Project Title: Identification of Cattle Production/Management Practices to Minimize Variation in Beef Tenderness

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Background

In May of 2002, the National Cattlemen's Beef Association, a contractor to the Beef Checkoff, acting under the auspices of the National Beef Instrument Assessment Plan II (NBIAP II), convened a group of industry experts, representing various sectors within the beef production chain, to develop an action plan for enhancing product tenderness. Following review and discussion of then-current scientific information concerning a broad array of factors that affect beef tenderness, conference participants identified three general areas of focus for future beef tenderness research: 1) "Instrumentation", 2)"Economics", and 3) "Optimum Production Practices." Working groups subsequently were formed to initiate and coordinate targeted research efforts within each of these three topic areas.

The primary goal of the Optimum Production Practices Working Group was to develop producer recommendations for implementation of a "best-practices" approach for reducing variability in beef tenderness. A growing body of scientific evidence suggests that numerous pre-harvest factors, both genetic and non-genetic, are associated with differences in beef tenderness. Moreover, recent studies have shown that implementing process control at specific points in the production chain could be effective for improving the quality and consistency of beef. Currently, however, there are no structured guidelines for quality management practices to ensure acceptable beef tenderness. In their action plan, members of the Optimum Production Practices Working Group recommended that a comprehensive review of the literature be conducted and a "white-paper", summarizing existing information concerning beef production practices and their effects on product tenderness, be developed.

Findings

Section I
The Importance of Efforts to Improve Beef Tenderness

Pre-harvest management of beef tenderness has become an important topic in today's cattle industry because: 1) erosion of consumer demand for beef over a period of approximately twenty years has caused cattle producers to become more clearly focused on satisfying the end-users of their product, 2) beef tenderness is a primary driver of consumer satisfaction and beef purchase decisions, and 3) recent structural changes in the beef industry, resulting in vertical alignment of the production, processing, and marketing sectors, have made it feasible to manage product attributes (such as tenderness) from "farm-to-table." This section provides a discussion of these factors, which underlie the fundamental importance of the industry's efforts to improve beef tenderness.

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An Industry in Transition

Sweeping structural changes are transforming U.S agriculture from a commodity-oriented industry dominated by small, independent producers, into a consumer-driven food production system comprised of larger, more vertically integrated firms focused on value-added production. According to Barkema and Drabenstott (1996), the underlying force driving agriculture toward this more industrialized, supply chain structure is consumer demand for conveniently prepared, highly nutritious, food products that fit faster-paced lifestyles.[1]

The cattle industry is no exception. Several decades of consolidation, driven by economies of scale, have resulted in a steady shift toward fewer and larger enterprises, particularly in the feeding, packing, and retail sectors of the beef industry. Additionally, changes in consumer eating patterns and food purchase behavior have forced beef producers to become more responsive to consumer demands for specific product attributes. As the beef industry has evolved structurally, commercial cow-calf producers have created opportunities for vertical alignment with feeders, packers and retailers forming producer-controlled cooperatives and strategic alliances. Cattle producers who operate in vertically coordinated business structures possess heightened awareness of consumer issues and have production goals that are more clearly focused on satisfying the end-users of their products. As Boehlje (1995) observed: "The produce-and-then-sell mentality of the commodity business is being replaced by the strategy of first asking consumers what they want as attributes in their food products and then creating or manufacturing those attributes in the products."[2]

Beef Demand – The Driving Force

The mid-1970s marked the emergence of a series of trends that, over time, would begin a major transformation of the U.S. beef industry – shifting the focus of cattle producers from almost single-minded pursuit of production-driven goals, to industry-wide emphasis on improving product quality, satisfying the needs of consumers, and building demand for beef. Per capita consumption of beef reached its pinnacle at 94.5 pounds in 1976 before spiraling downward in the years ahead. The lifestyles of American consumers were changing. More women had begun to enter the workforce and time devoted to in-home meal preparation began to decrease. Meal solutions featuring "convenience" would become increasingly popular in the years ahead. Beef consumption was identified as a major dietary source of calories, cholesterol, and saturated fatty acids and was implicated as a contributor to heart disease and the growing incidence of obesity in the U.S. population. American consumers received signals from a variety of sources discouraging the consumption of animal products, particularly red meat.

The beef industry of the mid-1970s was a highly segmented, commodity oriented, production-driven industry. Most commercial cattlemen focused on the "customer" – the person who represented the next immediate link in the beef chain (auction market, stocker operator, feeder, packer – in-other-words, the buyer) – and, in most cases, were either insulated or disconnected from the ground-swell of negative perceptions concerning beef that was developing among "consumers" – the actual end-users of their product.

The next two decades would be devastating to the beef industry. From 1980 through the first half of 1998, cumulative U.S. domestic beef demand, as reflected by the Beef Demand Index[3], decreased by more than 48%. During that same 18-year period, beef's market share (expressed as % of average annual per capita expenditures) declined by 15 percentage points, while poultry's market share nearly doubled[4]. Changes in consumer lifestyles and eating patterns, concerns about beef's safety and healthfulness, high beef prices relative to prices of competitive meats, and overall dissatisfaction with beef product performance all were frequently cited as factors that contributed to the precipitous erosion of beef demand. Dr. Wayne Purcell, VPI University, authored the following commentary describing the impact of shifts in meat

product demand on the beef production sector during the 1980s and early 1990s: "Consumers walked past the meat counter and bought poultry or fish. The divergence grew, and the numbers started to document a disaster. From 1979 through 1986, with per capita consumption in beef stable around 78 lb retail weight, the inflation-adjusted price for Choice beef at retail declined over 30 percent…Per capita consumption in beef was nearly 95 lb in 1976 and declined to the 65-lb level in 1993. The marketplace enacted the painful process of forced adjustment and downsizing and was headed toward an industry small enough to generate prices that would keep some producers in business. January 1 inventory numbers for beef cows was at a high of 45.7 million head in 1975, and declined to a low of 32.4 million head in 1990. Resources, including producers as the important human resource, were forced out of business and forced divestment and downsizing were the norms for two decades…"[5]

By the mid-1980s, with beef consumption continuing its downward spiral, beef industry leaders began to realize the enormity of their problem and recognized the need for change. Insight into the dynamics, which were forcing fundamental changes in the beef industry at that time, are reflected in the following comments made in 1986 by Robert Peterson (CEO of IBP, Inc.) during an interview with Meat Processing magazine: "It is important we recognize we are not going through a normal cycle. The red meat industry must learn to accept the fundamental changes, which have rocked our industry and are almost certainly irreversible. We must work on our own mental attitudes. We must think about new economic structures and new strategies to address the changing times. We must build a product the consumer wants, rather than the product we want them to have."[6]

In the early 1990s, beef producers began to embrace the principles of total quality management (TQM) and process control developed by "quality guru" W. Edwards Deming, who was credited with transforming post-WWII Japan into a leader in international business and industry and was viewed by many as the "father" of the modern "quality revolution" that began reshaping American industry in the 1980s. Attention was given to reducing costs throughout the beef chain[7], identifying product defects and quality shortfalls[8], learning more about the preferences, needs, and expectations of beef consumers[9], and linking segments of the beef chain to facilitate application of TQM principles and implementation of process control.[10] Improving demand became the beef industry's single most important goal and quality became an industry-wide priority.[11]

During the past five years, U.S. cattlemen have developed a renewed sense of optimism, as the beef industry's strategies to improve consumer demand for beef have begun to pay dividends. After a steady decline, spanning approximately two decades, consumer demand for beef has increased each year since 1998 and, at the time of this writing, the Beef Demand Index for 2003 shows a 15% increase over its low-point recorded in 1998. According to market analysts, the fact that beef demand strengthened, while 2003 cattle prices attained record highs and retail beef prices increased, provides evidence of a fundamental market shift reflecting significant changes in consumer eating patterns. The growing popularity of high-protein, low-carbohydrate diets – which advocate consumption of red meat as a dietary protein source and which have been supported by recent medical studies[12], [13] as being potentially beneficial in the fight against obesity – has been widely cited in recent popular press articles as clear evidence of a dramatic shift in eating patterns in the U.S.

For the past several years, beef producers have worked diligently to identify primary drivers of consumer demand and to become more responsive to consumer needs by improving the quality, safety and convenience of their products. While the exact cause and effect relationships underlying the recent upward shift in beef demand remain unclear at this time, the transition of the beef industry, from a traditional, production-driven commodity business, to

a modernized industry that emphasizes quality and meeting consumer needs, undoubtedly has contributed to the dramatic turnaround in beef demand.

Beef Tenderness and Flavor – Key Factors in Consumer Purchase Decisions
Delivering a quality eating experience is essential to the continued success of the beef industry's efforts to build consumer demand for beef products.[14] Consumer survey results suggest that eating quality (defined by most consumers simply as "taste") is a primary driver of food purchase decisions, across a variety of product categories. From 1983 to 2002, "taste" topped the list of factors considered "very important" by consumers when making food purchase decisions.[15] Feargal Quinn, founder and chief executive of Superquinn (a major supermarket chain in Ireland), summarized the overriding importance of taste in consumers' meat purchasing decisions as follows: "The end-product is taste…Customers won't pay for food to satisfy their nutritional requirements, neither will they pay for it to conform to their needs on food safety. These matters are paramount issues for them, certainly. But, they are make-or-break issues. If they are satisfied, they will consider buying; where they are not satisfied, they will increasingly refuse to buy at all…On the other hand, people will pay more for greater satisfaction, and taste is their measure of satisfaction in food…Meat producers who are customer-driven must seek to influence the factors that affect taste, all the way from the field to the table."[16]

Research involving U.S. consumers, characterized as frequent beef users, suggests that consumers' overall perceptions of the taste of beef are associated with three primary sensory attributes – tenderness, flavor, and juiciness.[17] In a recent study conducted at Colorado State University, 489 consumers, selected to be representative of the age, income, and ethnic background of the U.S. population, were asked to identify the sensory attribute (tenderness, flavor, or juiciness) they considered most important when purchasing beef. Tenderness was considered most important when making beef purchase decisions by 52% of consumers, whereas 38% listed flavor as most important, and 11% considered juiciness to be the most important driver of beef purchases.[18] Others have reported strikingly similar results. Huffman et al. (1996) asked consumers to identify the beef sensory attribute that most influenced their eating satisfaction when dining at home or at a restaurant: 51% identified tenderness, 39% identified flavor, and 10% identified juiciness.[19] Though tenderness is considered to be the fundamental determinant of a beef product's performance with respect to eating quality,[20] the contribution of beef flavor to the overall eating experience cannot be overlooked. Research conducted to identify various factors that determine beef customer satisfaction has suggested that, for cuts like the clod, top round, and top sirloin, flavor might be the more important driver of customer satisfaction.[21]

Experimental market research has established a direct link between the eating qualities (tenderness and flavor) of beef and actual purchase behavior of beef consumers. In a study conducted by Boleman et al. (1997), consumers evaluated sensory properties of beef strip loin steaks that had been pre-classified into three tenderness categories using Warner-Bratzler shear force (WBSF) measurements: tender (WBSF = 2.27 to 3.58 kg), intermediate (WBSF = 4.08 to 5.40 kg), and tough (WBSF = 5.90 to 7.21 kg). The steaks were identified to consumers using color-coded labels and participants were not aware that pre-determined tenderness differences existed among the groups. After sampling and assessing the sensory properties of the tender, intermediate and tough steaks, participants were presented with two opportunities to purchase representative steaks from the three tenderness categories. In the first segment of the experiment, participants were offered color-coded steaks from all three groups at the same price ($3.85/lb). They still had no knowledge of the pre-determined tenderness differences among the groups, so their purchase decisions were based solely on their previous eating experiences. Under these experimental conditions, 55% of the steaks purchased by consumers were from the tender category, 12% were from the intermediate group, and 32% of steaks purchased previously had been classified as

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tough. In the second segment of the experiment, the tenderness differences were revealed and participants were offered steaks verified to be tender, intermediate, or tough at prices of $4.35/lb, $3.85/lb, and $3.35/lb, respectively. When consumers were aware of the tenderness differences among the steaks and tender steaks were offered at premium prices, nearly 95% of the steaks purchased were from the tender category.[22]

Additional insight into consumers' willingness-to-pay for superior beef tenderness was provided by an in-store experiment involving meat shoppers in Midwest supermarkets conducted by Lusk et al. (1999).[23] That study utilized beef ribeye steaks that had been classified, using WBSF measurements, as either "guaranteed tender" or "probably tough".[24] In the first segment of the study, shoppers who participated in the experiment were presented with a free steak (the steak was labeled "blue" indicating to researchers that the steak had been classified as "probably tough"). The shoppers were then asked to evaluate cooked samples of two different steaks – one coded with a blue label ("probably tough"), the other with a red label ("guaranteed tender"). The meaning of the labeling difference (blue vs. red) was not divulged to the shoppers. After sampling the two steaks, shoppers were asked which steak they preferred. If they selected the blue-label steak, their participation in the experiment was concluded and they were allowed to keep their free (blue-label) steak. Shoppers who preferred the red-label steak, based on their independent evaluations of tenderness, were given the option of either keeping their free blue-label steak or submitting a bid to upgrade to a red-label steak. In this segment of the study, 69% of the consumers preferred the red-label steak and 36% were willing to pay extra to upgrade. Those opting to upgrade were willing to pay an average of $1.23/lb more to obtain the more tender red-label steak. The second segment of the study was identical to the first except that the steaks were labeled as "guaranteed tender" or "probably tough", providing shoppers with specific product label information about the differences between the steaks, in addition to their own assessment of the differences in sensory properties of the steak samples. When consumers were informed that the two steaks represented two tenderness categories – "guaranteed tender" and "probably tough" – 84% of the participants preferred the "guaranteed tender" steak and 51% were willing to pay more to upgrade from a "probably tough" steak to a "guaranteed tender" steak. In this segment of the study, those opting to upgrade were willing to pay an average of $1.84/lb more to obtain the "guaranteed tender" steak.[23]

Umberger et al. (2000) used a similar approach to determine consumers' willingness to pay for beef flavor preferences associated with differences in marbling (high vs. low marbling scores) and cattle production system/origin (U.S. corn-fed vs. Argentine grass-fed). Tenderness was held constant in all comparisons to isolate the effects of flavor on consumer purchase behavior. In comparisons of U.S. corn-fed with Argentine grass-fed, all products had a Slight degree of marbling, to eliminate quality grade effects. Results demonstrated that consumers were able to detect flavor differences associated with differences in marbling and production system and were willing to pay higher prices to obtain steaks that had the flavor characteristics that they preferred. Consumers in that study tended to prefer the flavor characteristics associated with high (rather than low) marbling levels and the flavor of U.S. corn-fed (rather than Argentine grass-fed) beef.[25]

Platter et al. (2004) used experimental auction techniques to examine the relationships of marbling and WBSF to consumer purchasing behavior and to prices that consumers were willing to pay for beef strip loin steaks. In that study, consumers (representative of primary U.S. population demographics) evaluated the sensory properties of beef strip loin steaks from 550 beef carcasses. The carcasses had marbling scores ranging from Traces to Slightly Abundant and the steaks had WBSF values ranging from 2.3 to 7.5 kg. After the consumers had evaluated sensory properties of the steaks, they were asked (without obligation) to participate in a variation of a sealed-bid Vickrey auction in which they could purchase steaks that were identical to those they had sampled. Results showed that marbling and WBSF both were important indicators

of the probability that consumers would purchase a steak. In addition, the prices consumers were willing to pay to purchase steaks increased as marbling score increased and as WBSF decreased. Consumers in that study were likely to purchase steaks if they had marbling scores of Modest[50] or greater (average Choice or higher quality grade) and (or) WBSF values of 3.9 kg or lower.[26]

Results of the studies detailed above are significant to the beef industry because they provide compelling evidence, which suggests that efforts to improve the eating qualities of beef, if successful, can have a positive influence on consumer purchase behavior. These studies, using actual transactions (rather than relying upon consumers' statements concerning their willingness or intent to purchase), confirm that differences in tenderness and flavor not only influence the likelihood that a consumer will purchase a beef product, but also affect the prices that shoppers are willing to pay for beef. Beef consumers in these experiments associated eating satisfaction with product value and many of them were willing to pay premium prices for beef with the level of tenderness or the flavor characteristics they preferred. Furthermore, results of these studies demonstrate that, when consumers are informed that beef products have been pre-tested and verified to be tender, they become even more willing to pay premium prices for beef with superior tenderness.

Consumer-Focused Beef Production

In an effort to capitalize on the relationships of beef's eating qualities to consumer satisfaction and purchase behavior, today's cattle producers are becoming increasingly interested in designing coordinated production and processing systems to facilitate production of beef that consistently delivers a quality eating experience. A growing number of cattle producers are entering into partnerships or contractual arrangements with other industry segments, forming alliances and beef supply chains. Peck (2003) listed thirty-six different "consumer-based" beef programs currently involved in some form of vertical coordination activities.[27]

Existing beef alliances and supply chains exhibit a variety of distinctive features: a) Nearly all focus on improving quality and adding value to cattle and beef products. In addition, most feature value-based marketing agreements to provide economic incentives for production of cattle and beef carcasses that meet program specifications. b) Most are at least partially integrated (or vertically coordinated), with producers retaining some share of ownership through much or all of the beef value chain. This is an essential feature of the coordinated business structure because it provides cattle producers with an opportunity to capture a share of the product value that is added by the processing and marketing sectors and enables producer-participants to receive market signals directly from consumers. c) Many include breed specifications (based on genotype or phenotype) for program cattle, in an effort to improve consistency of genetic inputs into the system. d) Many include information systems that facilitate data acquisition, information sharing among program participants, and measurement of system performance. e) Some feature branded products designed to target consumer preferences for specific product attributes. f) Many involve source and/or process verification and some utilize third-party verification to instill consumer confidence in product quality, consistency, and safety.

In addition to the features described above, several vertically coordinated beef programs have adopted a total quality management (TQM) approach and utilize process control to ensure the quality and consistency of their products. For example, Ranchers Renaissance utilizes "twenty-four process control points, from ranch to retail" with the goal of "providing great eating experiences time after time."[28]

The concept of using a TQM approach for improving beef palatability was first introduced at the Strategy Workshop for the National Beef Quality Audit – 1991 by Morgan (1992), who

coined the term PACCP (Palatability Assurance Critical Control Points) to describe the idea.[29] Shortly thereafter, the implementation of PACCP systems to improve beef tenderness was advocated as a key action point in the 1994 National Beef Tenderness Plan.[30] The PAACP concept has been embraced in other countries as well and provided the platform for the development of Australia's beef grading scheme – Meat Standards Australia.[31]

The basic tenet of TQM is to improve the production system to prevent product defects, rather than inspecting finished products and removing those that do not conform to quality specifications. In normal systems of beef production, there are several points at which management decisions are made that can have either a positive or negative impact on subsequent product quality. The TQM approach focuses on control of processes at these key points in the production chain to produce the desired outcome, which, in the context of this discussion, is the improvement of the eating qualities of beef and reduction/elimination of undesirable eating experiences.

As development of coordinated beef production systems has gained momentum, interest in managing consumer-oriented traits such as tenderness has intensified. Research conducted at Colorado State University[32] demonstrated the effectiveness of process control (both pre-harvest and post-harvest) in a quality management system for improving tenderness, quality, and consistency of beef and identified two general pre-harvest process control points (genetic inputs and pre-slaughter cattle management) that could be used by producers who operate within vertically coordinated business structures to reduce the incidence of tenderness problems.[33] The following sections provide a review of the literature concerning effects of various pre-harvest factors on beef's eating qualities, with primary emphasis on beef tenderness.

Section II
Fundamental Sources of Variation in Beef Tenderness

Effective application of pre-harvest cattle management practices to enhance the tenderness of the final product requires a basic understanding of the fundamental causes of variation in beef tenderness. A comprehensive discussion of all of the various factors associated with differences in meat tenderness is beyond the scope of this review. However, a brief overview of some of the root causes of tenderness variation that appear to be associated with various pre-harvest factors is provided below to establish a foundation for further discussion.

Beef tenderness is a complex trait that is influenced directly by several basic physical and chemical properties of skeletal muscle, and indirectly by numerous other factors. Pre-harvest management practices are believed to influence tenderness via their effects on 1) the amount and solubility of intramuscular collagen, 2) the contractile state of sarcomeres at the onset of rigor mortis, 3) the rate and extent of postmortem degradation of structural proteins in the myofiber, 4) postmortem muscle pH, and 5) deposition of intramuscular fat.

Fundamental relationships between tenderness and the amount and solubility of collagen have been recognized for many years. The amount or concentration of intramuscular collagen differs among the various muscles in an animal's body. Muscles with high collagen content (e.g., locomotive muscles) tend to be tougher than muscles with lower collagen concentrations (e.g., muscles supporting the spinal column). However, it is the solubility of collagen (the ease with which collagen is degraded during cooking) that is the primary factor associated with connective tissue effects on tenderness in most animal-to-animal comparisons. Collagen solubility is influenced by the formation and maturation of intermolecular collagen crosslinks.[34] During collagen synthesis, chemical bonds form between amino acids in adjacent collagen molecules, resulting in reducible, heat-labile crosslinks, which contribute to the organization and structural stability of collagen

in the living animal.[35] Newly synthesized collagen, with its high proportion of reducible crosslinks, is easily degraded during cooking and, consequently, has little effect on tenderness, except in muscles with very high concentrations of connective tissue. However, as the animal matures, intermolecular collagen crosslinks stabilize to an insoluble, heat-resistant form. Maturation and stabilization of the intermolecular crosslinks reduces meat tenderness because mature collagen is no longer effectively degraded during cooking.[36] Pre-harvest management practices that influence either the amount or the solubility of intramuscular collagen can influence beef tenderness.

