# MARKER ASSISTED SELECTION FOR BEEF PALATABILITY CHARACTERISTICS

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## INTRODUCTION

Future success of the beef industry hinges on the ability to regain market share, and sustain demand from competing protein sources. Because of the 2000 National Beef Quality Audit (NBQA), aggregate concerns of several beef marketing segments (beef processors, purveyors, restaurateurs, and retailers) were made aware to the beef industry. The top three producer issues in the NBQA were low overall uniformity and consistency, inadequate tenderness, and low overall palatability (McKenna et al., 2002).

Many researchers have documented the importance of tenderness on beef palatability. Smith et al. (1987), Savell et al. (1989), and Miller et al. (1995) determined tenderness to be the most important palatability attribute of beef. While tenderness has, and will continue to be, one of the focal points for future beef research, many questions still surround the variation in beef tenderness (Wheeler et al., 1994).

Marbling score has been used in the U.S. beef industry as the primary predictor of beef palatability among carcasses with similar maturity characteristics (USDA, 2001a). Intramuscular fat has been shown to have a small, positive relationship with beef palatability, along with a small inverse relationship with Warner-Bratzler shear force (WBS; Wheeler et al., 1994). Interestingly, Boleman et al. (1997) revealed the willingness of consumers (78%) to purchase a product labeled “guaranteed tender” at a higher price.

Clearly, the value of tenderness cannot be disputed with regards to consumer perception of beef. Likewise, it is apparent that many different factors contribute to beef tenderness. Therefore, genetic evaluation of tenderness among different seedstock breeds has become a “top-of-mind” issue. Current research has begun to focus on specific genes that are highly associated with increased beef tenderness and palatability characteristics. Likewise, marker assisted selection (MAS) should be utilized in beef herds, along with economically important phenotypic traits, for genetic progress to made with respect to improving the uniformity and consistency of beef. The following will detail the significance of marbling and tenderness to overall beef palatability, as well as detail the use of objective genetic mapping for tenderness evaluation and subsequent implications for genetic selection.

## REVIEW OF LITERATURE

*Overview*

Palatability is defined as being "pleasant to the taste" (Webster's New Collegiate Dictionary, 824). Meat palatability is generally referred to as tenderness, juiciness and flavor of a cooked product. These three cooked meat characteristics are what consumers desire and what the beef industry is trying to supply on a consistent and uniform basis. Of these three palatability attributes, tenderness is the most influential to consumer preference (Savell et al., 1989). Miller et al. (1995) found that consumers preferred meat that offered increased tenderness and flavor. Variation in meat tenderness can be explained by examining multiple animal and/or carcass factors (marbling, physiological maturity, and breed/genetic effects).

*Marbling: A Palatability Attribute*

Interfascicular or intramuscular adipose tissue is a unique fat depot. This tissue can be distinguished from other fat reservoirs by its location within perimysial connective tissue located alongside myofibers. Postnatal growth of intramuscular fat involves substantial hypertrophy of the adipocytes and also appears to include a period of apparent hyperplasia of preadipocytes (Smith et al., 2000).

The "jury" is still out concerning the role marbling plays in the formulation of beef tenderness. Romans et al. (1965) documented that only 5% of the variation in beef tenderness is accounted for by differences in marbling, whereas Campion et al. (1975) determined that marbling explained 10% of the variation of cooked beef. Likewise, Armbruster et al. (1983) found that marbling explained 1% of the variation in tenderness after accounting for other sources of variation and only 1.2% when other sources of variation were ignored. Smith et al. (1984) noted that marbling accounted for more desirable panel scores and lower shear force ratings when wide ranges of marbling scores were present. However, within a tighter range of marbling scores (i.e., Small to Moderately Abundant), marbling had little or no effect on sensory panel ratings and shear force values (Smith et al., 1984). Conversely, McBee and Wiles (1967) found that shear force, sensory panel tenderness, juiciness and flavor improved as marbling increased. Dolezal et al. (1982a) found that steaks with a Modest or higher degree of marbling had increased overall palatability ratings in relation to steaks from carcasses with Slight degree of marbling. Smith and Carpenter (1974) noted that the perceived value of a fattened animal dates back to Biblical times. In the early 20$^{th}$ century, researchers seemed to further echo these findings. Hall (1910) postulated that an increase in tenderness is the direct result of decreased elasticity of connective tissue due to the deposition of fat therein. Nelson et al. (1930) documented an 18 to 30% decrease in shear force values for samples from fat animals in relation to the force required to shear samples from thin animals. Research has also shown that deposition of intramuscular fat leads to decreased rigidity of connective tissue due to adipose accretion within (Nishimura et al., 2000). In a study to determine the effect of differing physiological maturity (i.e., potential differences in connective tissue) across similar marbling scores, McPeake et al. (2001) reported a more favorable trend for various palatability characteristics when steaks were from carcasses with increased marbling levels (Table 1).

