received the Brahman allele with greater accuracy (Cowen et al., 1989) for cases for which the sire and progeny had the same genotype. An unbiased estimate of P_b was obtained from frequencies of offspring homozygous for one or the other of the sire's alleles. Markers are highly informative if P_b or the proportion of calves that were heterozygous for the sire's alleles (H_s) are small. Fifty-seven percent of the 196 markers had values ≤ .1 for P_b or H_s. Even though 43% of the markers did not seem to be highly informative, the expected information content [$I_c = 1 - 4H_s - P_b (1 - P_b)$] was relatively high. Expected information content is expressed relative to informativeness when there is no ambiguity in determining transmission of sire's alleles to offspring. Information content averaged .89 (ranged from .41 to 1) and was ≥ .95 for 42% of the markers, ≥ .9 for 63%, ≥ .8 for 84%, and ≥ .7 for 91%. Based on H_s only and ignoring P_b, information content ($I_H = 1 - H_s$) was considerably lower than I_c and averaged .75 (ranged from .29 to .98) and was ≥ .95 for only 4% of the markers, ≥ .9 for 13%, ≥ .8 for 44%, and ≥ .7 for 66%. An information content of .75 for I_H is equivalent to losing 25% of the progeny. Utilizing P_b cuts the loss by more than half to 11%. Additional gains in information content that could be gleaned from genotyping dams would be minimal for this population relative to the added cost. However, this may not be the case for other resource populations in which both of the sire's alleles are relatively common in the dam population (e.g., F_2). A cost-effective strategy might be to genotype dams for only those markers with intermediate P_b and intermediate to high H_s, especially if they fall in regions that are likely to contain QTL.

Genotype × Environmental Interaction. We present evidence of a QTL with effects that are masked by unknown environmental factors that are evidently more prevalent for some slaughter groups than for others. Certainly the presence of this interaction reduces, but does not eliminate, our confidence that the QTL is real. A consequence of the genotype × environment interaction is that the QTL will only be detectable in a fraction of experiments as long as the offending environmental factors remain unknown. This is disturbing in the sense that it is indistinguishable from false-positive QTL peaks that would also exhibit a tendency to come and go in different experiments.

Conversely, it does not seem sensible to ignore results such as these because it is conceivable that QTL might exhibit this kind of sensitivity to environmental factors. For example, Freking et al. (1999) observed that the difference between lambs expressing the callipyge phenotype and other genotypes for Warner-Bratzler shear force was twice as large for lambs slaughtered one year than for those slaughtered in another year ($P < .01$). The callipyge locus has well-documented, obvious effects on muscling and meat tenderness. Evidence such as that seen by Freking et al. (1999) that indicates even a locus with large effects can be environmentally sensitive is quite compelling. Genotype × environment interactions have been detected for a wide array of traits in a number of species. Examples include fitness (Fry et al., 1998) and bristle number (Gurganus et al., 1998) in *Drosophila melanogaster*; thrombosis (Burzotta et al., 1998), very-low-density lipoprotein levels (Senti et al., 1998), hemochromatosis (Burke et al., 1998), and bladder cancer (Taylor et al., 1998) in humans; heat loss and body composition in mice (Moody et al., 1997); and growth rate in chickens (Yalcin et al., 1997). Perhaps it is not unreasonable to think that genotype × environmental interactions might influence meat tenderness in cattle as well.

One context for the current study is to think of it as two experiments with Exp. 1 comprising two slaughter groups of steers and Exp. 2 comprising two slaughter groups of mostly heifers (a few steers). Aside from the differences in sex, the cattle were managed differently between the two experiments and slaughtered on different days. Significant QTL effects were observed for Exp. 1 but not for Exp. 2. The failure of Exp. 2 to replicate the findings of Exp. 1 might be the result of 1) a QTL × sex interaction, 2) a QTL × management interaction, or 3) spurious findings in Exp. 1. We have attempted to minimize the possibility of the third option by correcting statistical inferences for multiple testing across the genome and slaughter groups.

Genetic mapping of chromosomal regions influencing meat tenderness of 1/4-Brahman calves may result in the development of flanking marker systems that can be used to select for *Bos taurus* germplasm at chromosomal regions (loci) that affect tenderness while allowing Brahman germplasm at other loci that confer positive attributes such as parasite resistance, heat tolerance, maternal calving ease, and heterosis to remain in the population. Paradoxically, marker-assisted selection for meat tenderness in cattle containing *Bos indicus* germplasm may result in lower production costs because it would allow cattle producers to use *Bos indicus* germplasm (absent germplasm that confers meat toughness) while producing a high-quality (tender) product.

Implications

A quantitative trait locus (QTL) on BTA15 seems to affect Warner-Bratzler shear force measured 14 d after slaughter. The QTL effect was only observed for one of four slaughter groups. This is disturbing in the sense that significant results can only be expected to be repeated for a fraction of future experiments. Apparently, unknown environmental factors were present for three of the four slaughter groups that masked the effect of the QTL. Sensitivity of the QTL effect to environmental factors indicates that use of markers in the region for genetic improvement may be complicated. Future research to elucidate the cause of the QTL × slaughter group interaction may reveal improved strategies for controlling unwanted variation in meat tenderness.

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