Another principle factor underlying differences in beef tenderness is the contractile state of muscle during the onset of rigor mortis. Pre-rigor bovine muscle shortens (individual contractile units in muscle cells, called sarcomeres, contract and shorten) if chilled too quickly (to temperatures below approximately 10°C) during the first few hours postmortem – a phenomenon referred to as "cold-shortening."[37] Cold-shortened muscles, with sarcomeres that have shortened to 20 to 40% of their relaxed length, are appreciably tougher than are muscles that experience rigor onset in a more relaxed state.[38] The cooling rate of a muscle is determined not only by ambient temperature, but also by carcass mass and by thickness of the external fat layer covering the muscle.[39] Correspondingly, pre-harvest practices that affect carcass mass and (or) fatness can indirectly affect tenderness by influencing carcass chill rate. Under current commercial processing conditions in the U.S., cold-shortening is thought to be a problem only in very lean and (or) light-weight beef carcasses.[40]

Fresh beef naturally tenderizes during postmortem storage at refrigerated temperatures. This tenderization process, commonly referred to as "aging", is caused by the degradation (proteolysis) of key structural proteins in the muscle cell by enzymes (proteases) that occur naturally in skeletal muscle. The protease system thought to be responsible for most of the proteolysis that occurs in bovine muscle during the early postmortem period is the calpain system.[41] The calpain system is comprised of two proteases (μ-calpain and m-calpain), both of which require the presence of calcium ions for activity (μ-calpain requires lower concentrations of calcium for activity than does m-calpain and Ca++ levels in postmortem muscle normally are high enough to activate μ-calpain, but not m-calpain). The calpain system also includes a specific calpain inhibitor (calpastatin), which functions to regulate the action of the proteases. When calpastatin activity is low in postmortem muscle tissue, the calpains (primarily μ-calpain) actively degrade key protein structures in the muscle, causing the muscle to lose structural integrity and become more tender during storage. Conversely, when calpastatin activity is high, degradation of structural proteins by the calpains is limited, which reduces both the rate and extent of tenderization during postmortem storage. Calpain activity is highest during the early postmortem period and is influenced by early postmortem muscle temperature and pH (calpain activity decreases with decreasing muscle temperature and pH).[42] Correspondingly, the rate and extent of postmortem tenderization are influenced by a variety of factors known to affect carcass chill rate and (or) the rate of muscle pH decline. In addition, there are known genetic effects on calpastatin activity, which are associated with differences in rate and extent of postmortem tenderization.

Takahashi (1996) presented experimental evidence supporting "the calcium theory of meat tenderization," challenging the widely held belief that the calpain system is exclusively responsible for postmortem tenderization of meat. Results of a series of experiments, presented by Takahashi (1996), suggest that calcium ions may exert direct, non-enzymatic tenderization effects in postmortem muscle. A calcium ion concentration of 0.1 mM, was shown to be associated with weakening or degradation of several structural elements in muscle tissue including weakening of Z-disks, weakening of rigor linkages between actin and myosin, splitting of titin filaments, fragmentation of nebulin filaments and desmin molecules, and weakening of intramuscular collagen.[43] It is particularly noteworthy that these structural changes were shown to occur within an acidic pH range (pH < 6.1), which is consistent with the normal pH of postmortem

muscle tissue. Collectively, these structural changes could account for most of the aging effects that normally are observed in postmortem muscle tissue. Furthermore, several of the changes are nearly identical to those normally attributed to calpains. In these experiments, however, a protease inhibitor, leupeptin, prevented calpain activity. These findings, though not widely recognized, are cited here because they seem to explain several of the changes in postmortem muscle tissue that have been difficult to attribute to the effects of calplains and because the theory, if proven, could have important implications with respect to pre-harvest management of beef tenderness via modification of calcium metabolism in cattle.

Postmortem muscle pH is an intrinsic property of meat that reflects the collective effects of multiple pre-harvest and post-harvest factors on postmortem muscle metabolism. Shortly after a beef animal is harvested, pH of the carcass musculature begins a gradual decline from a near-neutral value (approximately 7 or slightly higher) to a final level, approximately 24 hours later, of about 5.5 (5.4 to 5.7) in normal beef carcasses.[44] The gradual decline in muscle pH is caused by accumulation of lactic acid in the muscle tissue. In postmortem skeletal muscle, anaerobic glycolysis converts glycogen (a polysaccharide stored in muscle tissue) into lactic acid and ATP, the latter of which is used by the muscle for energy. The amount of lactic acid produced in postmortem muscle tissue, and the final pH of the muscle, essentially is determined by the amount of glycogen in the muscle at the time of harvest, which is affected by several factors including temperament and sex of the animal, diet, pre-harvest handling practices and the glycolytic potential of the muscle.[45] Investigations of the relationship between tenderness and final muscle pH suggest that muscles with final pH values ranging from 5.8 to 6.2 (slightly higher than normal) generally are toughest. Final muscle pH values below 5.8 and above 6.2 seem to be associated with greater tenderness. Studies have shown that the rate of postmortem muscle pH decline also has important implications with respect to beef tenderness. Even muscles that attain a final pH that is within the normal range of pH values can differ widely with respect to rate of pH decline due to differences in rate of postmortem glycolysis.[46] Comparisons of beef muscles with slow vs. fast rates of glycolysis, have shown that slow-glycolyzing muscles (i.e., those with high pH values during the first few hours postmortem) are more likely to cold-shorten, undergo less proteolysis during postmortem aging, and are less tender than fast-glycolyzing muscles.[47] However, if the rate of glycolysis is too fast (as can sometimes result with the application of low-voltage ES to pre-rigor beef carcasses) and high-temperature, low-pH conditions prevail during the early postmortem period, beef muscles can experience toughening associated with rigor- shortening (also termed heat-shortening).[48]

Marbling (intramuscular fat deposited in the perimysial connective tissue layer that surrounds groups or "bundles" of muscle fibers) is positively related to beef tenderness[49] and continues to be used as a primary indicator of beef quality in U.S. beef markets, even though the correlation between marbling and tenderness is relatively low.[50] Among the numerous theories that have been advanced to explain the effects of marbling on meat tenderness,[51] those that most likely explain the direct contribution of marbling to tenderness are predicated upon its relationship to physical density of cooked meat, its role as an insulator in pre-rigor muscle, and its ability to prevent drying and hardening of muscle proteins during cooking. As explained by Smith (2003), "*chunks of fat distributed throughout a section of beef make it more tender because fat globules are less resistant to shear force than are muscle fibers and connective tissue,*" … because "*the deposition of marbling in beef muscles can help insulate muscle fibers against cold-shortening*" … and "*because fat surrounding muscle fibers decreases the extent of protein coagulation/hardening that occurs when meat is cooked to a higher degree-of-doneness.*"[52] Marbling also may play an important indirect role in assurance of acceptable beef tenderness. Its presence in beef reflects several other factors – some genetic, some environmental – that are known to have a positive influence on beef tenderness.

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Section III
Effects of Various Pre-Harvest Factors on Beef Tenderness

A growing body of scientific evidence suggests that a number of different pre-harvest factors influence the eating qualities of beef and could be managed systematically to impart desired quality characteristics to the end product. Pre-harvest factors which might be considered for use as potential process control points in cattle production systems to enhance beef tenderness, include 1) pre-harvest diet and nutritional management, 2) use of hormonal implants or other growth modifiers, 3) animal breed or genotype, 4) temperament and (or) ante-mortem stress, 5) sex classification of the animal, and 6) health status, medical treatment history, and techniques used to administer animal health products.

Pre-Harvest Nutritional Management and Dietary Effects
The literature concerning the effects of pre-harvest diet on beef tenderness spans several decades and includes a vast array of reports covering a variety of topics. Those topics most pertinent to the development of strategies for pre-harvest nutritional management of beef tenderness include: 1) dietary energy intake and comparisons of grain vs. forage diets, 2) variation in the length of time animals are fed a high-concentrate diet, 3) the age at which the finishing period is initiated, and 4) dietary supplementation to enhance beef tenderness.

Dietary Energy Intake and Comparisons of Grain-Fed and Forage-Fed Beef. The importance of dietary energy intake and grain finishing to the development of desired beef quality characteristics has long been recognized. Animal nutrition texts published in the early 1900s[53,54] expressed the common belief that cattle fed intensively on high-energy, grain diets produced beef with superior tenderness, flavor, and juiciness when compared with cattle finished on lower-energy, forage-based diets. Cattle produced specifically for the U.S. dressed beef trade in the early 1900s represented two primary types: 1) "Beef Cattle" ("fat" steers and heifers exhibiting a predominance of Angus, Hereford, or Shorthorn breeding) finished on grain diets by Corn-Belt farmer-feeders and 2) "Texas and Western Range Cattle" (branded, unimproved cattle from Texas and the western range states), some of which were finished in mid-western feedlots, but most of which were shipped to market directly off of grass.[55] Market preferences at that time favored the quality characteristics of beef produced by beef-type, grain-fed steers, so cattle buyers and packers began utilizing live animal and carcass indicators of breed and feeding history, such as conformation (which was influenced by inherent differences in muscularity, but also by fat deposition), "finish" (amount, character, quality and distribution of fat), and amount of marbling (intramuscular fat), to reflect differences in "quality" and value among market cattle and carcass beef.[56] These early attempts to distinguish grain-fed beef from forage-fed beef for marketing purposes, provided the foundation for the first USDA beef grading system, the essential elements of which are still in use today. The following excerpt from the first Official United States Standards for Grades of Carcass Beef (USDA, 1926) describes a steer carcass that would qualify for the highest grade – Prime or No. A1 – and specifies a number of carcass traits, the development of which would require a period of intensive grain feeding.
"A Prime, or No. A1, grade steer carcass … is relatively short and blocky, and is heavily and uniformly fleshed throughout … The exterior of the carcass, including shanks and neck, is entirely covered with a smooth, brittle, slightly creamy-white fat … The interior walls are well covered … Flesh is firm, velvety, very fine-grained, and of a light or cherry-red color and, in the thicker cuts, possesses an abundance of marbling."[57]

Today's cattle production systems are designed specifically to produce grain-fed beef, which is demanded by most mainstream U.S. markets (both domestic and export). In current U.S.

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cattle production systems, most market cattle (young steers and heifers) are either placed in feedlots for grain finishing as weaned calves (calf-feds) or grown for a period of time on various forage-based diets, until they are approximately 12 to 18 months old (yearlings and long-yearlings, respectively), before placement in feedlots for finishing. Typical commercial cattle finishing diets consist of more than 70% grain on an as-fed basis and are designed to maximize rates of growth and fat deposition. Though today's cattle are marketed at leaner endpoints than in years past, cattle buyers and packers still utilize evidence of external fat deposition (in live cattle) and degree of marbling (in beef carcasses) as primary criteria for determining when cattle are market-ready. The majority of "fed" cattle in the U.S. are harvested when it is estimated (using visible indicators of external fat deposition or, in some feedyards, ultrasound measurements of % intramuscular fat) that they have deposited a sufficient amount of marbling to produce a carcass with a USDA quality grade of at least low Choice (minimum marbling score of "Small"), without being overly fat (USDA yield grade of 3 or better).

Although the majority of market cattle in the U.S. are finished on grain, there has been a recent resurgence of interest in forage finishing of cattle due to possible dietary health-benefits associated with consumption of forage-fed beef. Beef produced by cattle fed forages is leaner and has higher levels of conjugated linoleic acid (CLA) than beef produced by grain-fed cattle,[58] a fact that has captured the interest of a small segment of cattle producers and some health-conscious beef consumers. Conjugated linoleic acid in the human diet is thought to have anticarcinogenic and antiatherogenic properties, and may prevent onset of diabetes and reduce body fat mass.[59]

Studies comparing quality characteristics of forage-fed and grain-fed beef have demonstrated that grain feeding improves several carcass indicators of beef quality. Grain-fed cattle produce carcasses with brighter-colored, finer-textured lean,[60] whiter fat,[61] and more marbling,[62] all of which enhance acceptability of fresh retail beef.[63] In addition, most comparisons of forage-fed and grain-fed beef suggest that grain feeding improves tenderness.[64]

The greater tenderness of grain-fed beef has been attributed to several different factors. As noted earlier, grain-fed beef generally has more marbling than does forage-fed beef and, even though the magnitude of the relationship between marbling and tenderness has been characterized as low to moderate, higher marbling scores seem to be consistently associated with increased beef tenderness.[65] Grain feeding also increases collagen solubility[66] and reduces the risk of cold-shortening during chilling.[63] The reduced risk of cold-shortening for grain-fed cattle is associated with the effects of grain-feeding on carcass mass and fatness. Due to higher energy intake, grain-fed cattle grow faster and fatten more quickly than do forage-fed cattle.[67] Consequently, grain-fed cattle produce heavier-weight, fatter carcasses[68] that chill more slowly and have faster glycolytic rates[69] compared with lighter-weight, leaner carcasses produced by forage-finished cattle. The slower cooling rates and faster glycoltyic rates of muscles in carcasses produced by grain-fed cattle not only makes them less susceptible to cold-shortening, but also may increase the rate and extent of tenderization associated with muscle proteolysis (aging) during the early postmortem period.[64]

The beneficial effect of grain feeding on collagen solubility is believed to be associated with the effect of energy intake on pre-harvest growth rate.[70] In rapidly growing cattle, rates of collagen synthesis and degradation are elevated.[71] Correspondingly, following a brief period of rapid growth, due to intensive feeding, muscles of fast growing cattle have higher proportions of newly synthesized, soluble collagen than do muscles of slower-growing cattle.[72] According to data presented by Wu et al. (1981), the positive effects of intensive feeding and rapid growth on collagen synthesis and degradation occur within the first six weeks of the grain-finishing period.[71]

Results of several studies involving trained sensory panels suggest that grain feeding of cattle not only increases tenderness, but also improves beef flavor.[60, 63, 67, 68] Moreover, most U.S. consumers seem to prefer the flavor of grain-finished beef to that of forage-finished beef. In a recent marketing test involving consumers in Chicago and San Francisco, U.S. corn-fed beef was compared with Argentine grass-fed beef (tenderness was held constant in these comparisons to isolate the effects of flavor on consumer preference). Of 226 consumers who participated in that experiment, 141 (62%) preferred the flavor of corn-fed beef, 51 (23%) preferred the flavor of grass-fed beef, and 34 (15%) expressed no preference.[73]

Compared with beef from cattle finished on grain diets, beef produced by grass-fed cattle has different concentrations of several flavor precursors, the most important of which reside in the fat tissue.[74] Sensory panelists often characterize the less desirable flavor of forage-fed beef as "grassy" or "dairy/milky", compared with the "beef fat" flavor normally associated with grain-fed beef.[75] Larick et al. (1987) identified fourteen different compounds in the volatiles of melted subcutaneous fat of forage-fed cattle, which were positively correlated with "grassy" flavor of beef loin steaks. The compound most closely correlated with "grassy" flavor in their study was phyt-2-ene. Moreover, two lactones, δ-tetradecalactone and δ -hexadcalactone, were negatively correlated with "grassy" flavor and, therefore, were considered to be indicative of a grain-fed beef flavor.[76] Researchers at the University of Tennessee isolated several volatiles that were associated with flavor differences between grass-fed and grain-fed beef and were able to effectively mimic the characteristic "beef fat" flavor of grain-fed ground beef by spiking ground beef from forage-fed cattle with pentanal, toluene and m-xylene.[74]

Time-On-Feed Effects. Though only a small number of cattle targeted for U.S. beef markets are forage-finished, a great number of young, stocker cattle are backgrounded on various forages (grazed or harvested) for several months before receiving high-concentrate, finishing diets.[77] Cattle that are grown on relatively low-energy, forage diets must be fed a high-concentrate diet for a sufficient period of time in order to develop the carcass quality characteristics and beef palatability attributes typically associated with those of grain-fed beef.

Zinn et al. (1970) documented a relationship between the number of days cattle were fed a high-energy, grain diet (time-on-feed) and beef tenderness.[78] Further study of the relationship between tenderness and time-on-feed has shown that most improvements in tenderness occur during the early portion of the finishing period (before 112 days on feed),[79, 80, 81] and that finishing periods longer than approximately 100 days seem to provide little additional improvement in tenderness (see Figure 1).[81, 82, 83] In fact, feeding yearling cattle a high-concentrate, finishing diet for periods longer than 180 days has been shown to be detrimental to tenderness due to increased maturity of long-fed cattle.[78]

Figure 1. Relationship Between Days on Feed
and Shear Force (Source: May et al., 1992)

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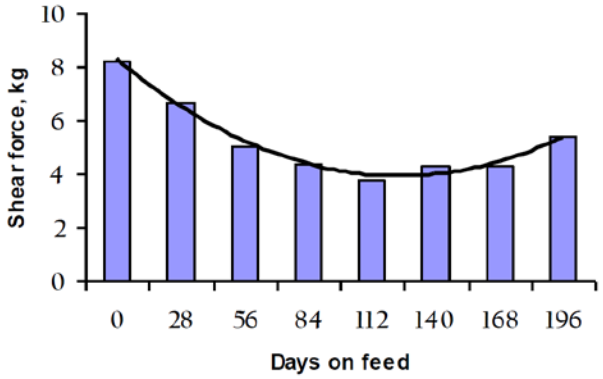

Increased time-on-feed also has been shown to improve beef flavor desirability.[83] Harrison et al. (1978) reported that the flavor of cooked beef fat became more desirable as length of the feeding period increased (from 0 to 49 to 98 days on feed)61 and Larick et al. (1987) determined that sensory panel scores for "grassy" flavor of steaks and ground beef decreased steadily with increased time-on-feed, from 0 to 112 days on feed.[76] Melton et al. (1982) studied flavor changes in ground beef during a 140-day finishing period, and found that intensity of cooked "beef fat" flavor (characteristic of grain-fed beef) increased, whereas intensity of flavors characterized as "milky-oily", "sour", and "fishy" (which sensory panelists associated with grass-fed beef) decreased, as time-on-feed increased. In their study, most of the changes in these flavor intensities occurred between 56 and 84 days on feed, with few additional flavor changes occurring after 84 days on feed, leading the authors to conclude that finishing periods of 80 to 90 days are required to produce desired, grain-fed beef flavor characteristics.[84]

Age of Cattle When Finishing Period is Initiated. The chronological age at which cattle enter a feedlot and are started on a high-concentrate, finishing diet represents another important source of variation in several pre-harvest factors that can influence beef tenderness, including duration of the finishing period (time-on-feed), deposition of intramuscular fat, and age/maturity at harvest. The greatest numbers of feeder cattle currently placed in commercial feedlots in the U.S. represent one of two age classes: calves (weaned calves entering the feedlot at 7 to 8 months of age) and yearlings (cattle entering the feedlot at approximately 12 months of age).[77] Cattle placed in feedlots as calves ("calf-feds") typically are fed for periods of 150 to 210 days and harvested at ages of 12 to 14 months, whereas cattle placed on feed as yearlings typically are fed for periods of 90 to 180 days and are usually about 16 to 18 months old at harvest. Placing young, lightweight calves on high-energy finishing diets accelerates fat deposition, causing them to finish at relatively young ages and comparatively light final weights. In contrast, backgrounding young cattle on low-energy, forage diets (as is common in most stocker programs) delays fat deposition, allowing cattle finished as yearlings to attain heavier weights and older ages before they fatten.[85] As a result, it is common for finished live weights of cattle fed as calves vs. yearlings to differ by as much as 100 pounds or more when fed to the same fat thickness endpoint.[86] Based on current market specifications for carcass weight and grade, relatively large, late-maturing cattle types are most suitable for calf-fed programs, whereas smaller, earlier maturing cattle types are most suitable for yearling programs.[87]

Studies that have compared growth and carcass characteristics of calf-fed and yearling-fed cattle harvested at the same fat thickness, or same carcass fat percentage, consistently have demonstrated the relationships described above. However, there is little agreement among different research trials concerning effects of age at feedlot entry on marbling score. Results of some trials suggest that carcasses from calf-feds have more marbling than carcasses produced by yearlings when the two age classes are compared at the same thickness of subcutaneous fat.[88, 89] Other trials have shown that cattle finished as calves and those finished as yearlings produce carcasses with similar marbling scores,[85, 90] while still others have reported higher

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marbling scores for yearlings.[86, 87] In comparisons involving calf-fed vs. yearling-fed cattle, marbling differences seem to be associated with differences in days on feed and (or) with energy intake of the yearlings during backgrounding. When the number of days on feed is much greater for calves than for yearlings, marbling differences tend to favor the calf-fed cattle. On the other hand, when the number of days on feed is similar for calves and yearlings, marbling scores for the two groups tend to be similar or may favor the yearlings. Moreover, if yearlings are backgounded on moderate-energy, pre-finishing diets, they tend to produce carcasses with as much or more marbling as carcasses produced by calf-feds. Miller et al. (1987) examined the effect of pre-finishing diet (moderate- vs. low-energy) on beef quality characteristics of yearling-fed steers harvested at 20 months of age. In their study, steers backgrounded on a moderate-energy pre-finishing diet required only 56 days on a finishing diet to deposit a Small degree of marbling (minimum requirement for the Choice grade).[80]

Only a few studies have compared the tenderness of beef produced by calf-fed and yearling-fed cattle. Results reported by Dikeman et al. (1985) and Brewer et al. (2003) suggest that placing cattle on high-concentrate finishing diets as calves may improve beef tenderness,[87, 89] whereas, Schoonmaker et al. (2002) reported similar shear force values for steaks produced by calf-feds and yearlings.[88]

Studies that have shown differences in beef tenderness between calf-fed and yearling-fed cattle have attributed the tenderness differences to the effects of animal age at harvest. Wulf et al. (1996a) reported a negative relationship between animal age at harvest and tenderness among Limousin steers fed as calves and harvested at ages ranging from 15 to 18 months.[91] In addition, Johnson et al. (1990) reported that calf-fed steers produced loin steaks that received higher panel ratings for tenderness and connective tissue amount than did loin steaks produced by yearling-fed steers and determined that longissimus muscle samples from calf-fed steers also had a higher percentage of heat-soluble (less mature) collagen than did *longissimus* samples from yearling-fed steers.[92] Harris et al. (1997) compared beef tenderness of calf-fed and yearling-fed steers harvested at the same age and found no difference in tenderness due to age at the initiation of the finishing period.[93] Collectively, these results seem to suggest that differences in tenderness, occasionally observed between calf-fed and yearling-fed cattle are associated with maturity differences and their effects on collagen solubility. If that is the case, then chronological age at harvest should be a more effective pre-harvest process control point than the age at which the finishing period is initiated.

Recent studies have investigated the use of early weaning as a herd-management strategy, particularly when feed resources for lactating cows are limited. Early weaning programs typically involve removing calves from cows when the calves are approximately 100 days old; conventional weaning normally occurs at approximately 200 days of age. In some cases, early-weaned calves are placed directly on high-concentrate diets and are finished at even younger ages than those of conventional calf-feds. Results of studies that have compared the effects of early weaning vs. normal weaning on carcass traits and beef tenderness, suggest that early weaning has little effect on either marbling score[94, 95] or tenderness.[88, 96, 97]

Dietary Supplementation to Enhance Beef Tenderness. Recent studies of the effects of pre-harvest diet on beef tenderness have focused on supplementation of the finishing diet to enhance tenderness via nutritional modification of muscle calcium levels. Interest in this area of research is based on the premise that pre-harvest elevation of intracellular muscle calcium levels may enhance activity of the calcium-dependent proteases (μ-calpain and m-calpain), thereby increasing the rate and extent of tenderization due to muscle proteolysis during the early postmortem period.