*Theories*

Carpenter and Smith (1974) detailed several theories relating marbling and tenderness. The ***bite theory*** hypothesizes that within a certain bite-size portion of cooked meat, marbling reduces the overall mass per unit of volume, which in turn lowers bulk density. Bulk density is the amount, distribution, and chemical or physical state of intramuscular fat and moisture. The ***strain theory*** suggests that as intramuscular fat is being formed, a portion is deposited within the perimysium or endomysium thereby decreasing the strength of connective tissue fibers. Increased accumulation of marbling causes the actual rigidity of the connective tissue to be weakened resulting in increased tenderness. This proposed theory can be affirmed by a recent study done by Nishimura et al. (1999) which found the development of adipose tissue in *longissimus dorsi* muscle appears to disorganize the structure of the intramuscular connective tissue and contributes to the tenderization of highly marbled beef from Wagyu cattle. Increased tenderness is the result of connective tissue that is more heat susceptible; the direct result of structural changes causing more efficient collagen solubilization. The *lubrication theory* states that as heat is applied to meat, intramuscular fat dissolves. The cooked fat and meat juices combine and serve as lubrication during the chewing process. Pearson (1966) found sustained juiciness (the sensation of juiciness perceived during continued chewing) to be related to intramuscular fat content. The *Insurance theory* suggests that increased amounts of intramuscular fat allow different preparation opportunities to be utilized that could affect degree of doneness. Marbling would provide some insurance that meat cooked too extensively or too rapidly would still be relatively palatable.

Breed Differences Brahman and Brahman-crossbred cattle, in relation to other breeds, have been shown to have lower marbling scores and tenderness ratings. Sherbeck et al. (1995) showed that carcasses from Hereford steers had higher marbling scores in relation to carcasses of 25 or 50% Brahman descent. Hereford carcasses had an increased proportion of USDA Choice than did carcasses from Brahman decent (44 versus 19 and 14%, respectively) and a smaller percentage of USDA Standard grade carcasses than Brahman-crossbred carcasses (0 versus 19 and 18%, respectively). Nevertheless, Wheeler et al. (1994) documented that carcasses originating from *Bos taurus* and *Bos indicus* steers experienced a small, positive relationship between marbling score and palatability. It can be disputed how much appreciable difference between *Bos indicus* and *Bos taurus* breeds for marbling deposition actually exist. Nonetheless, sensory panel tenderness differences do exist between these two diverse biological types of cattle due to biochemical differences in Zebu breeds (Koch et al., 1988). Zebu breeds have increased calpastatin activity, the endogenous inhibitor of calpain, when compared to cattle of British decent (Wheeler et al., 1994). While proteolysis will be discussed later, it has been documented that the calpain proteases (m- and $\mu$-calpain) play an important role in beef tenderness as a result of postmortem aging.

*Environmental Factors Effecting Palatability*

Time-on-Feed Traditionally, to increase marbling deposition, feedlot managers tend to increase the amount of time that animals are fed a high-concentrate finishing ration. Increased time-on-feed increases the probability that animals will produce carcasses with a more desirable quality grade (Zinn et al., 1970; Tatum et al., 1980; May et al., 1992).

The interaction between quality grade and palatability, as well as marbling and carcass value, has led researchers to hypothesize exactly how many days on feed are actually necessary for cattle to be acceptable in terms of palatability. Dolezal (1982b) suggested that feeding a high-grain ration for at least 90 d was necessary for acceptable palatability. May et al. (1992) and Van Koevering et al. (1995) suggest feeding animals for 84 and 119 d for palatability to be acceptable. Duckett et al. (1993) found that marbling levels doubled between 84 and 112 days on feed, but did not differ from day 0 to 84 or from day 112 to 196. Nash et al. (1999) utilized ultrasound technology to monitor changes in marbling deposition and predicted USDA Quality Grade in feedlot heifers relative to days on feed. The percent grading Choice increased from 20% at d 84 to 80% at d 100 and 120, with little change occurring there after.

Implants Beef industry segmentation is a major problem surrounding the problems with consistency and uniformity. Time-on-feed and breed differences have already been discussed, however, management regimes which utilize different implant protocols are undoubtedly a “hot topic” when considering the potential impact implants have on carcass quality. Anabolic implants are used routinely during the feedlot phase in order to promote increased gain and feed efficiency. Duckett’s (1997) review of 36 research trials determined implants caused a mean reduction of 24% in marbling and a 14.5% reduction in the number of carcasses grading Choice. Roeber et al. (2000) revealed that different implant strategies resulted in increased hot carcass weights and larger *longissimus dorsi* area while decreasing marbling scores and consumer preference of steaks. Duckett et al. (1999) found a reduction in marbling score when comparing implanted cattle with non-implanted controls. Research also exists that portrays the fact that certain implant regimes differ in their effect on carcass quality. Gerken et al. (1995) found that use of single implants containing 140 mg trenbolone acetate or the combination of 24 mg 17-ß estradiol and 120 mg trenbolone acetate had little appreciable effect on marbling or beef tenderness in genetically identical steers. Within this same trial, carcasses from cattle implanted with a single estrogenic implant containing 20 mg estradiol benzoate and 200 mg progesterone had significantly reduced marbling scores and decreased tenderness of top sirloin steaks when compared to the previously mentioned implant treatments.

*Marker Assisted Selection*

Genetic improvement of livestock primarily focuses on selection for quantitative traits, since most traits of economic importance including beef palatability are quantitative traits (i.e., controlled by many genes). In the past, most genetic improvement has been achieved through selection using estimated breeding values based on the phenotype of the individual and/or its relatives (Dekkers, 1999). The availability of molecular genetic tools has equated into increased genetic progress achieved via the ability to select on specific DNA markers for quantitative trait loci (QTL). Markers arise from research where a candidate gene of known effect is shown to influence a certain phenotypic attribute or where a specific genomic region is determined to significantly influence a particular trait. Meuwissen and Goddard (1996) documented several factors that affect the response to MAS: size of QTL variance, heritability of trait, and selection for phenotypic traits that are difficult to measure (i.e., carcass and sex-limited traits). In terms of carcass traits (heritability approximately 0.27), when displayed in terms of the percentage extra response from MAS, the maximum response was found during the first generation and declined substantially by generation five (64% vs. 39%, respectively). Strictly using MAS for breeding decisions is not advisable due to the inability to predict what is happening with other background genes (i.e., population differences) that may affect other traits. Accordingly, Dekkers and van Arendonk (1998) developed methods to optimize selection on a known QTL, leading to a greater response in both the short and long term when selection on the QTL is balanced with selection based on phenotypic information. This is further enhanced when QTL exhibit dominance.

Very few cattle breed associations have EPDs for WBS or sensory evaluated tenderness. Furthermore, little economic incentive has existed in the past for beef producers to select for tenderness. Therefore, selection for tenderness has not been practiced. The economic incentive to select for tenderness now exists due to the formation of various beef alliances and branded beef programs that could use this as marketing leverage. There are, however, substantial difficulties associated with the mass collection of WBS data. Therefore, research has focused on identifying gene markers that are highly associated with different palatability characteristics. Currently, the thyroglobulin, leptin, and calpastatin genes have been identified due to their strong relationship with marbling deposition and tenderness.

*Thyroglobulin*

Thyroglobulin is a glycoprotein hormone that is synthesized from the thyroid follicular cell and iodinated upon release. Thyroglobulin is the carrier for triiodothyronine (T3) and thyroxin (T4) and is stored in the lumen. When either of these hormones is needed, thyroglobulin is transported across the apical membrane where these hormones are cleaved and released into the blood. These hormones have been shown to affect both in vitro and in vivo adipocyte growth and differentiation (Ailhaud et al., 1992). Likewise, T3 and T4 have also been associated with marbling deposition in Wagyu cattle (Mears et al., 2001).

The TG5 polymorphism occurs in the 5' leader sequence of the thyroglobulin gene and has been highly associated with intramuscular fat deposition in long-fed cattle (Barendse, 2001). Cattle that are heterozygous or homozygous for the delta T allele (e.g., CT or TT) have higher marbling scores than cattle that are homozygous for the delta C allele (e.g., CC), with the delta locations defined as the beginning of the start of the first exon (Barendse, 1997). Additionally, steers exhibiting the delta T allele had increased growth performance and marbling deposition. Interestingly, no association was found for rump fat thickness or hot carcass weight. These results imply that selecting cattle based on this DNA marker should not result in subcutaneous fat thickness changes, a major factor affecting USDA yield grades for beef carcasses.