Research conducted at Iowa State University in the late 1990s demonstrated that treatment of cattle with oral boluses containing vitamin D_3 (daily dosages of 5 or 7.5 million IU/hd,

administered for 8 days prior to harvest) increased plasma calcium levels and significantly improved beef tenderness.[98] In subsequent studies, researchers at Oklahoma State University were able to produce similar results by feeding high levels of vitamin D_3 (daily dosages of 5 to 7.5 million IU/hd) in cattle finishing diets for the last 7 to 10 days before harvest.[99] Additional investigations involving the use of dietary supplementation of vitamin D_3 to enhance beef tenderness have documented that vitamin D_3 supplementation increases calcium levels in blood[100, 101] and muscle tissue;[102] however, a concomitant increase in activity of the calcium-dependent proteases has not been demonstrated. Montgomery et al. (2002) reported that supplementation of vitamin D_3 at dietary levels ranging from 0.5 million to 7.5 million IU/hd daily for 9 days before harvest had no effect on activities of calpain or calpastatin.[102] In addition, Swanek et al. (1999) reported that feeding vitamin D_3 at a level of 7.5 million IU/hd daily for 8 days reduced activities of both μ-calpain and calpastatin, and had no effect on activity of m-calpain.[99] Furthermore, the effects of vitamin D_3 supplementation on tenderness have been inconsistent. Seven different studies reporting Warner-Bratzler shear force values for steaks produced by control vs. vitamin D_3 supplemented cattle (receiving daily dosages ranging from 0.5 to 7.5 million IU/hd, for periods of 2 to 10 days before harvest) were reviewed. Collectively, these seven studies reported a total of 116 direct comparisons of shear force for control vs. vitamin D_3 beef, representing several different muscles and a variety of postmortem aging times. Of the 116 comparisons between control and vitamin D_3 beef, only 24 comparisons showed significant improvement in shear force with vitamin D_3 supplementation.[99, 100, 101, 102, 103, 104, 105]

Even if vitamin D_3 supplementation produced more consistent results with respect to improving beef tenderness, there are concerns associated with feeding cattle high doses of vitamin D_3. Feeding high levels of vitamin D_3 to cattle, even for a brief time period, can result in vitamin D toxicity, which is characterized by weight loss, loss of appetite, and decreased feed intake. Scanga et al. (2001) reported that after just two days of supplementation, cattle receiving more than 1 million IU/day of vitamin D_3 exhibited reduced feed consumption.100 Karges et al. (2001) also observed lower feed intake for cattle fed 6 million IU of vitamin D_3/day for 4 or 6 days[101] and Montgomery et al. (2002) reported significant weight losses for cattle fed 5 or 7.5 million IU vitamin D3 /day for 9 days.[102]

Additionally, supplementing cattle finishing diets with high levels of vitamin D_3 substantially increases residue levels of vitamin D_3 and its metabolites, 25-hydroxyvitamin D_3 and ^{1,25} dihydroxyvitamin D_3, in various edible tissues including skeletal muscle, liver, and kidney. Montgomery et al. (2000) reported that daily doses of 5 million and 7.5 million IU of vitamin D_3 fed to cattle during the final 10 days of the finishing period increased the concentration of vitamin D_3 in the liver by 71- and 114-fold, respectively, and increased vitamin D_3 concentrations in top round steaks, strip loin steaks, and kidney tissue by approximately 24-fold.[103] The Food and Nutrition Board of the National Academy of Sciences has established a Tolerable Upper Intake Level (UL) for vitamin D_3 of 50 μg/day (for children 1 to 18 years old and adults ≥18 years old).[106] Based on vitamin D_3 residue levels reported by Montgomery et al. (2000), a person would exceed the UL for daily vitamin D_3 intake if they consumed more than about 625 g of beef or approximately 80 g of liver from cattle supplemented with high levels of vitamin D_3.

Montgomery et al. (2002) advocated reducing the daily dose of vitamin D_3 to 0.5 million IU/hd to avoid residue problems in muscle and liver, whereas Foote et al. (2004) fed 25-hydroxyvitamin D_3, rather than vitamin D_3, to produce beef with substantially lower residues of vitamin D_3. Both approaches seemed to reduce concentrations of vitamin D_3 in muscle and liver. Improvements in tenderness were observed in 4 of 8 comparisons involving cattle fed 0.5 million IU of vitamin D_3/day,[102] whereas feeding 25-hydroxyvitamin D_3 seemed to increase postmortem proteolysis but did not ($P > 0.05$) improve tenderness.[105]

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Alternative nutritional approaches for improving beef tenderness by increasing pre-harvest muscle calcium levels have been explored. Studies in dairy cows have shown that plasma calcium levels are increased by oral administration of large doses of soluble calcium or by feeding anionic diets, leading researchers to test similar approaches in finishing cattle. Hanson et al. (2002) administered 150 g of calcium to beef steers 35 to 125 minutes before harvest by drenching the cattle with solutions of calcium chloride or calcium propionate. Results of their study showed that calcium chloride tended to increase serum (but not muscle) calcium level, whereas calcium propionate tended to increase *longissimus* muscle (but not serum) calcium concentration; however, neither treatment significantly affected tenderness.[107] Spears et al. (2002) investigated the addition of 4% calcium propionate (to increase soluble calcium availability) or 2% NH4Cl (to create a negative dietary cation-anion balance) to cattle finishing diets for a period of 7 days before harvest. Plasma calcium levels were slightly higher in steers fed calcium propionate, but were not influenced by feeding the anionic diet. However, both treatments reduced dry matter intake and average daily gain. Neither *longissimus* muscle calcium concentrations nor Warner-Bratzler shear force values were affected by feeding calcium propionate or the anionic diet.[108]

In a recent pilot study conducted at Colorado State University, Machado et al. (2003) fed steers an anionic diet for the final 14 days of finishing before harvest. In their study, cattle finishing diets were supplemented with a modified form of BioChlor™, a product manufactured by Biovance Technologies, Inc., which is used specifically for the formulation of anionic diets for dairy cattle. Compared with negative controls, cattle fed the anionic diet (containing BioChlor™) produced strip loin steaks with significantly lower shear force values. Moreover, in this trail, feed intake and average daily gain were unaffected by diet.[109]

Although the prospect of enhancing beef tenderness via dietary supplementation is appealing to cattle producers, experimental trials conducted thus far have demonstrated only limited success. Of those tested, the approach that seems most promising for eventual commercial application, if proven to be effective, is the feeding of pre-harvest diets with a negative cation-anion balance. Further research is planned to validate the positive results observed in the preliminary trial conducted by Machado et al. (2003).

Effects of Hormonal Implants and Other Growth Modifiers

Hormonal Implants. Beef production systems in the U.S. typically involve the use of hormonal implants during one or more phases of production prior to harvest. Implants, used commercially for growing and finishing cattle, significantly increase rate and efficiency of live weight gain, primarily by increasing protein accretion. Commercial cow-calf producers, particularly those who market their calf-crops as weaned feeder steers and heifers, frequently administer implants to calves during the suckling period to increase weaning weights. Moreover, most stocker cattle are implanted at the beginning of the growing period to improve weight gains, and nearly all feedlot cattle receive one or more implants during finishing to enhance feedlot performance. The number of implants administered during finishing depends upon the duration of the finishing period. Cattle fed fewer than 130 days typically receive only one finishing implant, whereas cattle fed for 130 days or more often receive two implants. Lightweight calves, fed for 230 days or more, could receive up to three implants during finishing.[110] From birth to harvest, cattle may receive as many as 6 or more total implants,[111] though 2 to 4 lifetime implants would be most common. While nearly all cattle in mainstream production channels receive some number of implants, there are increasing numbers of cattle produced for specific branded beef programs that never receive implants. A growing number of "all natural" beef programs (e.g., B3R Country Meats, Laura's Lean Beef, Coleman Natural Beef, Country Natural Beef, Maverick Ranch Natural Meats, Nolan Ryan's

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Tender Aged Beef, and others) specify that hormonal implants will not be used at all or, in some cases, will not be used within 100 days of harvest.[27]

A number of different implant products are commercially available for use in cattle. The active ingredients approved for use in cattle implants are steroid hormones, broadly classified either as estrogens (estrogen-like activity) or androgens (testosterone-like activity). Specific active ingredients contained in cattle implants include three estrogens: estradiol 17-βB, estradiol benzoate, and zeranol; and two androgens: testosterone propionate and trenbolone acetate. In addition, some implants contain progesterone. Implants differ considerably with respect to potency of anabolic activity, due to variation in dosages of their respective active ingredients. Low-dose estrogenic implants tend to have the mildest anabolic effects, whereas high-dose, combination implants (i.e., those containing both estrogen and androgen) are the most potent in terms of anabolic activity. As a general rule, low-potency implant products are used in lightweight suckling calves and stocker cattle, whereas moderate- and high-potency products are used more frequently during finishing. If more than one implant is administered during finishing, the initial implant is usually a low- to moderate-potency implant, while the terminal implant may be low-, moderate-, or high-potency, depending upon performance goals and market specifications. Because high-potency implants can decrease marbling, feeders who are trying to maximize quality grade performance for high-quality beef markets normally use low- to moderate-potency terminal implants, whereas feeders who are more interested in maximizing growth performance and yield, normally will use terminal implants with relatively high potency. Table 1 on the following page characterizes the most commonly used cattle implant products.

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Table 1. Most Commonly Used Implant Products in U.S. Beef Production Systems Implant product (trade name)	Active ingredients	Implant classification	Relative potency	Phase of production[a]	Class of cattle
Component E-C [b]	10 mg estradiol benzoate, 100 mg progesterone	Estrogen	Low	C, S	Steers, Heifers
Component E-S [b]	20 mg estradiol benzoate, 200 mg progesterone	Estrogen	Moderate	S, F	Steers
Component E-H [b]	20 mg estradiol benzoate, 200 mg testosterone propionate	Combination	Moderate	S, F	Heifers
Component T-S [b]	140 mg trenbolone acetate	Androgen	Moderate	F	Steers
Component T-H [b]	200 mg trenbolone actetate	Androgen	Moderate	F	Heifers
Component TE-IS [b]	80 mg trenbolone acetate, 16 mg estradiol 17-β	Combination	Moderate	F	Steers
Component TE-S [b]	120 mg trenbolone acetate, 24 mg estradiol 17-β	Combination	High	F	Steers
Component TE-IH [b]	80 mg trenbolone acetate, 8 mg estradiol 17-β	Combination	Moderate	F	Heifers
Component TE-H [b]	140 mg trenbolone acetate, 14 mg estradiol 17-β	Combination	High	F	Heifers
Component TE-200 [b]	200 mg trenbolone acetate, 20 mg estradiol 17-β	Combination	Very High	F	Steers
Component TE-G [b]	40 mg trenbolone acetate, 8 mg estradiol 17-β	Combination	Low	S	Steers, Heifers
Compudose [b]	25.7 mg estradiol 17-β	Estrogen	Low	C, S, F	Steers, Heifers
Encore [b]	43.7 mg estradiol 17-β	Estrogen	Low	C, S. F	Steers, Heifers
Finaplix-H [d]	200 mg trenbolone acetate	Androgen	Moderate	F	Heifers
Ralgro [c]	34 mg zeranol	Estrogen	Low	C, S, F	Steers, Heifers
Ralgro Magnum [c]	72 mg zeranol	Estrogen	Moderate	F	Steers
Revalor-G [d]	40 mg trenbolone acetate, 8 mg estradiol 17-β	Combination	Low	S	Steers, Heifers
Revalor-IS [d]	80 mg trenbolone acetate, 16 mg estradiol 17-β	Combination	Moderate	F	Steers
Revalor-S [d]	120 mg trenbolone acetate, 24 mg estradiol 17-β	Combination	High	F	Steers
Revalor-IH [d]	80 mg trenbolone acetate, 8 mg estradiol 17-β	Combination	Moderate	F	Heifers
Revalor-H [d]	140 mg trenbolone acetate, 14 mg estradiol 17-β	Combination	High	F	Heifers
Revalor-200 d	200 mg trenbolone acetate, 20 mg estradiol 17-☐	Combination	Very High	F	Steers
Synovex-C e	10 mg estradiol benzoate, 100 mg progesterone	Estrogen	Low	C, S	Steers, Heifers
Synovex-S e	20 mg estradiol benzoate, 200 mg progesterone	Estrogen	Moderate	S, F	Steers
Synovex-H e	20 mg estradiol benzoate, 200 mg testosterone propionate	Combination	Moderate	S, F	Heifers
Synovex-Choice e	100 mg trenbolone actetate, 14 mg estradiol benzoate	Combination	Moderate	F	Steers and Heifers
Synovex-Plus e	200 mg trenbolone acetate, 28 mg estradiol benzoate	Combination	Very High	F	Steers and Heifers

[a] C = calfhood (suckling period); S = stocker (growing period); F = feedlot (finishing period).
[b] Vetlife, Overland Park, KS.
[c] Schering Plough Animal Health, Union, NJ.
[d] Intervet, Inc., Middlesboro, DE.
[e] Fort Dodge Animal Health, Overland Park, KS.

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The use of anabolic implants represents a highly cost-effective means of improving growth performance of growing and finishing cattle. However, many in the beef industry have become concerned that too frequent use of implants and (or) use of newer-generation, high-potency implant products are detrimental to beef quality. Research conducted to examine the effects of steroidal implants on beef quality characteristics suggests that use of improperly designed implant programs can result in reduced marbling scores, increased carcass maturity, an increase in the incidence of dark cutting beef carcasses, and decreased beef tenderness.[112]

Numerous studies have documented that, in general, implanted cattle have lower marbling scores than do non-implanted cattle; however, not all implant programs significantly reduce marbling.[113, 114] Implant programs that cause the least reduction in marbling typically involve either the use of a single finishing implant[115, 116, 117] or the use of successive implants with relatively low potencies.[118, 119, 120] Morgan (1997), following a review of several studies involving a variety of different implant programs, concluded that marbling is influenced by both the number and the potency of implants administered during finishing and that implant programs which involve the use of high-potency implants, administered multiple times, tend to produce the greatest reductions in marbling.[121] Additionally, Foutz et al. (1990) suggested that the detrimental effects of implants on marbling are most pronounced if a high-potency, terminal implant is administered late in the finishing period (i.e., too near the date of harvest).[122] Correspondingly, implant programs that are designed to minimize reductions in marbling score typically specify that terminal implants be administered 70 to 120 days before the projected harvest date.[110]

Results of recent studies suggest that timing of the initial finishing implant may be as important as the timing of the terminal implant in the design of implant programs for finishing cattle targeted for high-quality beef markets. Bruns et al. (2001) determined that implants administered early in the finishing period tended to decrease the rate of intramuscular fat deposition and suggested that delaying administration of the initial finishing implant could help mitigate the detrimental effects of implants on marbling.[123] Studies that have evaluated delayed implant programs support the practice of delayed administration of the initial finishing implant as an effective strategy for maintaining carcass quality grade performance.[124]

Platter et al. (2003b), in a study of lifetime implant effects on beef quality, determined that implants administered at branding (during the suckling period) or at weaning (at the beginning of the growing period) did not affect marbling scores in steers subsequently harvested after finishing. However, in their study, the cumulative number of implants administered during an animal's lifetime had a significant effect on marbling. Steers receiving either 4 or 5 lifetime implants produced carcasses with lower marbling scores than did steers receiving only 2 finishing implants.[125]

Information concerning the effects of implants on carcass indicators of physiological maturity is limited. However, studies that have reported data comparing carcass maturity characteristics for implanted vs. non-implanted cattle suggest that carcasses produced by implanted cattle tend to have more advanced skeletal maturity characteristics.[121, 126, 127] Reiling and Johnson (2003) reported that carcasses from implanted steers not only were assigned more advanced skeletal maturity scores, but also had higher ash content of the 9th-11th thoracic cartilaginous buttons (an objective measure of skeletal ossification) than did carcasses produced by non-implanted control steers.[104] Research comparing the effects of type of implant on carcass maturity suggests that implants containing only estrogens[128, 129] or combination implants containing both estrogen and androgen[115, 126] tend to increase skeletal maturity among cattle harvested at similar ages, whereas implants containing only androgens do not seem to affect carcass maturity.[115, 130] As is the case with marbling, skeletal maturity seems to be influenced by both the number[131] and potency[104, 126] of implants administered during finishing.

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The cumulative effect of multiple estrogenic implants administered throughout an animal's lifetime also seems to increase the rate of skeletal maturation. Pritchard et al. (2003) administered implants to steers at 2 months of age, at weaning, at feedlot entry, and after 70 days of finishing, so that steers in each implant treatment group received a total of four lifetime implants. Estrogenic, androgenic, and combination implants differing in potency were used to create three different implant programs described by the authors as low-potency (Ralgro, 3X; Ralgro Magnum, 1X), intermediate-potency (Ralgro, 3X; Ralgro Magnum + Component T-S, 1X), and high-potency (Synovex-C, Revalor-G, Synovex-S, Revalor-S). In that study, all three lifetime implant programs increased carcass skeletal maturity, compared with a non-implanted control, regardless of potency. [120] In another study of lifetime implant effects, Platter et al. (2003) found that implanting steers at branding (approximately 60 to 100 days old) with a low-potency estrogenic implant (Synovex-C) caused a small, but significant increase in carcass maturity when the steers were later harvested at 16 to 18 months of age. In addition, Platter et al. (2003b) reported that steers receiving 4 or 5 lifetime implants had more advanced carcass maturity characteristics than did steers receiving 0, 2 or 3 lifetime implants.[125]

Among cattle harvested prior to 18 months of age, implant effects on carcass maturity usually are inconsequential, because carcasses produced by implanted cattle less than 18 months old normally would be classified as A-maturity. However, when cattle are implanted multiple times and harvested at ages of 20 months or older (which would be common for backgrounded cattle fed as long-yearlings), implant effects on carcass maturity can result in severe carcass price discounts due to an increase in the incidence of B-maturity, or older carcasses. Paisley et al. (1999) examined the effects of four winter-grazing implant treatments on carcass maturity characteristics of fall-weaned steer calves grazed through the winter and summer seasons, placed on a finishing diet as long-yearlings (16 to 18 months old), and harvested at 20 to 22 months of age. The steers all received a Synovex-C suckling implant at ages of 2 to 4 months. At ages of 7 to 9 months one of four winter-grazing implant treatments were administered – 1) no implant (control), 2) Synovex-C, 3) Synovex-S, or 4) Revalor-G. All steers then received a Ralgro summer-grazing implant at ages of 12 to 14 months followed by a single Revalor-S finishing implant at ages 16 to 18 months. In their study, all three winter-grazing implant treatments resulted in more advanced skeletal maturity characteristics compared with the non-implanted control group. In addition, estrogenic implants administered during the winter-grazing period tended to result in more advanced skeletal maturity characteristics than did the combination winter-grazing implant, supporting the premise that estrogens tend to have a greater effect on carcass maturity than do androgens. Percentages of B-maturity or older carcasses for the four treatment groups were: 9.5% for control steers, 33.3% for Synovex-C, 26.8% for Synovex-S, and 20.9% for Revalor-G.[132] These results clearly demonstrate the carcass maturity problems that can occur when multiple implants containing estrogens are administered to cattle that are backgrounded on forages for extended periods, finished as long-yearlings, and harvested at relatively advanced ages.

Though anabolic implants do not cause dark cutting beef, the use of certain implant schemes seem to be associated with more frequent occurrence of the dark cutting condition.[121] Because the dark cutting condition occurs relatively infrequently among fed steers and heifers (2.3% according to the most recent National Beef Quality Audit[133]), implant effects on the incidence of dark cutting beef carcasses are difficult to ascertain unless large numbers of cattle are studied.

Scanga et al. (1998) analyzed a large database, consisting of records for 15,439 pens of cattle, to examine the effects of implants on the incidence of dark cutting beef carcasses. Pen records collected over a three-year period were obtained from nine commercial feedyards and represented a sample of over 2.6 million commercially finished steers and

heifers. For steers, the lowest incidence of dark cutters occurred when the finishing implant program consisted of an implant/re-implant sequence of estrogen/estrogen or estrogen/combination, whereas the incidence of dark cutters was highest when a combination/combination sequence was used. For heifers, the lowest incidence of dark cutters occurred when only androgenic implants were used during the finishing period and the highest incidence of dark cutters occurred when an implant/re-implant sequence of androgen/estrogen was used. Moreover, the occurrence of the dark cutting condition was reduced, for both steers and heifers, when terminal implants were administered 100 days or more from the harvest date.[134]

While the effects of hormonal implants on growth performance and carcass grade traits have been reasonably well characterized, comparatively few studies have examined the effects of implants on beef tenderness. Of the studies that have investigated implant effects on tenderness, nearly all report data for the longissimus muscle and most include measurements of Warner-Bratzler shear force (WBS). Correspondingly, data from available reports that included WBS measurements of longissimus samples from both implanted and non-implanted (control) steers or heifers were compiled to review existing information on implants and tenderness. Results from nineteen different trials, examining an array of different implant programs and their effects on WBS, are summarized in tabular form on the following pages (Table 2). Data presented in Table 2 show the change in WBS due to the implant effect (mean of implanted group – mean of non-implanted control group) for each treatment vs. control comparison. Positive values for change in WBS (i.e., increased shear force compared with control) reflect a decrease in tenderness, whereas negative values (i.e., decreased shear force compared with control) reflect an increase in tenderness.