*Leptin*

Leptin is a protein hormone that has been implicated in the control of food intake and body composition in mammals (Geary et al., 2003). Leptin is produced primarily by white adipose tissue and, to a lesser extent, in the placenta, skeletal muscle, and stomach fundus in rats in response to fattening (Margetic et al., 2002). In skeletal muscle, leptin plays an important role in glycogen synthesis, glucose transport, and lipid partitioning (Margetic et al., 2002). As adipocytes become larger, more leptin mRNA is present (Auwerx and Staels, 1998; Masuzaki et al., 1995) and peripheral leptin concentrations increase (Ahima and Flier, 2000). Mice that are homozygous for an obesity condition (ob/ob) are the prototypical experimental subjects that set the stage for the discovery of leptin. These mice lack the leptin gene and are overweight. Both leptin deficiency (Tartaglia et al. 1995) and resistance (in *db/db* mice having a defective leptin receptor; Lee et al., 1996) are characterized by hyperphagia and reduced energy expenditure.

Studies have also been conducted to determine the significance of circulating leptin concentration on carcass characteristics of feedlot cattle. Serum leptin is positively correlated with ($P < 0.001$) ribeye fat thickness ($r = 0.32$), KPH ($r = 0.18$), marbling score ($r = 0.18$), and yield grade ($r = 0.28$; Minton et al., 1998). Geary et al. (2003) also found that serum concentrations of leptin were significantly associated with carcass composition and quality grade; these researchers concluded that leptin may be beneficial as an additional indicator of fat content in feedlot cattle. Currently, however, there is no commercially available application that utilizes serum leptin concentration as a predictor of beef quality grade or palatability.

DNA analysis for the leptin gene has also received research attention. Fitzsimmons et al. (1998) reported that alleles of the BM1500 microsatellite were associated with carcass fat measures in a population of 154 unrelated beef bulls. Likewise, Buchanan et al. (2002) determined that a cytosine (C) to thymine (T) transition that encoded an amino acid change of an arginine to a cysteine was identified in exon 2 of the leptin gene. Further results from this trial indicated that the T allele is associated with fatter carcasses (whole body fat) and the C allele with leaner carcasses. Not suprisingly, British breeds (i.e., Angus and Hereford) had a higher frequency of the T allele (0.59 and 0.57, respectively) whereas continental breeds (i.e., Charolais and Simmental) had a higher occurrence of the C allele (0.54 and 0.58, respectively).

*Calpastatin*

Postmortem management of beef plays a particularly important role in helping to reduce the variation in beef tenderness at the consumer level (Koohmaraie, 1996).

Increased tenderness in meat is caused by endogenous enzymatic activity in the form of the calpains (m- and μ-calpain), which occur naturally in the muscle. The calpain proteases are different in the amount of calcium required for activation; μ-calpain requires micromolar concentrations of calcium (200-300 μM) and m-calpain requires millimolar calcium concentrations (~10mM) for activation to occur. Calpastatin is an endogenous substrate that inhibits the calpain proteases. According to Koohmaraie (1992), when normal postmortem conditions are realized, m-calpain is very stable in the body due to insufficient calcium present for its' activation. Furthermore, a gradual decline in activity occurs with μ-calpain as calcium in the body is depleted and calpastatin loses activity very rapidly. Calpastatin is hydrolyzed by calpain proteases when greater quantities of protease are present in relation to inhibitor (Shannon and Goll, 1985). Prediction equations show 24-h calpastatin activity and 0-h μ-calpain activity account for 41% of the variation in WBS in beef aged 14 d (Shackelford et al., 1991). Likewise, research conducted by Johnson et al. (1990) and Calkins et al. (1988) found WBS values to be correlated with both calpastatin (r = 0.41) and μ-calpain activity (r = -0.71), respectively.

A DNA marker for the calpastatin gene has now been developed. Researchers with Australia's Commonwealth Scientific and Industrial Research Organization (Bindon, 2002) reported two variants of the calpastatin gene, one associated with tenderness and the other with increased toughness. While both alleles have been found in all breeds tested, there appear to be clear differences in genotype frequency within breeds; Zebu breeds have a greater frequency of the genotype associated with toughness (i.e., '11') relative to British, Belmont Red, and Santa Gertrudis cattle (i.e., '22'). In this trial, the estimated difference between the '11' and the '22' genotype for WBS was 1.34 kg (Bindon, 2002). However, this value represents the extremes of the distribution tested and not a random population sample. Likewise, Chung et al. (2001) found genetic polymorphisms among individuals for two different domains of the Calpastatin locus (domain I = CAST67 and domain IV = CAST28). Results from this trial also indicate that use of calpastatin genotypes in MAS programs can improve carcass traits and calpastatin activity.