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Table 2. Implant Effects on Warner-Bratzler Shear Force of the *Longissimus*

Study		N	Sex class	Suckling implants	Growing implants	Finishing implants	Change in WBS, kg (implanted – control)	Implant effect
Apple et al. (1991), JAS 69:4437	1 2 3 4	72	Steers	NI NI NI NI	NI NI NI NI	RA (4X) SS (4X) SS+FS (4X) RA+FS (4X)	0 -0.08 +0.29 +0.34	NS NS NS NS
Barham et al. (2003) JAS 81:3052	1 2	2,748	Steers	NI NI	NI NI	SS_1 /SS_2 SS_1 /RS_2	+0.13 +0.07	NS NS
Calkins et al. (1986), JAS 62:625	1 2	24	Steers	RA CD (9 wk)	RA (2X) CD (8 mo)	RA (2X) --	+0.15 +0.17	NS NS
Foutz et al. (1997), JAS 75:1256	1 2 3 4	140	Steers	NI NI NI NI	CD NI NI NI	SS_1 RS_1 SS+FS_1 SS+FS_1 /FS_2	+0.43 +0.32 +0.12 +0.41	C < I C < I NS C < I
Gerken et al. (1995), JAS 73:3317	1 2	24	Steers	NI NI	NI NI	SS_1 RS_1	+0.58 +0.67	NS NS
Huck et al. (1991), JAS 69(S1):560	1 2 3 4	80		NI NI NI NI	NI NI NI NI	SS_1 /SS_2 SS_1 /SS+FS_2 SS+FS_1 /SS_2 SS+FS_1 /SS+FS_2	+0.22 +0.22 +0.45 +0.04	NS NS NS NS
Hunt et al. (1991), JAS 69: 2452	1	30	Steers	NI	NI	CD+F- 120_1	-0.20	NS
Platter et al. (2003), JAS 81:984	1 2 3 4 5 6 7 8 9 10	550	Steers	NI NI NI SC NI SC SC SC SC SC	NI RA SS SS RA_1 /SS_2 RA SS RA_1 /RA_2 RA_1 /SS_2 RA_1 /SS2	SS_1 /RS_2 SS_1 /RS_2 SS_1 /RS_2 NI_1 /RS_2 SS_1 /RS_2 SS_1 /RS_2 SS_1 /RS_2 SS_1 /RS_2 SS_1 /RS_2 RS_1 /RS_2	+0.41 +0.92 +0.65 +0.65 +0.61 +0.58 +0.51 +0.51 +0.60 +0.84	C < I C < I C < I C < I C < I C < I C < I C < I C < I C < I
Pritchard et al. (2000), JAS(S1) 78:195	1 2 3	310	Steers	RA RA SC	RA RA RG	MG_1 MG+TS_1 SS_1 / RS_2	-0.18 +0.04 +0.13	NS NS NS
Reiling & Johson (2003), JAS 81:135	1 2	123	Steers	NI NI	NI NI	RA_1 /RS_2 RS_1 /RS_2	+0.22 +0.52	NS C < I
Roeber et al. (2000), JAS 78:1867	1 2 3 4 5 6 7	298	Steers	NI NI NI NI NI NI NI	NI NI NI NI NI NI NI	EN+TS_1 /NI_2 RA_1 /SP_2 RA_1 /RS_2 RS_1 /RS_2 RS_1 /NI_2 NI_1 /SP_2 SP_1 /NI_2	+0.21 +0.44 +0.34 +0.31 +0.54 +0.45 +0.32	NS NS NS NS C < I NS NS
Rumsey et al. (1999), JAS 77:1726	1	58	Steers	NI	NI	SS_1	+0.95	C < I

Table 2 cont'd on next page

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Study		N	Sex class	Suckling implants	Growing implants	Finishing implants	Change in WBS, kg (implanted – control)	Implant effect
Samber et al. (1996), JAS 74:1470	1 2 3 4 5 6	560	Steers	NI NI NI NI NI NI	NI NI NI NI NI NI	RA_1/SS_2 $/RS_3$ RA_1/RS_2 $/RS_3$ $DI/SS_1/RS_2$ $DI/RS_1/RS_2$ RS (3X)-LP RS (3X)-HP	+0.16 +0.17 +0.06 +0.43 +0.34 +0.28	NS NS NS C < I C < I C < I
Scheffler et al. (2003), JAS 81:2395	1 2 3	128	Steers	NI NI NI	NI NI NI	$NI_1/NI_2/RS_3$ NI_1/RS_2 $/RS_3$ RS_1/RS_2 $/RS_3$	+0.1 +0.3 +0.5	NS NS C < I
Tipton et al. (2002), TAES Report, 2002 Beef Cattle Research in Texas, Texas A&M University	1 2 3 4 5 6	239	Steers	NI NI NI NI NI NI	NI NI NI NI NI NI	SS_1/SS_2 SS_1/RS_2 SS_1/SP_2 SP_1/NI_2 CD_1/NI_2 RS_1/NI_2	+0.46 +0.29 +0.97 +0.80 +0.23 +0.45	NS NS C < I C < I NS NS
Milton and Horton (1996), Revalor-IS Tech. Bull. Ref. 1, Intervet, Inc.	1 2 3 4	193	Steers	NI NI NI NI	NI NI NI NI	NI_1/RS_2 RG_1/RS_2 RIS_1/RS_2 SS_1/RS_2	+0.13 +0.11 +0.13 +0.18	NS NS NS NS
Crouse et al. (1987), JAS 64:1434	1	58	Heifers Spayed Heifers	NI NI	Ni NI	FH_1 FH_1	-0.05 -0.54	NS NS
Kerth et al. (2003), JAS 81:1728	1 2 3 4 5	96	Heifers	NI NI NI NI NI	NI NI NI NI NI	NI_1/RH_2 RH_1/NI_2 RH_1/RH_2 RIH_1/RH_2 SH_1/RH_2	+0.05 -0.56 -0.31 -0.15 -0.10	NS NS I < C NS NS
Nichols et al. (1996), Revalor-H Tech. Bull. 3, Hoechst-Roussel Agri-Vet.	1 2 3 4	600	Heifers	NI NI NI NI	NI NI NI NI	MGA FH_1+MGA RH_1 RH_1+MGA	+0.09 +0.08 +0.23 +0.26	NS NS C < I C < I

[a] Acronyms used: CD (Compudose 200), DI (delayed implant; initial implant at 30 days on feed), FH (Finaplix-H), FS (Finaplix-S, 140 mg trenbolone acetate), F-120 (Finaplix-120, 120 mg trenbolone acetate), HP (14.5% crude protein in finishing diet), LP (12.5% crude protein in finishing diet), MG (Ralgro Magnum), MGA (Melegestrol Acetate, Pharmacia and Upjohn Co., fed in finishing diet), NI (no implant administered), RA (Ralgro), RG (Revalor-G), RH (Revalor-H), RIH (Revalor-IH), RIS (Revalor-IS), RS (Revalor-S), SC (Synovex-S), SH (Synovex-H), SP (Synovex-Plus), SS (Synovex-S), TS (Component T-S). Subscript numbers denote order implants were administered; 1 = initial implant, 2 = first re-implant, 3 = second re-implant.

[b] NS = not significant ($P > .05$); C < I = WBS for control is lower ($P < .05$) than WBS for implant treatment; I < C = WBS for implant treatment is lower ($P < .05$) than WBS for control.

Sixteen studies comparing WBS values for implanted vs. non-implanted steers were reviewed. Collectively, these studies involved 61 direct WBS comparisons between implanted and non-implanted steers. Of the 61 comparisons (Table 2), 22 comparisons (36%) showed a significant increase in WBS (indicative of increased toughness), 39 (64%) showed no change in WBS, and none showed a significant decrease in WBS. Of the 22 comparisons that showed an increase in WBS for implanted vs. non-implanted steers, all but 2 involved the use of relatively high-potency combination (estrogen + androgen) implant treatments. Further examination of the tabular data for steers revealed the following patterns: a) When steers received only estrogenic implants, either once or multiple times, 2 of 12 comparisons (17%) showed a significant reduction in tenderness, measured by WBS; b) when steers were implanted either once or multiple times, but only one time with the combination of estrogen plus androgen, 13 of 37 comparisons

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(35%) showed a significant reduction in tenderness; and c) when steers were implanted two or more times with the combination of estrogen plus androgen, 7 of 12 comparisons (58%) showed a significant reduction in tenderness. Data presented in Table 2 suggest that, implant programs for steers that involve the use of relatively high-potency, combination implants may result in reduced beef tenderness, particularly when implants containing both estrogen and androgen are used repetitively.

Only three studies comparing WBS values for implanted vs. non-implanted heifers were identified and reviewed. Collectively, these studies involved 11 direct WBS comparisons between implanted and non-implanted heifers. Of the 11 comparisons for heifers (Table 2), 2 comparisons (18%) showed a significant increase in WBS, 8 (73%) showed no change in WBS, and 1 (9%) showed a significant decrease in WBS, associated with the use of implants. These data seem to suggest that, among heifers, anabolic implants have little or no effect on tenderness. However, existing information is simply too limited to support any valid inferences concerning the effects of heifer implant programs on tenderness.

An important question is whether or not implant-induced reductions in tenderness are of sufficient magnitude to affect consumer satisfaction. Only a few studies have examined the effects of implants on consumer ratings of beef tenderness and overall product performance. The Beef Customer Satisfaction study, a large in-home consumer test conducted by the National Livestock and Meat Board (1995), was one of the first studies to document a relationship between implant history of cattle and consumers' evaluations of product performance. Results of that study showed that implanting with a single implant (either estrogenic, androgenic, or combination) or with an implant/re-implant sequence of estrogen/estrogen or estrogen/combination did not affect consumer ratings for "Overall Like." However, steaks produced by cattle implanted with two successive androgen/androgen or combination/combination implants, during finishing, received lower consumer ratings for "Overall Like."[9]

In a more recent study, Roeber et al. (2000) compared consumer ratings for tenderness of beef from steers either not implanted, or implanted using one of seven different finishing implant strategies. In their study, consumers rated loin steaks from non-implanted steers and steers implanted once with a mild estrogen + androgen combination as significantly more tender than steaks produced by steers receiving one high-potency combination implant, two high-potency combination implants, or one very high-potency combination implant during finishing.[135]

Barham et al. (2003) compared tenderness ratings for steaks produced by 3/8 *Bos indicus*, 5/8 *Bos taurus* steers representing three implant treatment groups: Group 1 – non-implanted steers, Group 2 – steers implanted with two estrogens during finishing, and Group 3 – steers implanted with an estrogen implant and re-implanted with a high-potency combination implant during finishing. Trained sensory panel ratings were lower for samples from implanted cattle (Groups 2 and 3) compared with samples from non-implanted cattle (Group 1); however, consumer ratings for tenderness (scored from 1 to 8: 1 = extremely tough, 8 = extremely tender) did not differ among the three groups.[136] In that study, consumers also were asked to classify the tenderness of each beef sample as either "acceptable" (sample assigned a score of 1) or "unacceptable" (sample assigned a score of 2). Unfortunately, the investigators chose to analyze the resulting binomial data using a least squares model, an inappropriate statistical approach that seems to have led to an erroneous interpretation of their results. The authors reported least squares means and standard errors for "tenderness acceptability" of 1.2 ± 0.05, 1.2 ± 0.05, and 1.8 ± 0.07, for Groups 1, 2, and 3, respectively. Based on a two-point scoring system, where 1 = "acceptable" and 2 = "unacceptable," 80% of the tenderness acceptability ratings for steaks in Groups 1 and 2 would have to be scores of 1 ("acceptable") and 20% would have to be scores of 2 ("unacceptable") to obtain means

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of 1.2 for the two groups. Similarly, to obtain a group mean of 1.8, 20% of tenderness acceptability ratings for steaks in Group 3 would need to be scores of 1 ("acceptable"), and 80% would have to be scores of 2 ("unacceptable"). Frequency differences of this magnitude, if tested using a x^2 analysis, would produce a statistically significant difference between groups with as few as 5 observations per group. Therefore, it appears that, in this study,[136] the proportion of steaks rated as "unacceptable" should be interpreted as being higher for steers in Group 3 (estrogen followed by combination re-implant), than for steers in Groups 1 (non-implanted control) and 2 (estrogen followed by estrogen re-implant).

Platter et al. (2003b) compared consumer acceptability of steaks produced by steers receiving 0, 2, 3, 4, or 5 lifetime implants. All steers that received 2 or more implants received a high-potency combination implant as the terminal finishing implant. Consumers rated steaks from steers receiving no implants as more tender than steaks produced by steers implanted with 2, 3, 4, or 5 lifetime implants, but were unable to detect tenderness differences among steaks produced by steers implanted with 2 to 5 lifetime implants. In addition, implants administered during the pre-finishing period (at branding, weaning or backgrounding) did not affect consumer tenderness ratings, suggesting that the reduction in tenderness detected by consumers was associated with the finishing implant protocol (moderate-potency estrogenic initial implant, followed by a high-potency combination product at re-implant).[125]

In the latter study (Platter et al., 2003_b), consumers were specifically asked if they were satisfied with the overall eating quality of the beef they sampled, and their responses showed that the use of implants significantly reduced consumer satisfaction. Approximately 74% of consumers indicated that they were satisfied with the overall performance of steaks from non-implanted cattle, whereas significantly fewer consumers (64%) indicated that they were satisfied with the performance of steaks from implanted cattle.[125]

Existing information suggests that producers who are interested in reducing the incidence of beef quality problems should avoid the use of overly aggressive implant programs. Implant programs featuring a maximum of two or three lifetime implants, with use of no more than one high-potency combination implant, administered 100 days or more before the anticipated harvest date, seem to be associated with the fewest detrimental effects on carcass quality characteristics and the lowest frequency of unsatisfactory eating experiences among beef consumers.

Feed Additives. Supplementing finishing diets for heifers with melengestrol acetate (MGA) is a common practice in the commercial feeding industry. Melengestrol acetate is an orally active progestin that, when included in the diets of heifers, suppresses estrus and improves growth performance.[137] Dietary supplementation with MGA increases circulating levels of estrogen in heifers, similar to the effect of implanting with a mild estrogenic implant. Correspondingly, MGA is particularly effective for enhancing growth performance of heifers implanted with androgenic implants. Nichols et al. (1996) reported data suggesting that including MGA in diets of feedlot heifers had no effect on WBS or trained sensory panel ratings for tenderness.[138] Heifers supplemented with MGA normally will show signs of estrus within 2 to 7 days of MGA withdrawal. The increased physical activity and stress associated with behavioral estrus in heifers, following MGA withdrawal, can result in a very high incidence of dark cutting carcasses. Consequently, to avoid problems with dark cutters, most feeders do not remove heifers from MGA-supplemented diets more than 24 hours before harvest.

In June 2003, the U.S. Food and Drug Administration approved the use of ractopamine hydrochloride for use in feedlot cattle. Shortly thereafter, Elanco Animal Health introduced Optaflexx (the trade name for ractopamine hydrochloride) – a new cattle feed ingredient

designed to increase live weight gain, improve feed efficiency, and increase carcass yields of lean beef. Ractopamine hydrochloride is a beta-adrenergic agonist and has been marketed under the trade name Paylean for use in swine since 1999.

Optaflexx, is mixed into cattle finishing diets and provided to feedlot steers and heifers during the final 28 to 42 days before harvest. Research trials conducted to provide scientific data for FDA approval of the new feed ingredient showed that Optaflexx, when fed to steers at the recommended dosage of 200 mg/hd/d for the last 28 days of the finishing period, increased average daily gains by approximately 20% and improved feed efficiency (F/G) by almost 16%. In addition, Optaflexx was shown to increase ribeye area and carcass leanness (measured as % protein in the carcass), but did not affect marbling score, quality grade, carcass maturity, lean color, the incidence of "dark cutting" carcasses, or beef tenderness.[139, 140] Elanco Animal Health recently initiated several large feeding trials to provide additional scientific information concerning the effects of Optaflexx on cattle growth performance and beef quality characteristics.

Genetic Inputs and Their Effects on Beef Tenderness
Optimizing cowherd productivity across the broad range of beef production environments in the U.S. requires the use of diverse biological types of cattle that differ with respect to size, milk production, growth and maturing rates, and adaptability to regional differences in feed resources and climatic conditions. The high degree of genetic diversity among and within the various breeds and biological types of cattle currently utilized in U.S. beef production systems, while advantageous from a production standpoint, is a primary source of variation in beef tenderness. Correspondingly, the selective use of breeds and selection of specific genetic lines within breeds, both merit consideration as pre-harvest process control points for managing beef tenderness.

Breed Effects. The most comprehensive comparison of cattle breed differences in carcass and meat quality characteristics is the ongoing Germ Plasm Evaluation (GPE) Program at the U.S. Meat Animal Research Center at Clay Center, Nebraska.[141, 142, 143] Tenderness differences (expressed as mean differences in longissimus shear force) among several cattle breeds evaluated in Cycles IV through VII[144, 145, 146, 147] of the GPE Program are shown in Figure 2.

For the purposes of this review, seventeen breeds, evaluated in the most recent cycles of the GPE Program, were chosen specifically to represent the following categories: a) British breeds – four breeds of British origin (Angus, Hereford, Red Angus and Shorthorn) that collectively account for a very high proportion of the maternal genetics in U.S. commercial beef herds; b) Continental European breeds – five Continental breeds (Charolais, Gelbvieh, Limousin, Salers, and Simmental) used extensively in U.S. crossbreeding systems; c) Tropically adapted breeds – three *Bos indicus* breeds, including the most widely used heat-tolerant breed in the U.S. (Brahman) and two additional Zebu breeds (Boran and Nellore), plus a heat-tolerant, non-Zebu breed (Tuli); and d) Specialty Breeds – two high-muscle breeds (Belgian Blue and Piedmontese), a high-marbling breed (Wagyu), and a Continental European breed (Pinzgauer), which has consistently ranked among the most tender of breed groups in the GPE program. Within each GPE cycle, Hereford-Angus reciprocal crosses have been used as a reference. Correspondingly, shear force data in Figure 2 are presented as mean breed-group deviations from the appropriate H X A reference group (breed-group mean shear force - mean shear force for H X A reference group, calculated on a within-cycle basis) to eliminate Cycle-to-Cycle differences in mean shear force. Age-constant data are presented to reflect breed differences in tenderness among cattle fed and managed alike and harvested at similar ages.

Research has shown that, among the various breeds of cattle commonly used in U.S. production systems, the most pronounced between-breed tenderness differences exist between *Bos indicus* and *Bos taurus* breeds. Cattle of the various *Bos indicus* breeds

consistently have been shown to produce beef that is less tender than beef from *Bos taurus* breeds of cattle.[144, 145] This breed effect on tenderness is clearly reflected in Figure 2. Among all seventeen breeds compared in Figure 2, the three *Bos indicus* breeds ranked highest for mean shear force (i.e., lowest for tenderness). Among the *Bos taurus* breeds, Salers, Belgian Blue, and Gelbvieh ranked highest for shear force (lowest for tenderness), whereas Pinzgauer, Angus, and Wagyu ranked lowest for shear force (highest for tenderness). A number of breeds represented in Figure 2 were similar with respect to tenderness. For the majority of breed comparisons, within-breed variation in tenderness has been shown to be as great or greater than observed variation in tenderness among breeds.[148]

Rankings of the same seventeen breed groups, based on age-constant, mean marbling score deviations from the H X A reference, are shown in Figure 3. The five breeds ranking highest for marbling (in order from highest to lowest) included Red Angus, Shorthorn, Wagyu, Angus, and Pinzgauer. Interestingly, four of these breeds also were among the "top five" breeds with respect to tenderness (Figure 2). The only exception was the Shorthorn breed, which ranked 2nd for marbling and 9th for tenderness. The five breeds ranking lowest for marbling (in order from lowest to highest) were Belgian Blue, Piedmontese, Brahman, Limousin, and Gelbvieh. Of these five breed groups, all but two groups were ranked among the lowest six breeds with respect to tenderness (Figure 2). The two exceptions were the Piedmontese breed, which ranked 16th for marbling, but 4th for tenderness, and the Limousin breed, which ranked 14th for marbling and 6th for tenderness. Across all breeds, breed-group means for marbling score accounted for approximately 26% of the variation in breed-group means for shear force.

Existing evidence suggests that, among cattle fed and managed alike, and harvested at relatively young ages, a significant amount of the explained genetic variation in tenderness can be attributed not only to differences in marbling, but also to differences in post-rigor calpastatin activity.[149] Calpastatin is the inhibitory regulator of the calpains – the calcium-dependent enzymes in muscle tissue that are believed to be responsible muscle proteolysis and the resulting tenderization that occurs naturally in beef during the postmortem aging period. Calpastatin activity in post-rigor muscle influences the rate and extent of muscle proteolysis during aging. Beef produced by cattle that express high calpastatin activity ages more slowly than does beef produced by cattle that express lower activity of calpastatin. As a result, beef from high-calpastatin genotypes is noticeably tougher than beef produced by low-calpastatin genotypes in the early postmortem period, and typically remains tougher throughout most of the aging period (Figure 4).

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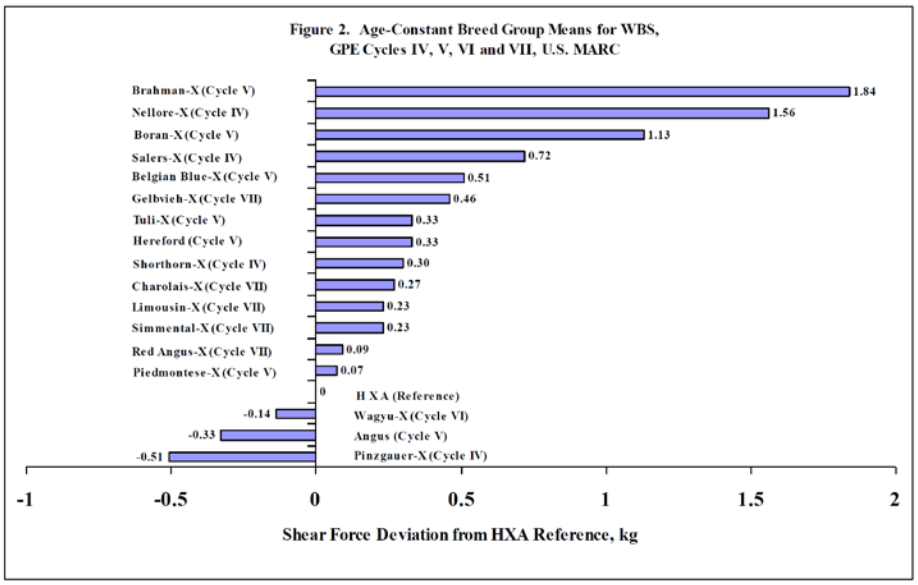

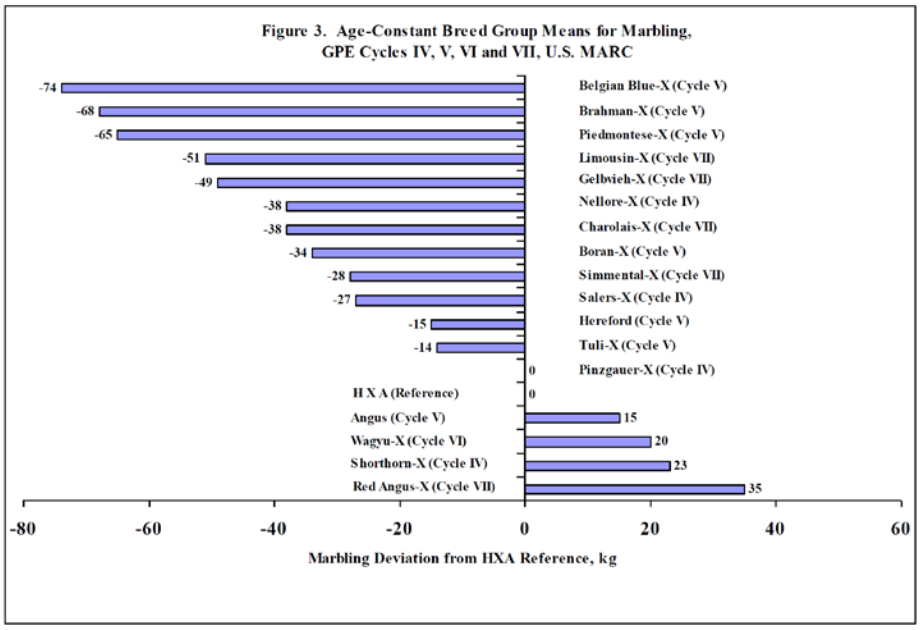

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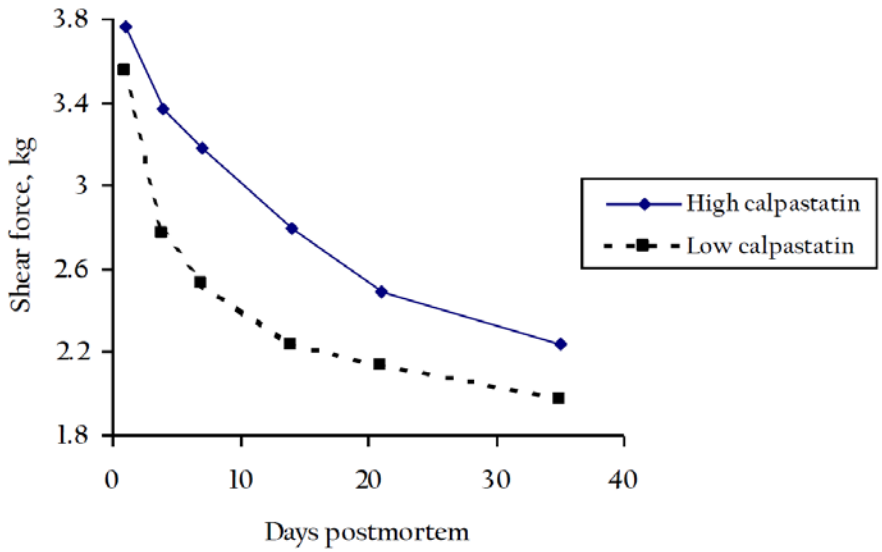
Figure 4. Postmortem Aging Curves for Genotypes with High vs. Low Calpastatin Activities (Source: O'Connor et al., 1997)



Only a limited amount of information concerning between-breed differences in calpastatin activity has been reported. However, it is reasonably well documented that calpastatin activity, measured at 24 hours postmortem, is the primary factor related to beef tenderness differences between *Bos taurus* and *Bos indicus* cattle.[150] In addition, some of the genetic effects on tenderness in *Bos taurus* cattle breeds have been attributed to differences in calpastatin activity.[151] Data presented by Shackelford et al. (1994) suggest that among the *Bos taurus* breeds, Gelbvieh crosses tend to express a relatively high calpastatin activity. In their study, the mean calpastatin activity for Gelbvieh crosses was similar to that expressed by Nellore (*Bos indicus*) crosses.[149] In addition, Shackelford et al. (1994) presented data suggesting that calpastatin activity for the Limousin breed was lower than calpastatin activities for several other Continental breeds (Charolais, Gelbvieh, Pinzgauer). Wulf et al. (1996b) reported data showing that Limousin-sired steers and heifers had lower longissimus calpastatin activities than did Charolais-sired steers and heifers,[151] and O'Connor et al. (1997) reported that the Simmental breed effect in *Bos indicus* and *Bos taurus* composites was associated with comparatively low calpastatin activities.[152] These between-breed differences in calpastatin activity are based on limited data and should not be interpreted as conclusive evidence of specific breed effects on calpastatin activity; however they do seem to explain the relative rankings of the Gelbvieh, Limousin, and Simmental breeds for shear force in Figure 2.

A unique breed, with respect to its carcass and meat quality traits, is the Piedmontese. Piedmontese cattle have been selected specifically to exhibit a phenotype characterized by extreme muscle hypertrophy (i.e., "double-muscling"). It is now known that double muscling in cattle results from inactivation of the myostatin gene (for review, see Arnold et al., 2001).[153] Myostatin, is a negative regulator of muscle cell growth that controls the number of muscle cells in the developing embryo. A mutation at the "mh" gene locus inactivates the myostatin gene, causing the developing animal to produce a higher-than-normal number of muscle cells. It is the increased number of muscle cells (hyperplasia) that causes animals to express the double-

muscled phenotype. Genotypes that have two active alleles (+/+) at the mh gene locus exhibit a normal phenotype, those with only one active allele (mh/+) are heavy-muscled, and those with two inactive alleles (mh/mh) exhibit extreme muscle hypertrophy. Due to their history of within-breed selection for double muscling, the Piedmontese and Belgian Blue breeds both have a high intra-population frequency of the inactive mh gene. Studies consistently have shown that Piedmontese crosses produce tender beef despite their tendency to have relatively low marbling levels.[144, 145, 154] In some studies, the Belgian Blue breed also has been shown to produce relatively tender beef; however, existing evidence seems to suggest that beef produced by Belgian Blue crosses is not as tender as beef from Piedmontese crosses.[155]

The relative tenderness of beef produced by double muscled cattle has been attributed to its lower connective tissue (collagen) content compared with that of beef from normal cattle.[156,157] Wheeler et al. (2001) compared tenderness of myostatin genotypes (+/+, mh/+, and mh/mh) differing in Piedmontese inheritance (0, 25, 50, or 75% Piedmontese) and determined that mh/+ and mh/mh genotypes produced *longissimus, gluteus medius, biceps femoris*, and *semimembranosus* muscles that were more tender than corresponding muscles from +/+ genotypes. A significant result of their study was the finding that round and sirloin muscles (muscles with inherently high amounts of connective tissue) from mh/mh (double muscled) genotypes were similar in tenderness to *longissimus* muscle (a muscle with a relatively low amount of connective tissue) from +/+ (normal) genotypes.[158]

Heritability of Tenderness and Potential for Within-Breed Improvement. The recent Carcass Merit Traits project (sponsored by NCBA and several U.S. cattle breed associations), evaluated tenderness of approximately 7,200 progeny of several sires representing each of 14 different breeds. Results of that study documented wide ranges in sire-group means for shear force, both among and within breeds. The range for sire-group shear force means, calculated within breeds, ranged from a low of 0.77 kg in the breed with the least among-sire variation to a high of 2.99 kg in the breed with the greatest variability among sires.[159] These findings imply that there may be considerable potential for improving beef tenderness within breeds by identification and selection of “tender” vs. “tough” sires.

Genetic parameter estimates for shear force from a number of different studies are presented in Table 3. Heritability estimates for shear force, summarized in Table 3, suggest that tenderness is moderately heritable in *Bos taurus* and *Bos taurus* X *Bos indicus* cattle populations,[144, 145, 149, 151, 152, 160] but only lowly heritable in pure strains of Brahman cattle.[161, 162] These estimates imply that within-breed selection for low shear force (i.e., increased tenderness) could be effective for improving beef tenderness in most cattle breeds; however expected genetic progress would be relatively slow, especially in the Brahman breed.

Seedstock and commercial cattle breeders currently rely on traditional methods, such as progeny testing, to obtain beef tenderness information for selection purposes. The time and expense required to change tenderness via traditional selection methods have been major impediments to genetic improvement of beef tenderness. As a result, many cattlemen have emphasized selection for alternative traits that are related to differences in tenderness, such as marbling and (or) percentage of intramuscular fat in the longissimus (% IMF). Marbling can be measured in progeny groups, with greater ease and less expense compared with tenderness measurements such as shear force, and % IMF can be measured ultrasonically in the breeding animals themselves or in their progeny.

Marbling has been shown to be a moderately heritable to highly heritable trait in most experimental cattle populations (Table 3). In populations in which *Bos taurus* cattle are the predominant type, estimates of the genetic correlation between marbling and shear force reflect a moderately strong, favorable genetic relationship between the two traits.[144, 149, 151,

[160] However, in the limited number of studies involving *Bos indicus* populations, genetic correlations seem to reflect an unfavorable genetic relationship between marbling and shear force.[152, 162] These estimated genetic relationships, if accurate, suggest that efforts to improve tenderness by within-breed selection for increased marbling would be effective in *Bos taurus* breeds, but likely would not be effective in *Bos indicus* breeds. Only a few studies have examined the genetic relationship between calpastatin activity and beef tenderness (Table 3). However, the limited number of estimates of the genetic correlation between calpastatin activity and shear force reflect a relatively strong genetic relationship between the two traits.

Table 3. Genetic Parameter Estimates for Shear Force, Marbling, and Calpastatin Activitiy in *Bos taurus* and *Bos indicus* cattle

	Heritability estimate			Genetic correlation with Shear Force	
Study	**Shear Force**	**Marbling or %IMF**	**Calpastatin activity**	**Marbling or %IMF**	**Calpastatin activity**
Bos taurus-X:					
Wulf et al. (1996), JAS 74:2394	0.31	0.16	0.52	-0.53	1.14
Bos taurus-X & *Bos indicus*-X:					
Koch et al. (1982), JAS 55:1319	0.31	0.40	--	-0.25	--
Shackelford et al. (1994), JAS 72:857	0.53	0.93	0.65	-0.57	0.50
Wheeler et al. (1996), JAS 74:1023	0.37	0.73	--	-0.55	--
Wheeler et al. (2001), JAS 79:1209	0.24	0.57	--	-0.30	--
O'Connor et al. (1997), JAS 75:1822	0.31	0.52	0.15	0.31	0.17
Bos indicus:					
Elzo et al., (1998), JAS 76:1810	0.17	0.16	--	-0.06	--
Riley et al. (2003), JAS 81:54	0.14	0.34	0.07	0.13	0.73

Results reported by Shackelford et al. (1994) and Wulf et al. (1996b) suggest that in predominantly *Bos taurus* populations, calpastatin activity is highly heritable.[149, 151] The high heritability estimate for calpastatin activity, coupled with the strong genetic correlation between calpastatin activity and shear force, suggests that within-breed selection for reduced 24-hour calpastatin activity may be an effective strategy for improving beef tenderness in *Bos taurus* cattle. In contrast, low heritability estimates for calpastatin activity have been reported in *Bos indicus* composite breeds (3/8 Brahman)[152] and in purebred Brahman cattle.[162] The low heritablity estimate for calpastatin activity in the Brahman breed implies that efforts to improve tenderness via within-breed selection for reduced calpastatin activity may be relatively ineffective, despite the strong genetic relationship between tenderness and calpastatin activity.

Because carcass and meat quality traits are difficult to measure phenotypically and, in most cases, are moderately or highly heritable, they are excellent candidate traits for marker-assisted selection. Currently, there are three gene markers – one for marbling and two for tenderness – that are commercially available for use by U.S. cattle breeders. Genetic Solutions Pty Ltd., a company based in Brisbane, Australia, has commercialized two gene markers, which are marketed undenr the trade name GeneSTAR.

GeneSTAR Marbling is a PCR-based RFLP test that distinguishes between alleles of the thyroglobulin promoter gene, which have been linked to marbling differences in cattle. Based on this DNA test (typically performed on a hair sample obtained from the animal to be tested), cattle are classified according to the number of copies ("stars") of the favorable thyroglobulin allele that they possess: 0-Star (no copies), 1-Star (1 copy), 2-Star (2 copies). The difference in the percentage of Choice grade carcasses (% Choice) between 2-Star and 0-Star genotypes has been reported to be approximately 19%. Information reported by Genetic Solutions suggests

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that the frequency of the favorable thyroglobulin allele is highest in high-marbling cattle breeds such as Wagyu, Angus, and Red Angus and lowest in lower-marbling breeds, such as the *Bos indicus* breeds.

GeneSTAR Tenderness is a DNA marker test for two variants of the bovine calpastatin gene on chromosome 7. As with the marbling marker, GeneSTAR Tenderness classifies cattle according to the number of favorable alleles ("stars") they possess (0-Star, 1-Star, or 2-Star). Data reported by Genetic Solutions suggests that 2-Star cattle produce beef with lower shear force values (approximately 0.40 kg lower) compared with beef from 0-Star cattle. Frequencies of 2-Star genotypes have been reported to be approximately 80% in British breeds, about 55% in the Santa Gertrudis breed (a 3/8 Brahman composite), and 32% in the Brahman breed. Frequencies of 0-Star genotypes are reported to be 18% in the Brahman breed, 8% in the Santa Gertrudis breed, and less than 2% in British breeds.[163]

More recently, Page et al. (2002) identified single nucleotide polymorphisms in the μ-calpain gene that were associated with tenderness differences in cattle. Genotypes with μ-calpain alleles that encode isoleucine at position 530 and glycine at position 316 were found to produce tougher beef than genotypes possessing μ-calpain alleles that encode valine at position 530 and alanine at position 316.[164] The difference in shear force for animals possessing 0 vs. 2 copies of the favorable allele has been reported to be approximately 0.45 kg.165 This test recently was commercialized by Frontier Beef Systems, LLC and is offered under the trade name TenderGENE.

The introduction of these commercially available gene markers for marbling and tenderness has generated tremendous interest among cattlemen and may represent a significant step in the quest to improve tenderness genetically. However, there currently is a scarcity of scientific documentation concerning the effectiveness of these DNA-based tests. Results of controlled selection experiments are needed to determine how well these markers identify genetic differences in marbling and tenderness within various cattle breeds.

Short-term Strategies for Genetic Improvement of Beef Tenderness. As beef producers become more consumer-focused, selection strategies that balance improved cattle performance with genetic improvements in product quality and tenderness are receiving greater emphasis. While, within-breed selection for improved tenderness – by progeny testing or with the assistance of gene marker information – represents a logical long-term strategy for managing beef tenderness, achieving significant genetic progress via within-breed selection for tenderness currently requires substantial investments of time and capital. An alternative short-term, less expensive, approach for genetic improvement of tenderness is the selective control of breed inputs into coordinated beef production systems.[166]

One effective strategy for influencing tenderness via the selective use of breeds is to moderate the percentage of *Bos indicus* breeding in market steers and heifers, particularly if this can be accomplished without sacrificing the production advantages of *Bos indicus* crossbred breeding females in subtropical or tropical environments. Dikeman (1995), following a review of then-current information concerning *Bos indicus* breed effects on beef tenderness, advocated a maximum limit of one-quarter to three-eighths *Bos indicus* breeding to avoid beef toughness problems.[167] Sherbeck et al. (1995) conducted a study for the American Hereford Association to determine if cattle with 25% or 50% Brahman breeding could be included in the Certified Hereford Beef (CHB) Program, without negatively impacting product tenderness. Results of that study determined that Hereford crossbreds with 25% Brahman breeding could be included in the CHB Program without increasing the risk of reduced tenderness, but that inclusion of cattle with 50% Brahman breeding would adversely affect tenderness of CHB.[168] In a study commissioned by the

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National Cattlemen's Beef Association, a contractor to The Beef Checkoff, to develop a prototype quality system to produce tender beef, Tatum et al. (1997) used a maximum constraint of 3/8 *Bos indicus* inheritance, which effectively mitigated any breed effects on beef tenderness.[169] The Nolan Ryan Tender Aged Beef™ Program currently guarantees the tenderness of beef produced by cattle with up to 50% Brahman inheritance and has reported a very low frequency of returned products due to toughness.[52]

When it is not possible to document actual percentages of *Bos indicus* inheritance among groups of cattle, live animal and (or) carcass specifications, based on phenotype, can assist in the assurance of acceptable tenderness. Sherbeck et al. (1996) established relationships between phenotypic indicators of the percentage of *Bos indicus* breeding and differences in beef tenderness. In their study, steaks from steers classified as more than 3/8 Brahman (based on visual evaluation of phenotypic evidence of *Bos indicus* breeding among the live animals) were less tender than steaks from steers classified as less than 3/8 Brahman, based on phenotype. In addition, steaks from carcasses with hump height measurements of 7.6 cm were less tender than steaks from carcasses with hump heights less than 6.4 cm.[170] Several branded beef programs have adopted program specifications that utilize carcass hump height as a phenotypic indicator of *Bos indicus* breeding. Of the 40 beef marketing programs currently certified by USDA-AMS, 35 programs have a maximum carcass hump height specification of 2 inches.[171]

O'Connor et al. (1997) suggested that substituting a tropically adapted *Bos taurus* breed for the *Bos indicus* breed component in the development of heat-tolerant composites might be a viable strategy for managing tenderness. Their study involved mating Senegus (Senepol X Red Angus) bulls to Simbrah (5/8 Simmental, 3/8 Brahman) cows to produce a heat-tolerant composite consisting of 1/4 Red Angus, 1/4 Senepol (a tropically adapted *Bos taurus* breed), 5/16 Simmental, and 3/16 Brahman. Beef produced by these cattle was as tender (based on shear force) as beef produced by Red Angus X Simmental crosses and more tender than beef produced by Simbrah cattle.[152] Data presented in Figure 2 suggest that the Tuli breed may represent another viable substitute for the *Bos indicus* breed component in the development of tropically adapted composites. The Tuli – a Sanga type, tropically adapted breed – was comparable in tenderness to the Hereford and Shorthorn breeds in the GPE Program.

British breeds of cattle, most notably the Angus breed, have a long-standing reputation for producing high-quality beef. Data in Figure 2 suggest that all of the major British breeds produce relatively tender beef, while the Angus breed excels in tenderness. Presently, twenty-three of the forty branded beef programs certified by USDA feature the breed name "Angus" in the brand names of their products. In all 23 Angus-based programs, cattle must be ≥ 51% black to be eligible for certification and, in four programs, cattle that meet a "Red Angus genotype" requirement are included. Three additional breed-based programs feature beef produced by Hereford or Hereford-crossbred cattle.[171] Additional breeds that may merit consideration for selective use in crossbreeding systems designed for production of tender beef (based on data presented in Figure 2) include the Wagyu breed, the Piedmontese breed, and several of the more tender Continental breeds (Charolais, Limousin, Pinzgauer, and Simmental).

For beef programs that already involve collection of tenderness data for sire-identified progeny groups, preferential use of specific sires is another effective short-term approach to the genetic improvement of tenderness. Tatum et al. (1999) presented data suggesting that selection of "tender" sires and (or) elimination of "tough" sires, based on progeny differences in shear force was highly effective for reducing the rate of non-conformance to tenderness specifications in a model beef quality system designed for the production of tender beef. [32]

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Pre-Harvest Stress, Cattle Temperament, and Beef Tenderness

Relationships between pre-harvest stress and meat quality characteristics have been recognized for many years. Pre-harvest stress, either acute or prolonged, depletes muscle glycogen stores, resulting in the production of beef with an abnormally high final muscle pH (see Section II) and a characteristically dark lean color (referred to as "dark cutting" beef).[172, 173] Pre-harvest conditions, which cause any form of physical or psychological stress among cattle, can result in muscle glycogen depletion and increase the incidence of dark cutting beef. Common pre-harvest stressors in cattle include: a) aggressive handling, excitement, or physical exertion of cattle before, during, or following transport to the processing plant; b) long transit periods and (or) schedule delays preventing prompt unloading of cattle transported to processing plants; c) mixing of cattle from different sources before harvest, prompting physical activity as animals re-establish an order of social dominance within the mixed group; d) extremes in climatic conditions, including both extremely hot weather and cold, wet weather; e) extended fasting periods or prolonged feeding of very low-energy diets before harvest; and f) females exhibiting behavioral estrus near the time of harvest.

Carcasses produced by cattle subjected to pre-harvest stress exhibit varying degrees of the dark cutting condition, depending upon the extent of ante-mortem glycogen depletion and the final pH of the carcass musculature.[45] Final muscle pH within a range of 5.4 to 5.7 is considered normal for beef. As muscle pH increases above 5.7, lean color becomes progressively darker. Beef carcasses with slightly higher-than-normal final muscle pH values, ranging from 5.8 to 6.2, exhibit a lean color that is only slightly dark; however, a number of studies have shown that muscle pH values within this range are associated with a comparatively high frequency of meat toughness problems.[174, 175] Watanabe et al. (1996) documented a relationship between final muscle pH and the rate of meat tenderization occurring during the postmortem aging period and determined that the slowest "aging rate" occurred in muscle with a final pH of approximately 6.0.[176] In the latter study (Watanabe et al., 1996), it was hypothesized that differences in aging rate (and tenderness) among muscles differing in pH could be the result of two separate mechanisms involved in post-mortem tenderization, including: 1) the widely accepted theory of post-mortem tenderization involving the calpain protease system, and 2) the theory proposed by Takahashi (1996) involving direct effects of calcium on postmortem changes in structural proteins in the myofiber[43] (see Section II).

Wulf et al. (1996b) documented a relationship between lean color and tenderness at various aging times ranging from 1 to 35 days postmortem (Figure 5). In their study, *longissimus* shear force was strongly related to differences in muscle color (dark lean > normal lean > pale lean), especially during the first 7 days post-harvest.