## CONCLUSIONS AND IMPLICATIONS TO GENETIC IMPROVEMENT OF BEEF CATTLE

It is quite evident that reproduction and growth traits are still major factors in maintaining profitable beef production. However, only around 10% of fed cattle processed in the United States meet the requirements for upper 2/3 USDA Choice or Prime grade carcasses (McKenna et al., 2002). Several breed associations are now compiling ultrasound information for development of EPDs for marbling, ribeye area, and fat thickness. Likewise, DNA markers now exist that determine if certain animals express certain genes that are highly associated with beef palatability. Pricing grids now exist that reward higher levels of marbling; therefore, the economic incentive for increased marbling will continue to be important in the future. One should note that genetic selection for marbling will not always yield a tender product (i.e., the phenotypic relationship between marbling and tenderness is not especially high.) Consequently, some cattle with relatively high marbling will produce meat that is unacceptable in tenderness, and some cattle with low levels of marbling will produce meat that is very desirable in tenderness. Many researchers continually point out the fact that marbling accounts for little of the variation in beef tenderness. However, taste panel ratings indicate that with increased marbling score, the chance for an undesirable eating experience is reduced (McPeake et al., 2001). Therefore, genetic selection based on both marbling and tenderness traits should be conducted in the future to help insure a highly palatable beef product for the consumer.

While the entire captive supply should not be comprised of Choice or Prime carcasses, by emphasizing carcass traits during genetic selection producers can have the ability to address these areas of concern. One should note, however, that MAS alone is not the beef industry's "silver bullet" for solving the beef quality and tenderness equation. Marker assisted selection translates into one of the many ingredients involved in the recipe for genetic selection. Beef producers should utilize this tool, along with phenotypic records for quantitative traits, to insure both short and long term genetic progress.

The importance of expected progeny differences (EPD) as a tool for genetic selection cannot be questioned. In yesteryears, beef producers would evaluate “traditional” EPDs for birth weight, weaning weight, yearling weight, milk, and scrotal circumference in order to increase genetic progress for reproduction, maternal, and growth traits within the herd. However, the beef industry has undergone a fundamental shift in beef marketing from a commodity based, low-cost system that offers little incentive for a quality product, to a value-based marketing system where dollars are passed along the production chain based on product quality and value. This shift has now forced beef producers to be information gatherers: from collection and analysis of carcass data, to incorporation of carcass EPDs in selection decisions. While MAS requires more sophisticated sampling and decision making, it also adds to conventional selection and allows for exploitation of specific genetic effects.

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Table 1. Least squares means and pooled standard errors for palatability attributes stratified by quality grade category[h]

| | Quality grade category[a] | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Trait*[b] | HSMA | HSMB | LSMA | LSMB | HSEA | HSEB | LSEA | LSEB | SE |
| Tenderness | 6.14[de] | 5.43[ef] | 5.52[ef] | 5.43[ef] | 5.44[ef] | 5.43[ef] | 5.17[f] | 5.04[f] | 0.26 |
| Juiciness | 5.76[d] | 5.68[d] | 5.82[d] | 5.53[d] | 5.61[d] | 5.66[d] | 5.56[d] | 5.68[d] | 0.21 |
| Connective tissue | 6.33[cde] | 5.66[f] | 5.83[ef] | 5.78[ef] | 5.88[def] | 5.69[f] | 5.61[f] | 5.57[f] | 0.26 |
| Flavor intensity | 5.90[de] | 5.72[ef] | 5.78[ef] | 5.50[f] | 5.63[ef] | 5.80[ef] | 5.63[ef] | 5.62[ef] | 0.16 |
| Beef fat flavor | 1.53[cd] | 1.48[cd] | 1.47[cd] | 1.55[cd] | 1.44[d] | 1.45[d] | 1.43[d] | 1.46[cd] | 0.15 |
| Overall Acceptability | 5.44[def] | 5.04[efg] | 5.01[fg] | 4.92[fg] | 4.87[fg] | 4.99[fg] | 4.63[g] | 4.51[g] | 0.22 |

[a]Quality grade categories defined as High Small, A maturity; High Small, B maturity; Low Small, A maturity, Low Small, B maturity; High Select, A maturity; High Select, B maturity; Low Select, A maturity; Low Select, B maturity (HSMA, HSMB, LSMA, LSMB, HSEA, HSEB, LSEA, and LSEB, respectively).

[b]Tenderness: 1=extremely tough, 8=extremely tender; Juiciness: 1=extremely dry, 8=extremely juicy; Connective tissue: 1=abundant, 8=none; Flavor intensity: 1=extremely bland, 8=extremely intense; Beef fat flavor: 1=none detectable, 3=very strong; Overall acceptability: 1=extremely undesirable, 7=extremely desirable

[cdefg]Means within a row with different superscripts differ ($P < 0.05$).

[h]Adapted from McPeake et al. (2001).