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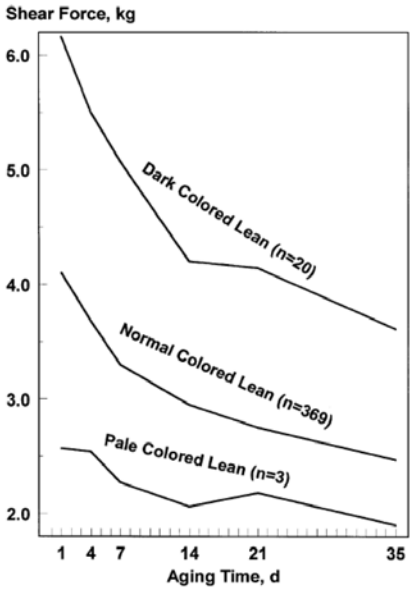
Figure 5. Effects of lean color and postmortem aging time on longissimus shear force
(Source: Wulf et al., 1996)



Moreover, differences in lean color were associated with marked differences in calpastatin activity (dark lean > normal lean > pale lean), suggesting that the observed tenderness differences likely stemmed from differences in early postmortem muscle proteolysis.[151]

Wulf et al. (1997) reported similar relationships among final muscle pH, objective measurements of muscle color (CIE values for L*a*b*), calpastatin activity, and beef *longissimus* tenderness.175 In that study, lower final muscle pH values were associated with lean colors characterized as more white than black (higher L*), more red than green (higher a*), and more yellow than blue (higher b*). In addition, final muscle pH and L*a*b* color measurements (particularly b*) were associated with differences in calpastatin activity, rate of postmortem aging, and beef tenderness (Figure 6). These relationships among muscle pH, muscle color, and beef tenderness constitute the basis for the recent development of color-based sorting technologies for categorizing beef carcasses into expected-tenderness groups[177, 178] and the use of maximum pH constraints in beef grading systems.[179]

Figure 6. Effects of b* value and postmortem aging time on *longissimus* shear force
(Source: Wulf et al., 1997)

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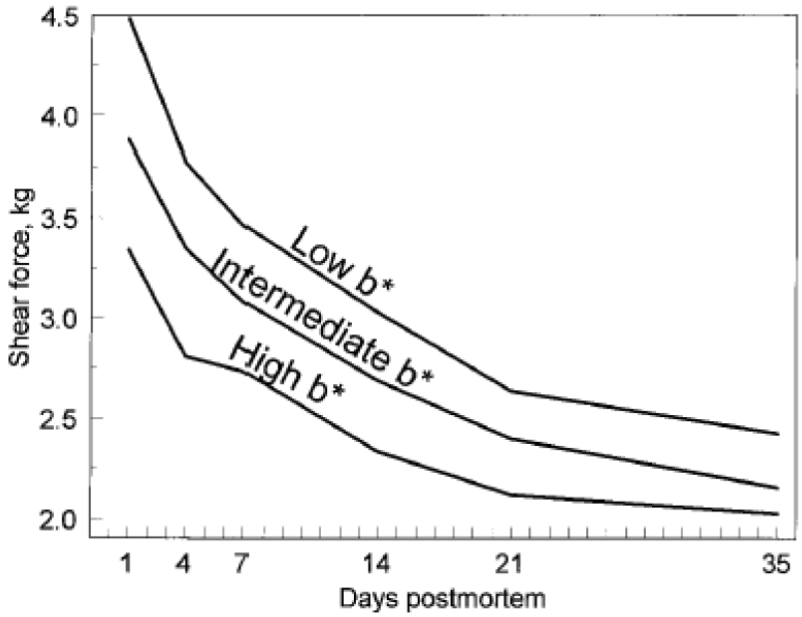

Cattle differ in behavior and temperament and, therefore, react differently when subjected to various pre-harvest stressors. Research has begun to identify relationships between cattle temperament (i.e., their excitability or tendency to become agitated when handled) and the incidence of stress-related beef quality problems. Voisinet et al. (1997) used a subjective scoring system to quantify differences in cattle behavior during restraint in a hydraulic squeeze-chute (1 = calm, little movement; 2 = squirming, occasional shaking of restraint device; 3 = continuous, vigorous movement and shaking of restraint device; 4 = frenzied, rearing, twisting, or violently struggling). In their study, cattle receiving temperament scores of 4 produced carcasses with a very high (25%) incidence of a slightly dark lean color, characterized by the researchers as a "border-line dark-cutting condition. In addition, cattle receiving temperament scores of 3 or 4 produced longissimus steaks that were significantly tougher than steaks produced by cattle receiving temperament scores of 1 or 2.[180] Wulf et al. (1997) presented data showing that cattle temperament score was significantly correlated with several longissimus muscle characteristics including muscle color, calpastatin activity, shear force, and sensory panel ratings for tenderness and flavor. In that study, cattle with more excitable temperaments tended to have higher final muscle pH measurements, darker muscle color, higher calpastatin activities, higher shear force values, and lower sensory panel ratings for tenderness and flavor compared with cattle having less excitable temperaments.[175]

More recently, Australian scientists have established a genetic relationship between "flight time" and beef tenderness. "Flight time" is an electronic measurement of the time required for an animal to travel a specified distance (approximately 2 meters) after it leaves a squeeze-chute, and is related to the animal's temperament (more excitable animals have faster flight times). Studies conducted by scientists at the Cooperative Research Centre for Cattle and Beef Quality have shown that "flight time" is moderately to highly heritable and has a relatively strong genetic correlation (r = -0.53) with *longissimus* shear force. Interestingly, phenotypic correlations between "flight time" and measures of tenderness were found to be very low, which led the researchers to conclude that "best practice" handling might overcome tenderness problems associated with poor temperament and pre-harvest stress.[181]

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Adopting management practices that reduce handling and environmental stress and preferential selection of cattle with calm temperaments are essential elements of effective beef quality management systems. Meat & Livestock Australia (2000) offers cattle producers a very useful set of practical guidelines for avoiding beef quality problems caused by pre-harvest stress.[182]

Sex Effects on Tenderness

Intact male cattle generally produce less tender beef than do steers because 1) elevated serum testosterone levels, coinciding with sexual development at 8 to 14 months of age, are associated with a concomitant increase in collagen content,[183, 184] and 2) higher calpastatin activity in the musculature of bulls causes their cuts to age more slowly compared with cuts from steers.[185] In addition, carcasses produced by bulls have less marbling than do carcasses of steers. [186]

To avoid beef tenderness problems, bull calves destined to become feeders should be castrated before they begin to develop the secondary sex characteristics of mature, intact males. In most cases, male calves designated for beef production are castrated shortly after birth, at branding (approximately 2 to 3 months old), or at weaning (5 to 8 months old). The NCBA Beef Palatability Task Force recommendations (NCBA, 1996) encouraged U.S. cattlemen to "castrate bull calves as early as possible, and prior to 7 months of age."[187] Martinez-Peraza et al. (1999) compared carcass and beef palatability traits of steers (castrated at branding, approximately 2 to 3 months of age) with late-castrates (castrated at approximately 10 months of age). Results of their study showed a significant reduction in quality grade performance, as well as a significant decrease in longissimus tenderness, associated with delayed castration.[188]

Studies comparing tenderness of beef produced by steers vs. heifers have produced ambiguous results. Research conducted more than twenty-five years ago, suggested either that beef from steers and heifers was similar in tenderness,[189, 190] or that beef from heifers was more tender than beef from steers.[191] However, contemporary studies suggest that heifers consistently produce beef that is less tender than beef produced by steers.[151, 152] Wulf et al., (1996b) suggested that the relatively high dosages of androgens used in heifer finishing implants may contribute to sex effects on tenderness;[151] however, Choat et al. (2003) recently compared non-implanted steers and heifers and reported that non-implanted heifers produced less tender longissimus steaks than did non-implanted steers.[192]

Wulf et al. (1997) reported that steers had lower temperament scores (i.e., were less excitable) than heifers and that muscles from steer carcasses had lower 24-hour calpastatin activities, lower final pH values, higher a* values, and higher b* values than did muscles from heifer carcasses.[175] Voisinet et al. (1997) also reported a difference in temperament between steers and heifers and attributed the difference to the more excitable behavior of the nulliparous female, which has been documented in various species and is thought to be associated with estrogen secretion.[193] Also worth noting is the fact that Scanga et al. (1998) documented a significantly higher occurrence of the dark cutting condition in intact heifers than in either steers or spayed heifers.[134] Collectively, these findings seem to suggest that differences in tenderness observed between steers and heifers in recent comparisons may be attributed, at least in part, to differences between the sex classes in temperament, reaction to pre-harvest stress, and associated differences in muscle pH.

Table 4. Effects of sex on longissimus muscle characteristics (Source: Wulf et al., 1997)

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Trait	Steer	Heifer	RSD	P_{sex}
Calpastatin activity (24-hr)	4.26	4.87	0.88	0.0001
Longissimus $pH_{24\text{-hr}}$	5.46	5.52	0.07	0.0001
L*	37.1	36.6	2.5	0.2623
a*	24.0	22.7	1.8	0.0001
b*	11.6	10.8	1.2	0.0002
Shear force, kg	2.60	3.03	0.59	0.0001
Panel tenderness	5.78	5.45	0.62	0.0022

Effects of Morbidity and Intramuscular Injections on Tenderness

Morbidity. Differences in costs associated with morbidity are the most important source of variation in profitability among groups of feedlot cattle,[194] which underscores the fundamental importance of effective cattle health-management programs. Morbidity during the finishing period has been shown to depress growth performance of finishing cattle, resulting in lighter carcass weights and lower marbling scores. However, based on a limited number of comparisons, animal health status and treatment history seem to have only minor effects on beef tenderness.

Gardner et al. (1999) studied the impact of bovine respiratory disease (BRD) on feedlot performance, beef carcass characteristics, and longissimus tenderness. In their study, steers that were treated for BRD had lower average daily gains and produced lighter-weight, leaner carcasses than did cattle that were not treated for BRD. Marbling score and longissimus tenderness did not differ for cattle treated for BRD vs. those not requiring treatment; however, cattle with respiratory tract lesions at the time of harvest had lower marbling scores and produced tougher longissimus steaks (aged for 7 days) than did cattle without lung lesions.[195]

Roeber et al. (2001) examined the effects of feeder cattle health management on morbidity rate, feedlot performance, carcass traits, and beef palatability characteristics. Two pre-conditioning programs for weaned calves were tested and both were shown to be effective for reducing rates of morbidity and mortality. Analysis of medical treatment records revealed that morbidity rate during the finishing period (measured as number of hospital visits) was associated with depressed average daily gain (early in the finishing period), decreased dressing percent, lighter carcass weights, reduced marbling scores, and lower carcass values. However, morbidity did not affect beef tenderness.[196]

Intramuscular Injections. Administration of animal health products via intramuscular injections not only can cause development of lesions near the site of injection, but also can influence tenderness of the surrounding muscle. George et al. (1995) determined that intramuscular injections administered to calves at branding and at weaning produced a high incidence of injection-site lesions that were still evident when the cattle were harvested several months later.[197]

An intramuscular injection causes trauma to the muscle at, and around, the injection site. Subsequent wound healing involves infiltration of connective tissue and fat into the traumatized muscle tissue – a process referred to as steatosis. The infiltration of connective tissue into the traumatized tissue causes significant toughening of the muscle tissue surrounding the lesion and has been shown to affect tenderness of the muscle up to three inches from the center of the lesion.[198] The implementation of state-level and national-level Beef Quality Assurance (BQA) programs, which include specific recommended guidelines for administering animal health products, has dramatically reduced the incidence of injection site lesions in beef cuts.[199, 200]

Figure 7. Effects of injection site lesions on tenderness of surrounding muscle tissue (Source: George et al., 1995)

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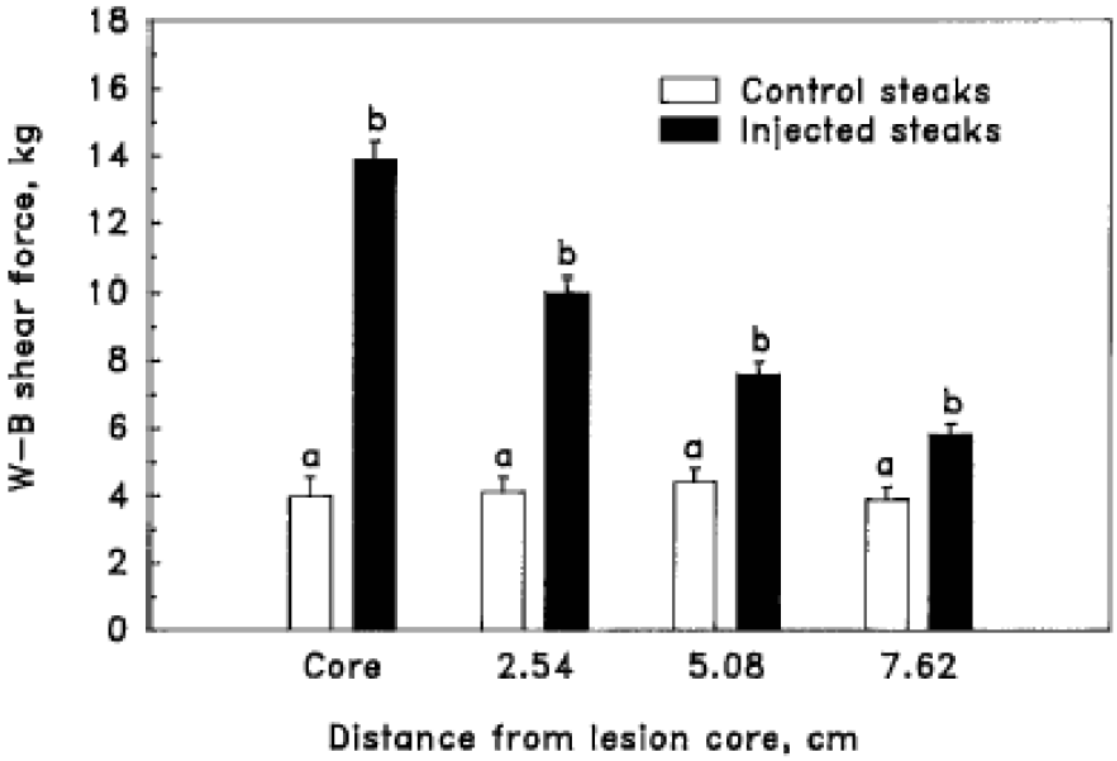

Section IV
A TQM Approach to Beef Grading

One of Deming's "14 Points for Management" is – "Cease dependence on inspection to achieve quality; eliminate the need for mass inspection by building quality into the product."[201] The current system for ensuring product quality in the U.S. beef industry involves "mass inspection" (i.e., USDA grading) of carcasses near the end of the production process. Although this system results in general categorization according to palatability differences, product value is lost, not only due to the imprecision of current grading methodology, but also, and more importantly, because products with "inferior" quality have been produced and must be merchandized at discounted prices.

For the past several years, the beef industry has aggressively supported efforts to identify and develop technologies and instrumentation that would permit beef tenderness to be measured or accurately predicted at the time of harvest. Accurate measurement or prediction of beef tenderness immediately post-harvest has proven to be challenging because: a) tenderness is a complex trait that is influenced by such a wide array of interacting factors, at all points in the beef chain from production to consumption; b) tenderness changes from day to day during postmortem aging – and the rate of postmortem tenderization differs among animals – so that tenderness differences among individuals measured at the time of harvest, even if accurate, do not always precisely reflect tenderness differences days or weeks later; and c) accurate measurement of tenderness of a single muscle does not always reflect the relative tenderness of other muscles in the carcass. Recent testing has characterized existing systems for measuring or predicting beef tenderness as lacking either practicality or precision.[202]

A practical, non-invasive, and precise measurement of tenderness at harvest would be a valuable tool for measurement of system performance and verification of product conformance to tenderness specifications. Yet, even if practical and more precise methods for measuring beef tenderness were available, their application would still involve "mass inspection" of finished products, and the inefficiencies associated with production of lower-value, non-conforming products would persist. Furthermore, even the most precise measurement of tenderness immediately post-harvest ultimately would represent only a partial prediction of the overall desired outcome, which is to meet or exceed the quality expectations of the consumer.

Rather than continued, singular focus on measurement and categorization of beef quality differences at the end of the production process, an alternative and more comprehensive approach – consistent with quality management philosophy – is to focus on understanding the causes of product variability and, then, work to improve the production process by measuring and monitoring critical variables known to affect variability in finished products. Using these concepts, Meat & Livestock Australia (MLA) incorporated TQM principles into their beef grading system – Meat Standards Australia (MSA). The MSA grading system identifies "critical control points" (CCPs) in various sectors of the beef chain (from production to meal preparation) that influence consumer acceptance of beef products. Eligibility of beef cuts for the various MSA grades requires adherence to specific beef production and processing methods, as well as conformance to several live animal and carcass specifications.

Development of the MSA grading system began with the implementation of an extensive, ongoing consumer-testing program. As consumers rated thousands of beef products, data simultaneously were collected to facilitate identification of CCPs, throughout the production chain, that were associated with consumers' likes and dislikes. Using the resulting database, a statistical model was constructed to predict palatability using the CCPs identified as being most important based on consumer information. According to Thompson (2002), the primary CCPs in the prediction model include: 1) *Bos indicus* % (and caracass hump height), 2) sex of the animal, 3) carcass weight (used in conjuction with skeletal ossification to represent the animal's 'growth path'), 4) Milk Fed Veal classification; 5) carcass hanging method – Achilles tendon, Tenderstretch (tendon), Tenderstretch (aitch bone), or Tendercut; 6) marbling score; 7) ultimate muscle pH; 8) length of aging period; and 9) cooking method. Use of hormonal growth promotants (HGPs) is another CCP being considered for use in the MSA system.[203]

A unique aspect of the MSA grading scheme is that the grades are assigned to cuts, not carcasses. Cuts from the same carcass are assigned individual (and in many cases, different) grades that reflect differences in expected eating quality performance among the various cuts of beef. The grading model computes a meat quality score (a combined index of tenderness, flavor, juiciness, and overall acceptability), which is then used to assign the various cuts to specific grades based on predicted consumer acceptability – Ungraded – unsatisfactory, 3 star – good every day, 4 star – better than every day, and 5 star – premium quality.

A key feature of the TQM grading approach developed by MLA is that it incorporates several important elements – animal-specific traits (such as genetics, sex, and age), control of processes in several sectors of the beef chain (including both pre-harvest and post-harvest processes), cut-specific quality differences, and consumer preferences – into the beef pricing system. As a result, a much clearer economic signal can be transmitted through the entire beef chain, which provides producers and processors with economic incentives to become more quality conscious and facilitates consumer-driven improvement in product performance. The MSA system is still being modified and refined, but it represents the best existing example of a TQM-grading approach for improving beef quality and tenderness.

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Implications

A comprehensive review of the literature concerning effects of beef production practices on product tenderness was conducted to serve as a basis for development of industry recommendations for pre-harvest management of market cattle to enhance beef tenderness. Based on this review, a "white paper" was developed to summarize the current state-of-knowledge with respect to pre-harvest management of beef tenderness. Major topics discussed include: 1) Fundamental sources of variation in beef tenderness; 2)Pre-harvest nutritional management and dietary effects; 3) Effects of hormonal implants and other growth modifiers; 4) Genetic inputs and their effects on beef tenderness; 5) Pre-harvest stress, cattle temperament, and beef tenderness; 6) Sex effects on tenderness; and 7) Effects of morbidity and intramuscular injections on tenderness. In addition, the importance of the industry's efforts to improve beef tenderness and a TQM approach to beef grading are briefly discussed.

References

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[1] Barkema, Alan and Mark Drabenstott. 1996. Consolidation and Change in Heartland Agriculture. Proceedings: Economic Forces Shaping the Rural Heartland. Federal Reserve Bank of Kansas City.
[2] Boehlje, Michael. 1995. Industrialization of Agriculture: What are the consequences? Conf. Proc. Industrialization of Heartland Agriculture. Ch. 3, Ag. Econ. Misc. Rep. No. 176, Soybean Research & Development Council. Available at www.agribiz.com/IQS.
[3] Research Institute on Livestock Pricing (www.aaec.vt.edu/rilp/).
[4] Cattle-Fax. 2001. Average annual per capita expenditures for meat. March 2001, Cattle and Beef Industry Statistics, National Cattlemen's Beef Association.
[5] Purcell, Wayne D. 2002. Demand for meats: Past, present, and a look ahead. Available at: www.aaec.vt.edu/rilp.
[6] Lefens, Mark. 1986. What's Going On? The New Reality. Meat Processing (January Issue, p. 30).
[7] Lambert, Charles D. 1991. Lost Opportunities in Beef Production. Mimeograph Report, pp. 1-10. National Cattlemen's Association, Englewood, CO.
[8] Smith, G.C., J.W. Savell, R.P. Clayton, T.G Field, D.B. Griffin, D.S. Hale, M.F. Miller, T.H. Montgomery, J.B. Morgan, J.D. Tatum, and J.W. Wise. 1992. Improving the consistency and competitiveness of beef. The Final Report of the National Beef Quality Audit – 1991. National Cattlemen's Association, Englewood, CO.
[9] NLSMB. 1995. Beef Customer Satisfaction: A comprehensive in-home product test among frequent beef users. National Live Stock and Meat Board, Chicago, IL.
[10] NCA. 1993. Executive Summary – Strategic Alliances Field Study. National Cattlemen's Association, Englewood, CO.
[11] Industry-Wide Long Range Plan Task Force. 1993. Beef Industry Long Range Plan Task Force Report. Beef Industry Council, Cattlemen's Beef Board, U.S. Meat Export Federation, and National Cattlemen's Association.
[12] Foster, G. D., H. R. Wyatt, J. O. Hill, B. G. McGuckin, C. Brill, B. S. Mohammed, P.O. Szapary, D.J. Rader, J. S. Edman, and S. Klein. 2003. A randomized trial of a low- carbohydrate diet for obesity. New England Journal of Medicine 348:2082-2090.
[13] Samaha, F.F., N. Iqbal, P. Seshadri, K.L. Chicano, D.A. Daily, J. McGrory, T. Williams, M. Williams, E.J. Gracely, and L. Stern. 2003. A low-carbohydrate as compared with a low-fat diet in severe obesity. New England Journal of Medicine 348:2074-2081.
[14] NCBA. 2001. Beef Industry Long Range Plan, 2001-2004. National Cattlemen's Beef Association, Centennial, CO.
[15] Food Marketing Institute. 2002. Factors "very important" to supermarket shoppers in food selections. FMI, Washington, DC.
[16] Quinn, F. 1999. Tracing the future of meat. In: Proc. 12th World Meat Cong., Dublin, Ireland. Session 2, pp. 1-10.
[17] Neely, T.R., C.L. Lorenzen, R.K. Miller, J.D. Tatum, J.W. Wise, J.F. Taylor, M.J. Buyck, J.O. Reagan, and J.W. Savell. 1998. Beef customer satisfaction: Role of cut, USDA quality grade, and city on in-home consumer ratings. J. Anim. Sci. 76:1027-1033.
[18] Platter, W.J., J.D. Tatum, K.E. Belk, P.L. Chapman, J.A. Scanga, and G.C. Smith. 2003a. Relationships of consumer sensory ratings, marbling score, and shear force value to consumer acceptance of beef strip loin steaks. J. Anim. Sci. 81:2741-2750.
[19] Huffman, K.L., M.F. Miller, L.C. Hoover, C.K. Wu, H.C. Brittin, and C.B. Ramsey. 1996. Effect of beef tenderness on consumer satisfaction with steaks consumed in the home and restaurant. J. Anim. Sci. 74:91-97.
[20] Miller, M.F., M.A. Carr, C.B. Ramsey, K.L. Crockett, and L.C. Hoover. 2001. Consumer thresholds for establishing the value of beef tenderness. J. Anim. Sci. 79:3062-3068.

BEEF®
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[21] Goodson, K.J., W.W. Morgan, T.L. Wheeler, S.D. Shackelford, M. Koohmaraie, J.O. Reagan, B.L. Gwartney, S.M. Courington, J.W. Wise, and J.W. Savell. 1999. Beef Customer Satisfaction II: The marketplace and beyond. National Cattlemen's Beef Association, Englewood, CO.
[22] Boleman, S.J., S.L. Boleman, R.K. Miller, J.F. Taylor, H.R. Cross, T.L. Wheeler, M. Koohmaraie, S.D. Shackelford, M.F. Miller, R.L. West, D.D. Johnson, and J.W. Savell. 1997. Consumer evaluation of beef of known categories of tenderness. J. Anim. Sci. 75:1521-1524.
[23] Lusk, J., J. Fox, T. Schroeder, J. Mintert, and M. Koohmaraie. 1999. Will consumers pay for guaranteed tender steak? Research Bulletin 3-99. Research Institute on Livestock Pricing. Available at: www.aaec.vt.edu/rilp.
[24] Shackelford, S.D., T.L. Wheeler, and M. Koohmaraie. 1996. Tenderness-based classification of beef. Mimeographed Report. Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE.
[25] Umberger, W.J., D.M. Feuz, C.R. Calkins, and K.M. Killinger. 2000. Consumer preference and willingness to pay for flavor in beef steaks. Paper presented at the 2000 IAMA Agribusiness Forum, Chicago, IL.
[26] Platter, W.J., J.D. Tatum, K.E. Belk, S.R. Koontz, P.L. Chapman, and G.C. Smith. 2004. Effects of marbling and shear force on consumers' willingness-to-pay for beef strip loin steaks. J. Anim. Sci. (accepted for publication).
[27] Peck, C. 2003. The Alliance Yellow Pages – 2003, Taking Control. Beef (August Issue, p. A1). Also available at www.beef-mag.com.
[28] Butler, J. 2002. Identifying opportunities during challenging times. Presented at the Taylor Beef Symposium, Colorado State University (December 4, 2002).
[29] Morgan, J.B. 1992. Tenderness problems and potential solutions. In: Improving the consistency and competitiveness of beef. The Final Report of the National Beef Quality Audit – 1991. National Cattlemen's Association, Englewood CO (pp. 180-187).
[30] NCA. 1994. National Beef Tenderness Executive Summary. National Cattlemen's Association. Englewood, CO.
[31] Polkinghorne, R., R. Watson, M. Porter, A. Gee, J. Scott, and J. Thompson. 1999. Meat Standards Australia, A PACCP based beef grading scheme for consumers. 1) The use of consumer scores to set grade standards. Proc. 45th Intl. Cong. Meat Sci. and Technol. 45:14-15.
[32] Tatum, J.D., K.E. Belk, M.H. George, and G.C. Smith. 1999. Identification of quality management practices to reduce the incidence of retail beef tenderness problems: Development and evaluation of a prototype quality system to produce tender beef. J. Anim. Sci. 77: 2112-2118.
[33] Tatum, J.D., G.C. Smith, and K.E. Belk. 2000. New approaches for improving tenderness, quality, and consistency of beef. Proc. Am. Soc. Anim. Sci., 1999. Available at: www.asas.org/jas/symposia/proceedings.
[34] Bailey, A.J., S.P. Robbins, and G. Balian. 1974. Biological significance of the intermolecular crosslinks of collagen. Nature 251:105.
[35] Light, N.D. and A.J. Bailey. 1979. Covalent crosslinks in collagen: Characterization and relationships to connective tissue disorders. In: Fibrous Proteins: Scientific, Industrial and Medical Aspects, Vol. 1, p. 151. Academic Press, New York.
[36] Bailey, A.J. 1972. The basis of meat texture. J. Food Sci. Agric. 23:995.
[37] Locker, R.H. and C.J. Hagyard. 1963. A cold shortening effect in beef muscles. J. Sci. Food Agric. 14:787.
[38] Marsh, B.B. and N.G. Leet. 1966. Studies in meat tenderness. 3. The effect of cold shortening on tenderness. J. Food Sci. 31:450.
[39] Marsh, B.B., P.R. Woodhams, and N.G. Leet. 1968. Studies in meat tenderness. 5. The effect on tenderness of cooling and freezing before the completion of rigor mortis. J. Food Sci. 33:12.

BEEF®
Funded by the Beef Checkoff

[40] Marsh, B.B. 1983. Effects of early-postmortem muscle pH and temperature on meat tenderness. Proc. Recip. Meat Conf. 36:131-135.
[41] Koohmaraie, M. 1992. Role of neutral proteinases in postmortem muscle protein degradation and meat tenderness. Proc. Recip. Meat Conf. 45:63-71.
[42] Koohmaraie, M., J. Schollmeyer, and T.R. Dutson. 1986. Effect of low-calcium-requiring calcium activated factor on myofibrils under varying pH and temperature. J. Food Sci. 51:28- 32.
[43] Takahashi. K. 1996. Structural weakening of skeletal muscle tissue during post-mortem ageing of meat: The non-enzymatic mechanism of meat tenderization. Meat Sci. 43:S67-S80.
[44] Page, J.K., D.M. Wulf, and T.R. Schwotzer. 2001. A survey of beef muscle color and pH. J. Anim. Sci. 79:678-687.
[45] Wulf, D.M., R.S. Emnett, J.M. Leheska, and S.J. Moeller. 2002. Relationships among glycolytic potential, dark cutting (dark, firm, and dry) beef, and cooked beef palatability. J. Anim. Sci. 80:1895-1903.
[46] Bendall, J.R. 1978. Variability in rates of pH fall and of lactate production in the muscles on cooling beef carcasses. Meat Sci. 2:91-104.
[47] O'Halloran, G.R., D.J. Troy, and D.J. Buckley. 1997. The relationship between early- postmortem pH and the tenderisation of beef muscles. Meat Sci. 45:239-251.
[48] Marsh, B.B., T.P. Ringkob, R.L. Russell, D.R. Swartz, and L.A. Pagel. 1988. Mechanisms and strategies for improving meat tenderness. Proc. Recip. Meat Conf. 41:113-118.
[49] McBee, J.L. and J.A. Wiles. 1967. Influence of marbling and carcass grade on the physical and chemical characteristics of beef. J. Anim. Sci. 26:701-704.
[50] Carpenter, Z.L. 1974. Beef quality grade standards – Need for modification? Proc. Recip. Meat Conf. 27:122.
[51] Smith, G.C. and Z.L. Carpenter. 1974. Eating quality of animal products and their fat content. Proc. Symposium on Changing the Fat Content and Composition of Animal Products. National Research Council, National Academy of Sciences, Washington, DC.
[52] Smith, G.C. 2003. The taste of beef. Presented at the New Brunswick Cattle Producers AGM & Beef Symposium. pp. 1-33.
[53] Bull, S. 1916. The Principles of Feeding Farm Animals. The Macmillan Co., New York.
[54] Henry, W.A. and F.B. Morrison. 1916. Feeds and Feeding. Henry-Morrison Publ. Co., Madison.
[55] Mumford, H.W. 1902. Market classes and grades of cattle with suggestions for interpreting market quotations. Illinois Agric. Exp. Sta. Bull. No. 78. Univ. of Illinois, Urbana.
[56] Gibbons, C.E. 1929. Advantages of standards for livestock and meats. USDA Misc. Publ. No. 33, Washington.
[57] USDA. 1926. Official United States Grades for Carcass Beef. United States Dept. of Agric., Washington, DC.
[58] French, P., C. Stanton, F. Lawless, E.G. O'Riordan, F.J. Monahan, P.J. Caffrey, and A.P. Moloney. 2000. Fatty acid composition, including conjugated linoleic acid, of intramuscular fat from steers offered grazed grass, grass silage, or concentrate-based diets. J. Anim Sci. 78:2849-2855.
[59] Belury, M.A. 2002. Dietary conjugated linoleic acid in health: physiological effects and mechanisms of action. Ann. Rev. Nutr. 22:505-531.
[60] Schroeder, J.W., D.A. Cramer, R.A. Bowling, and C.W. Cook. 1980. Palatability, shelf-life and chemical differences between forage- and grain-finished beef. J. Anim. Sci. 50:852- 859.
[61] Harrison, A.R., M.E. Smith, D.M. Allen, M.C. Hunt, C.L. Kastner, and D.H. Kropf. 1978. Nutritional regime effects on quality and yield characteristics of beef. J. Anim. Sci. 47:383-388.
[62] Schaake, S.L., G.C. Skelley, E. Halpin, L.W. Grimes, R.B.Brown, D.L. Cross, and C.E. Thompson. 1993. Carcass and meat sensory traits of steers finished on fescue and clover, summer forage, or for different periods in drylot. J. Anim. Sci. 71:3199-3205.

BEEF®
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[63] Bowling, R.A., G.C. Smith, Z.L. Carpenter, T.R. Dutson, and W.M. Oliver. 1977. Comparison of forage-finished and grain-finished beef carcasses. J. Anim. Sci. 45:209-215.
[64] Brewer, P. and C. Calkins. 2003. Quality traits of grain- and grass-fed beef: A review. 2003 Nebraska Beef Report, pp. 74-77. Univ. of Nebraska, Lincoln.
[65] Smith, G.C., Z.L. Carpenter, H.R. Cross, C.E. Murphey, H.C. Abraham, J.W. Savell, G.W. Davis, B.W. Berry, and F.C. Parrish, Jr. 1985. Relationship of USDA marbling scores to palatability of cooked beef. J. Food Quality 7:289-308.
[66] Schnell, T.D., K. E. Belk, J.D. Tatum, R.K. Miller, and G.C. Smith. 1997. Performance, carcass, and palatability traits for cull cows fed high-energy, concentrate diets for 0, 14, 28, 42, or 56 days. J. Anim. Sci. 75:1195-1202.
[67] Bowling, R.A., J.K. Riggs, G.C. Smith, Z.L. Carpenter, R.L. Reddish, and O.D. Butler. 1978. Production, carcass and palatability characteristics of steers produced by different management systems. J. Anim. Sci. 46:333-340.
[68] Hedrick, H.B., J.A. Paterson, A.G. Matches, J.D. Thomas, R.E. Morrow, W.C. Stringer, and R.J. Lipsey. 1983. Carcass and palatability characteristics of beef produced on pasture, corn silage and corn grain. J. Anim. Sci. 57:791-801.
[69] French, P., E.G. O'Riordan, F.J. Monahan, P.J. Caffrey, M.T. Mooney, D.J. Troy, and A.P. Moloney. 2001. The eating quality of meat of steers fed grass and/or concentrates. Meat Sci. 57:379-386.
[70] Aberle, E.D., E.S. Reeves, M.D. Judge, R.E. Hunsley, and T.W. Perry. 1981. Palatability and muscle characteristics of cattle with controlled weight gain: Time on a high energy diet. J. Anim. Sci. 52:757-763.
[71] Wu, J.J., C.L. Kastner, M.C. Hunt, D.H. Kropf, and D.M. Allen. 1981. Nutritional effects on beef collagen characteristics and palatability. J. Anim. Sci. 53:1256-1261.
[72] Fishell, V.K., E.D. Aberle, M.D. Judge, and T.W. Perry. 1985. Palatability and muscle properties of beef as influenced by preslaughter growth rate. J. Anim. Sci. 61:151-157.
[73] Fuez, D.M. and W.J. Umberger. 2001. Consumer willingness-to-pay for flavor in beef steaks: An experimental economics approach. Cornhusker Economics. Cooperative Extension, University of Nebraska, Lincoln.
[74] Melton, S.L. 1990. Effects of feeds on flavor of red meat: A review. J. Anim. Sci. 68:4421- 4435.
[75] Melton, S.L., M. Amiri, G.W. Davis, and W.R. Backus. 1982a. Flavor and chemical characteristics of ground beef from grass, forage-grain- and grain-finished steers. J. Anim. Sci. 55:77-87.
[76] Larick, D.K., H.B. Hedrick, M.E. Bailey, J.E. Williams, D.L. Hancock, G.B. Garner, and R.E. Morrow. 1987. Flavor constituents of beef as influenced by forage- and grain- feeding. J. Food Sci. 52:245-251.
[77] Klopfenstein, T., R. Cooper, D.J. Jordan, D. Shain, T. Milton, C. Calkins, and C. Rossi. 2000. Effects of backgrounding and growing programs on beef carcass quality and yield. Proc. Am. Soc. Anim. Sci., 1999. Available at: www.asas.org/jas/symposia/proceedings.
[78] Zinn, D.W., C.T. Gaskins, G.L. Gann, and H.B. Hedrick. 1970. Beef muscle tenderness as influenced by days on feed, sex, maturity and anatomical location. J. Anim. Sci. 31:307-309.
[79] McKeith, F.K., J.W. Savell, G.C. Smith, T.R. Dutson, and Z.L. Carpenter. 1985. Tenderness of major muscles from three breed types of cattle at different times-on-feed. Meat Sci. 13:151-166.
[80] Miller, R.K., H.R. Cross, J.D. Crouse, and J.D. Tatum. 1987. The influence of diet and time on feed on carcass traits and quality. Meat Sci. 19:303-313.
[81] May, S.G., H.G. Dolezal, D.R. Gill, F.K. Ray, and D.S. Buchanan. 1992. Effect of days fed, carcass grade traits, and subcutaneous fat removal on postmortem muscle characteristics and beef palatability. J. Anim. Sci. 70:444-453.

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[82] Tatum, J.D., G.C. Smith, B.W. Berry, C.E. Murphey, F.L. Williams, and Z.L. Carpenter. 1980. Carcass characteristics, time on feed and cooked beef palatability attributes. J. Anim. Sci. 50:833-840.
[83] Dolezal, H.G., G.C. Smith, J.W. Savell, and Z.L. Carpenter. 1982. Effect of time-on-feed on the palatability of rib steaks from steers and heifers. J. Food Sci. 47:368-373.
[84] Melton, S.L., J.M. Black, G.W. Davis, and W.R. Backus. 1982b. Flavor and selected chemical components of ground beef from steers backgrounded on pasture and fed corn up to 140 days. J. Food Sci. 47:699-704.
[85] Sainz, R.D. and R.F. Vernazza Paganini. 2004. Effects of different grazing and feeding periods on performance and carcass traits of beef. J. Anim. Sci. 82:292-297.
[86] Grona, A.D., J.D. Tatum, F.L. Williams, K.E. Belk, and G.C. Smith. 2002. An evaluation of the USDA Standards for feeder cattle frame size and muscle thickness. J. Anim.Sci. 80:560-567.
[87] Dikeman, M.E., K.N. Nagele, S.M. Myers, R.R. Schalles, D.H. Kropf, C.L. Kastner, and F.A. Russo. 1985. Accelerated versus conventional beef production and processing. J. Anim. Sci. 61:137-150.
[88] Schoonmaker, J.P., S.C. Loerch, F.L. Fluharty, H.N. Zerby, and T.B. Turner. 2002. Effect of age at feedlot entry on performance and carcass characteristics of bulls and steers. J. Anim. Sci. 80:2247-2254.
[89] Brewer, P., C. Calkins, R. Anderson, T. Klopfenstein, and R. Rasby. 2003. Carcass and palatability characteristics of calf-fed and yearling finished steers. 2003 Nebraska Beef Report, pp. 68-70. Univ. of Nebraska, Lincoln.
[90] Huffman, R.D., S.E. Williams, D.D. Hargrove, D.D. Johnson, and T.T. Marshall. 1990. Effects of percentage Brahman and Angus breeding, age-season of feeding, and slaughter end point on feedlot performance and carcass characteristics. J. Anim. Sci. 68:2243-2252.
[91] Wulf, D.M., J.B. Morgan, J.D. Tatum, and G.C. Smith. 1996a. Effects of animal age, marbling score, calpastatin activity, subprimal cut, calcium injection, and degree of doneness on the palatability of steaks from Limousin cattle. J. Anim. Sci. 74:569-576.
[92] Johnson, D.D., R.D. Huffman, S.E. Williams, and D.D. Hargrove. 1990. Effects of percentage Brahman and Angus breeding, age-season of feeding and slaughter end point on meat palatability and muscle characteristics. J. Anim. Sci. 68:1980-1986.
[93] Harris, J.J., D.K. Lunt, S.B. Smith, W.L. Mies, D.S. Hale, M. Koohmaraie, and J.W. Savell. 1997. Live animal performance, carcass traits and meat palatability of calf- and yearling-fed cloned steers. J. Anim. Sci. 75:986-992.
[94] Myers, S.E., D.B. Faulkner, F.A. Ireland, and D.F. Parrett. 1999. Comparison of three weaning ages on cow-calf performance and steer carcass traits. J. Anim. Sci. 77:323- 329.
[95] Fluharty, F.L., S.C. Loerch, T.B. Turner, S.J. Moeller, and G.D. Lowe. 2000. Effects of weaning age and diet on growth and carcass characteristics. J. Anim. Sci. 78:1759- 1767.
[96] Schoonmaker, J.P., M.J. Cecava, F.L. Fluharty, H.N. Zerby, and S.C. Loerch. 2004. Effect of source and amount of energy and rate of growth in the growing phase on performance and carcass characteristics of early- and normal-weaned steers. J. Anim. Sci. 82:273-282.
[97] Schoonmaker, J.P., F.L. Fluharty, S.C. Loerch, T.B. Turner, S.J. Moeller, and D.M. Wulf. 2001. Effect of weaning status and implant regimen on growth, performance, and carcass characteristics of steers. J. Anim. Sci. 79:1074-1084.
[98] Montgomery, J.L., F.C. Parrish, Jr., D.C. Beitz, R.L. Horst, E.J. Huff-Lonergan, and A.H. Trenkle. 1997. The use of vitamin D3 to improve beef tenderness. Proc. Recip. Meat Conf. 50:168.
[99] Swanek, S.S., J.B. Morgan, F.N. Owens, D.R. Gill, C.A. Strasia, H.G. Dolezal, and F.K. Ray. 1999. Vitamin D3 supplementation of beef steers increases longissimus tenderness. J. Anim. Sci. 79:912-918.

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Funded by the Beef Checkoff

[100] Scanga, J.A., K.E. Belk, J.D. Tatum, and G.C. Smith. 2001. Supranutritional oral supplementation with vitamin D3 and calcium and the effects on beef tenderness. J. Anim. Sci. 79:912-918.
[101] Karges, K., J.C. Brooks, D.R. Gill, J.E. Breazile, F.N. Owens, and J.B. Morgan. 2001. Effects of supplemental vitamin D3 on feed intake, carcass characteristics, tenderness, and muscle properties of beef steers. J. Anim. Sci. 79:2844-2850.
[102] Montgomery, J.L., M.A. Carr, C.R. Kerth, G.G. Hilton, B.P. Price, M.L. Galyean, R.L. Horst, and M.F. Miller. 2002. Effect of vitamin D3 supplementation level on the postmortem tenderization of beef from steers. J. Anim. Sci. 80:971-981.
[103] Montgomery, J.L., F.C. Parrish, Jr., D.C. Beitz, R.L. Horst, E.J. Huff-Lonergan, and A.H. Trenkle. 2000. The use of vitamin D3 to improve beef tenderness. J. Anim. Sci. 78:2615-2621.
[104] Reiling, B.A. and D.D. Johnson. 2003. Effects of implant regimens (trenbolone acetate-estradiol administered alone or in combination with zeranol) and vitamin D3 on fresh beef color and quality. J. Anim. Sci. 81:135-142.
[105] Foote, M.R., R.L. Horst, E.J. Huff-Lonergan, A.H. Trenkle, F.C. Parrish, Jr., and D.C. Beitz. 2004. The use of vitamin D3 and its metabolites to improve beef tenderness. J. Anim. Sci. 82:242-249.
[106] Institute of Medicine. 1999. Dietary Reference Intakes for Calcium, Phosphorus, Magnesium, Vitamin D, and Fluoride, The National Academy Press. National Academy of Sciences, Washington, D.C.
[107] Hanson, D., C. Calkins, and J. Horton. 2002. Oral dosage with NutroCal™ (calcium propionate) to enhance beef tenderness. 2002 Nebraska Beef Report, pp. 87-89. Univ. of Nebraska, Lincoln.
[108] Spears, J.W., T.E. Engle, W.R. Platter, K.E. Lloyd, K.E. Belk and J. Horton. 2003. Effects of high dietary calcium propionate and dietary cation-anion balance on calcium metabolism and *longissimus* muscle tenderness in finishing steers. Prof. Anim. Scientist. 19:424-428.
[109] Machado, T.J., K.E. Belk, T.E. Engle, J.A. Scanga, J.D. Tatum, and G.C. Smith. 2003. Effects on beef tenderness by supplementing Bio-Chlor to feedlot cattle. Final Research Report to Biovance Technologies, Inc. by the Department of Animal Sciences, Colorado State University, Fort Collins 80523-1171.
[110] Nichols, W.T., L. Choromanski, J.P. Hutcheson, S. Nordstrom, C.D. Reinhardt, T. Shelton, and G.E. Sides. Implant strategies for finishing cattle. Undated publication available from Intervet, Inc., Middlesboro, DE.
[111] Mader, T.L. 1997. Carryover and lifetime effects of growth promoting implants. Pages 88- 94 in Proc. OSU Symp.: Impact of Implants on Performance and Carcass Value of Beef Cattle, Oklahoma Agric. Exp. Sta., Stillwater, OK.
[112] Belk, K.E. 1992. Low quality grades – Effects of implants on maturity, marbling and incidence of dark cutting beef. In: Improving the consistency and competitiveness of beef. The Final Report of the National Beef Quality Audit – 1991. National Cattlemen's Association, Englewood CO (pp. 173-180).
[113] Duckett, S.L., F.N. Owens, and J.G. Andrade. 1997. Effects of implants on performance and carcass traits of feedlot steers and heifers. Pages 63-82 in Proc. Symposium: Impact of Implants on Performance and Carcass Value of Beef Cattle, P-957, Okla. State Univ. Stillwater.
[114] Nichols, W.T., M.L. Galyean, D.U. Thomson, and J.P. Hutcheson. 2002. Review: Effects of steroid implants on the tenderness of beef. Prof. Anim. Sci. 18:202-210.
[115] Apple, J. K., M. E. Dikeman, D. D. Simms, and G. Kuhl. 1991. Effects of synthetic hormone implants, singularly or in combinations, on performance, carcass traits, and *longissimus* muscle palatability of Holstein steers. J. Anim. Sci. 69:4437-4448.

BEEF®
Funded by the Beef Checkoff

[116] Johnson, B. J., P. T. Anderson, J. C. Meiske, and W. R. Dayton. 1996. Effect of a combined trenbolone acetate and estradiol implant on feedlot performance, carcass characteristics, and carcass composition of feedlot steers. J. Anim. Sci. 74:363-371.
[117] Rumsey, T. S., T. H. Elsasser, S. Kahl, and M. B. Solomon. 1999. The effect of roasted soybeans in the diet of feedlot steers and Synovex-S implants on carcass characteristics and estimated composition. J. Anim. Sci. 77:1726-1734.
[118] Mader, T. L., D. C. Clanton, J. K. Ward, D. E. Pankaskie, and G. H. Deutscher. 1985. Effect of pre- and post-weaning zeranol implant on steer calf performance. J. Anim. Sci. 61:546-551.
[119] Loy, D. D., H. W. Harpster, and E. H. Cash. 1988. Rate, composition and efficiency of growth in feedlot steers reimplanted with growth stimulants. J. Anim. Sci. 66:2668-2677.
[120] Pritchard, R. H., K. W. Bruns, and D. L. Boggs. 2003. A comparison of lifetime implant strategies or beef steers. Pages 70 –79 in 2003 South Dakota Beef Report. Available: http://ars.sdstate.edu/extbeef/2003_Beef_Report.htm.
[121] Morgan, J.B. 1997. Implant program effects on USDA beef carcass quality grade traits and meat tenderness. Pages 147-154 in Proc. Symposium: Impact of Implants on Performance and Carcass Value of Beef Cattle, P-957, Okla. State Univ. Stillwater.
[122] Foutz, C.P., D.R. Gill, H.G. Dolezal, T.L. Gardner, and R.T. Botts. 1990. Synovex-S and trenbolone acetate implants for feedlot steers. J. Anim. Sci. 68(Suppl. 1):472.
[123] Bruns, K.W., R.H. Pritchard, and T.A. Wittig. 2001. The effect of stage of growth and implant exposure on carcass composition and quality in steers. J. Anim. Sci. 79(Suppl. 1):31.
[124] Samber, J.A., J.D. Tatum, M.I. Wray, W.T. Nichols, J.B. Morgan, and G.C. Smith. 1996. Implant program effects on performance and carcass quality of steer calves finished for 212 days. J. Anim. Sci. 74:1470-1476.
[125] Platter, W.J., J.D. Tatum, K.E. Belk, J.A. Scanga, and G.C. Smith. 2003b. Effects of repetitive use of hormonal implants on beef carcass quality, tenderness, and consumer ratings of beef palatability. J. Anim. Sci. 81:984-996.
[126] Foutz, C.P., H.G. Dolezal, T.L. Gardner, D.R. Gill, J.L. Hensley, and J.B. Morgan. 1997. Anabolic implant effects on steer performance, carcass traits, subprimal yields, and *longissimus* muscle properties. J. Anim. Sci. 75:1256-1265.
[127] Pritchard, R.H. 2000. Comparison of estradiol-trenbolone acetate implant programs for yearling steers of two genotypes. In 2000 South Dakota Beef Report. Available: http://ars.sdstate.edu/BeefExt/BeefReports/2000/comparison_of_estradiol.htm.
[128] Vanderwert, W., L.L. Berger, F.K. McKeith, P.J. Bechtel, and T.R. Carr. 1984. Influence of zeranol dosage level in Angus bulls and late castrate cattle. J. Anim. Sci. 42:213.
[129] Prichard, D.L., D.D. Hargrove, and B.R. Robinson. 1984. Influence of creep feeding, Ralgro and breed type on weanling heifer development and composition. J. Anim. Sci. 59(Suppl. 1):225.
[130] Crouse, J.D., B.D. Schanbacher, H.R. Cross, S.C. Seideman, and S.B. Smith. 1987. Growth and carcass traits of heifers as affected by hormonal treatment. J. Anim. Sci. 64:1434-1440.
[131] Scheffler, J.M, D.D. Buskirk, S.R. Rust, J.D. Cowley, and M.E. Doumit. 2003. Effect of repeated administration of combination trenbolone acetate and estradiol implants on growth, carcass traits, and beef quality of long-fed Holstein steers. J. Anim. Sci. 81:2395-2400.
[132] Paisley, S.I., G.W. Horn, C.J. Ackerman, B.A. Gardner, and D.S. Secrist. 1999. Effects of implants on daily gains of steers wintered on dormant native tallgrass prairie, subsequent performance, and carcass characteristics. J. Anim. Sci. 77:291-299.
[133] McKenna, D.R., D.L. Roeber, P.K. Bates, T.B. Schmidt, D.S. Hale, D.B. Griffin, J.W. Savell, J.C. Brooks, J.B. Morgan, T.H. Montgomery, K.E. Belk, and G.C. Smith. 2002. National Beef Quality Audit – 2000: Survey of targeted cattle and carcass characteristics related to quality, quantity, and value of fed steers and heifers. J. Anim. Sci. 80:1212-1222.

BEEF®
Funded by the Beef Checkoff

[134] Scanga, J.A., K.E. Belk, J.D. Tatum, T. Grandin, and G.C. Smith. 1998. Factors contributing to the incidence of dark cutting beef. J. Anim. Sci. 76:2040-2047.
[135] Roeber, D.L., R.C. Cannell, K.E. Belk, R.K. Miller, J.D. Tatum, and G.C. Smith. 2000. Implant strategies during feeding: Impact on carcass grades and consumer acceptability. J. Anim. Sci. 78:1867-1874.
[136] Barham, B.L., J.C. Brooks, J.R. Blanton, Jr., A.D. Herring, M.A. Carr, C.R. Kerth, and M.F. Miller. Effects of growth implants on consumer perceptions of meat tenderness in beef steers. 2003. J. Anim. Sci. 81:3053-3056.
[137] Anderson, P.T. 1991. Implant programs for finishing heifers. Beef Cattle Extension Publication, Issue 21, University of Minnesota, pp. 1-15.
[138] Nichols, W.T., M.I. Wray, T.H. Montgomery, B. Schutte, J.B. Morgan, H.G. Dolezal, and D.P. Hutcheson. 1996. The effects of anabolic agents alone and in combination on feedyard performance, carcass characteristics, and meat quality of finishing heifers fed for 108, 131, of 143 days. Tech Bull. 3. Hoechst-Roussel Agri-Vet., Co., Somerville, NJ.
[139] Schroeder, A.L., D.M. Polser, S.B. Laudert, and G.J. Vogel. 2003. The effect of Optaflexx on growth performance and carcass traits of steers. Optaflexx Exchange, No.1. Elanco Animal Health, Greenfield, IN. pp 1-6.
[140] Schroeder, A.L., D.M. Polser, S.B. Laudert, and G.J. Vogel. 2003. The effect of Optaflexx on sensory properties of beef. Optaflexx Exchange, No.3. Elanco Animal Health, Greenfield, IN. pp 1-7.
[141] Koch, R.M., M.E. Dikeman, D.M. Allen, M. May, J.D. Crouse, and D.R. Campion. 1976. Characterization of biological types of cattle. III. Carcass composition, quality and palatability. J. Anim. Sci. 43:48-62.
[142] Koch, R.M., M.E. Dikeman, R.J. Lipsey, D.M. Allen, and J.D. Crouse. 1979. Characterization of biological types of cattle – cycle II: III. Carcass composition, quality and palatability. J. Anim. Sci. 49:448-460.
[143] Koch, R.M., M.E. Dikeman, and J.D. Crouse. 1982a. Characterization of biological types of cattle (cycle III). III. Carcass composition, quality and palatability. J. Anim. Sci. 54:35-45.
[144] Wheeler, T.L., L.V. Cundiff, S.D. Shackelford, and M. Koohmaraie. 1996. Characterization of biological types of cattle (Cycle IV): Carcass traits and longissimus palatability. J. Anim. Sci. 74:1023-1035.
[145] Wheeler, T.L., L.V. Cundiff, S.D. Shackelford, and M. Koohmaraie. 2001. Characterization of biological types of cattle (Cycle V): Carcass traits and longissimus palatability. J. Anim. Sci. 79:1209-1222.
[146] Cundiff, L.V., T.L. Wheeler, S.D. Shackelford, M. Koohmaraie, R.M. Thallman, K.E. Gregory, and L.D. Van Vleck. 2001a. Preliminary results from Cycle VI of the cattle Germplasm Evaluation Program at the Roman L. Hruska U.S. Meat Animal Research Center. Germplasm Evaluation Program Progress Report No. 20. USDA, ARS.
[147] Cundiff, L.V., T.L. Wheeler, K.E. Gregory, S.D. Shackelford, M. Koohmaraie, R.M. Thallman, G.D. Snowder, and L.D. Van Vleck. 2001b. Preliminary results from Cycle VII of the cattle Germplasm Evaluation Program at the Roman L. Hruska U.S. Meat Animal Research Center. Germplasm Evaluation Program Progress Report No. 22. USDA, ARS.
[148] Cundiff, L.V. 1992. Genetic selection to improve the quality and composition of beef carcasses. Proc. Recip. Meat Conf. 45:123-131.
[149] Shackelford, S.D., M. Koohmaraie, L.V. Cundiff, K.E. Gregory, G.A. Rohrer, and J.W. Savell. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield, and growth rate. J. Anim. Sci. 72:857-863.
[150] Whipple, G., M. Koohmaraie, M.E. Dikeman, J.D. Crouse, M.C. Hunt, and R.D. Klemm. 1990. Evaluation of attributes that affect longissimus muscle tenderness in *Bos taurus* and *Bos indicus* cattle. J. Anim. Sci. 68:2716-2728.

BEEF®
Funded by the Beef Checkoff

[151] Wulf, D. M., J. D. Tatum, R. D. Green, J. B. Morgan, B. L. Golden, and G. C. Smith. 1996b. Genetic influences on beef *longissimus* palatability in Charolais- and Limousin-sired steers and heifers. J. Anim. Sci. 74:2394-2405.
[152] O'Connor, S.F., J.D. Tatum, D.M. Wulf, R.D. Green, and G.C. Smith. 1997. Genetic effects on beef tenderness in *Bos indicus* composite and Bos taurus cattle. J. Anim. Sci. 75:1822-1830.
[153] Arnold, H., M.A. Della-Fera, and C.A. Baile. 2001. Review of myostatin history, physiology, and applications. Int. Arch. Biosci. 2001:1014-1022.
[154] Tatum, J.D., K.W. Gronewald, S.C. Seideman, and W.D. Lamm. 1990. Composition and quality of beef from steers sired by Piedmontese, Gelbvieh, and Red Angus bulls. J. Anim. Sci. 68:1049-1060.
[155] Liboriussen, T. 1982. Comparison of sire breeds represented by double muscled and normal sires. In: J.W.B. King and F. Menissier (ed.) Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production: Current Topics in Veterinary Medicine and Animal Science. Vol. 16. pp 637-643. Martinus Nijhoff, The Hague.
[156] Bailey, A.F., M.B. Enser, E. Dransfield, D.J. Restall, and N.C. Avery. 1982. Muscle and adipose tissue from normal and double muscled cattle: Collagen types, muscle fibre diameter, fat cell size, and fatty acid composition and organoleptic properties. In: J.W.B. King and F. Menissier (ed.) Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production: Current Topics in Veterinary Medicine and Animal Science. Vol. 16. pp 178. Martinus Nijhoff, The Hague.
[157] Dumont, B.L. and O. Schmitt. Conséquences de l'hypertrophie musculaire héréditaire sur la trame conjontive du muscle de bovin. Ann. Genet. Sel. Anim. 5:499-506.
[158] Wheeler, T.L., S.D. Shackelford, E. Casas, L.V. Cundiff, and M. Koohmaraie. 2001. The effects of Piedmontese inheritance and myostatin genotype on the palatability of *longissimus thoracis, gluteus medius, semimembranosus*, and *biceps femoris*. J. Anim. Sci. 79:3069-3074.
[163] Genetic Solutions. 2003. GeneNOTE 4: GeneSTAR® Tenderness – The first commercial gene marker test for beef tenderness. Available at www.genestar.com.au .
[164] Page, B.T., E. Casas, M.P. Heaton, N.G. Cullen, D.L. Hyndman, C.A. Morris, A.M. Crawford, T.L. Wheeler, M. Koohmaraie, J.W. Keele, and T.P.L. Smith. 2002. Evaluation of single-nucleotide polymorphisms in CAPN1 for association with meat tenderness in cattle. J. Anim. Sci. 80:3077-3085.
[165] Frontier Beef Systems. 2003. MARC calpain tenderness test offered by Frontier Beef Systems. News release available at: www.frontierbeefsystems.com .
[166] Cundiff, L.V. 1993. How breed variations affect carcass quality and cutability. Presented at the National Cattlemen's Association Annual Convention and Tradeshow, Phoenix, AZ. pp. 1-33.
[167] Dikeman, M.E. 1995. Carcass composition and quality of finished crossbred Brahman cattle. Proc. of the King Workshop. Arkansas Exp. Sta. Special Rep. No. 167. pp 77-88.
[168] Sherbeck, J.A., J.D. Tatum, T.G. Field, J.B. Morgan, and G.C. Smith. 1995. Feedlot performance, carcass traits, and palatability traits of Hereford and HerefordXBrahman steers. J. Anim. Sci. 73:3613-3620.
[169] Tatum, J.D., M.H. George, K.E. Belk, and G.C. Smith. 1997. Development of a Palatability Assurance "Critical Control Points" (PACCP) model to reduce the incidence of beef palatability problems. Final Report submitted to the National Cattlemen's Beef Association, pp 1-29. Department of Animal Sciences, Colorado State University, Fort Collins, CO.
[170] Sherbeck, J.A., J.D. Tatum, T.G. Field, J.B. Morgan, and G.C. Smith. 1996. Effect of phenotypic expression of Brahman breeding on marbling and tenderness traits. J. Anim. Sci. 74:304-309.
[171] Gerken, C.L. 2004. USDA Certified & Process Verified Programs. USDA, AMS. Available from Cara L. Gerken at Cara.Gerken@usda.gov.

BEEF®
Funded by the Beef Checkoff

[172] Ashmore, C.R., F. Carroll, L. Doerr, G. Tomkins, H. Stokes, and W. Parker. 1973. Experimental prevention of dark-cutting meat. J. Anim. Sci. 36:33.
[173] McVeigh, J. and Tarrant. 1981. The breakdown of muscle glycogen during behavioral stress in normal and beta-adrenoreceptor blocked young bulls. In: D.E. Hood and P.V. Tarrant (ed.) The Problem of Dark Cutting in Beef: Current Topics in Veterinary Medicine and Animal Science. Vol. 16. pp 430-439. Martinus Nijhoff, The Hague.
[174] Purchas, R.W. 1990. An assessment of the role of pH differences in determining the relative tenderness of meat from bulls and steers. Meat Sci. 27:129-140.
[175] Wulf, D.M., S.F. O'Connor, J.D. Tatum, and G.C. Smith. 1997. Using objective measures of muscle color to predict beef longissimus tenderness. J. Anim. Sci. 75:684-692.
[176] Watanabe, A., C.C. Daly, and C.E. Devine. 1996. The effects of the ultimate pH of meat on tenderness changes during aging. Meat Sci. 42:67-68.
[177] Wulf, D.M. and J.K. Page. Using measurements of muscle color, pH, and electrical impedance to augment the current USDA beef quality grading standards and improve the accuracy and precision of sorting carcasses into palatability groups. J. Anim. Sci. 78:2595-2607.
[178] Wyle, A.M., D.J. Vote, D.L. Roeber, R.C. Cannell, K.E. Belk, J.A. Scanga, M. Goldberg, J.D. Tatum, and G.C. Smith. 2003. Effectiveness of SmartMV prototype BeefCam System to sort beef carcasses into expected palatability groups. J. Anim. Sci. 81:441-448.
[179] Ferguson, D., J. Thompson, and R. Polkinghorne. 1999. Meat Standards Australia, A PACCP based beef grading scheme for consumers. 3) PACCP requirements which apply to carcass processing. Proc. 45th Intl. Cong. Meat Sci. and Technol. 45:18-19.
[180] Voisinet, B.D., T. Grandin, S.F. O'Connor, J.D. Tatum, and M.J. Deesing. 1997. Bos indicus-cross feedlot cattle with excitable temperaments have tougher meat and a higher incidence of borderline dark cutters. Meat Sci. 46:367-377.
[181] Burrow, H. 2002. Simple, indirect selection for beef tenderness. Mimeograph Report. CSIRO Livestock Industries, Rockhampton, Queensland, Australia. Available at: www.brahman.com.au.
[182] Meat & Livestock Australia. 2000. Tips & Tools On The Effect of pH on Beef Eating Quality (ISBN: 1 74036 355 8). Available at: www.mla.com.au .
[183] Boccard, R.L., R.T. Naude, D.E. Cronje, M.C. Smit, H.J. Venter, and E.J. Rossouw. 1979. The influence of age, sex, and breed of cattle on their muscle characteristics. Meat Sci. 3:261-266.
[184] Cross, H.R., B.D. Schanbacher, and J.D. Crouse. 1984. Sex, age, and breed related changes in bovine testosterone and intramuscular collagen. Meat Sci. 10:187-195.
[185] Morgan, J.B., T.L. Wheeler, M. Koohmaraie, J.W. Savell, and J.D. Crouse. 1993. Meat tenderness and the calpain proetolytic system in longissimus muscle of young bulls and steers. J. Anim. Sci. 71:1471-1476.
[186] Seideman, S.C., H.R. Cross, R.R. Oltjen, and B.D. Schanbacher. 1982. Utilization of the intact male for red meat production: A review. J. Anim. Sci. 55:826-840.
[187] NCBA. 1996. Final report of the beef palatability task force. pp 1-9. Natonal Cattlemen's Beef Association, Centennial, CO.
[188] Martinez-Peraza, M.J., K.E. Belk, J.D. Tatum, and G.C. Smith. 1999. Effects of age at castration, implant strategy, and aging on the tenderness of longissimus muscle steaks derived from steers, late castrates, and intact bulls. 1999 Beef Program Rep., Dept. of Anim. Sci., Colorado State Univ., Fort Collins. Pp 135-150.
[189] Gracia, E., J.D. Sink, L.L. Wilson, and J.H. Ziegler. 1970. Sex, sire, and physiological factors affecting muscle protein solubility and other characteristics. J. Anim. Sci. 31:42-46.
[190] Prost, E., E. Pelczyńska, and A.W. Kotula. 1975. Quality characteristics of bovine meat. II. Beef tenderness in relation to individual muscles, age and sex of animals and carcass quality grade. J. Anim. Sci. 41:541-547.

BEEF®
Funded by the Beef Checkoff

[191] Kropf, D.H. and R.L. Graf. 1959. The effect of grade, weight, and class of beef carcasses upon certain chemical and sensory evaluations of beef quality. Food Technol. 13:719-721.
[192] Choat, W.T., J.A. Paterson, B.M. Rainey, M.C. King, R.J. Lipsey, K.E. Belk, and G. C. Smith. 2003. The effects of cattle gender on feedlot performance, carcass characteristics, and muscle tenderness. Proc. West. Sec. Amer. Soc. Anim. Sci. 54:22-26.
[193] Voisinet, B.L., T. Grandin, J.D. Tatum, S.F. O'Connor, and J.J. Struthers. 1997. Feedlot cattle with calm temperaments have higher average daily gains than cattle with excitable temperaments. J. Anim. Sci. 75:892-896.
[194] Gardner, B.A., S.L. Northcutt, H.G. Dolezal, D.R. Gill, F.K. Ray, J.B. Morgan, and C.W. Shearhart. 1996. Factors influencing profitability of feedlot steers. An. Sci. Res. Rep., Oklahoma Agricultural Experiment Station, Oklahoma State University, Stillwater. P 164.
[195] Gardner, B.A., H.G. Dolezal, L.K. Bryant, F.N. Owens, and R.A. Smith. 1999. Health of finishing steers: Effects on performance, carcass traits, and meat tenderness. J. Anim. Sci. 77:3168-3175.
[196] Roeber, D.L., N.C. Speer, J.G. Gentry, J.D. Tatum, C.D. Smith, J.C. Whittier, G.F. Jones, K.E. Belk, and G.C. Smith. 2001. Feeder cattle health management: Effects on morbidity rates, feedlot performance, carcass characteristics, and beef palatability. Prof. Anim. Sci. 17:39-44.
[197] George, M.H., P.E. Heinrich, D.R. Dexter, J.B. Morgan, K.G. Odde, R.D. Glock, J.D. Tatum, G.L. Cowman, and G.C. Smith. 1995. Injection-site lesions in carcasses produced by cattle receiving injections at branding and at weaning. J. Anim. Sci. 73:3235-3240.
[198] George, M.H., J.B. Morgan, R.D. Glock, J.D. Tatum, G.R.Schmidt, J.N. Sofos, G.L. Cowman, and G.C. Smith. 1995. Injection-site lesions: Incidence, tissue histology, collagen concentration, and muscle tenderness in beef rounds. J. Anim. Sci. 73:3510-3518.
[199] Roeber, D.L., R.C. Cannell, K.E. Belk, J.A. Scanga, G.L. Cowman, and G.C. Smith. 2001. Frequency of injection-site lesions in beef top sirloin butts. J. Anim. Sci. 79:2615-2618.
[200] Roeber, D.L., R.C. Cannell, W.R. Wailes, K.E. Belk, J.A. Scanga, J.N. Sofos, G.L. Cowman, and G.C. Smith. 2002. Frequencies of injection-site lesions in muscles from rounds of dairy and beef cow carcasses. J. Dairy Sci. 85:532-536.
[201] Deming, W.E. 1986. Out of the Crisis. Massachusetts Institute of Technology, Center for Advanced Educational Services, Cambridge, MA.
[202] Wheeler, T.L., D. Vote, J.M. Leheska, S.D. Shackelford, K.E. Belk, D.M. Wulf, B.L. Gwartney, and M. Koohmaraie. 2002. The efficacy of three objective systems for identifying beef cuts that can be guaranteed tender. J. Anim. Sci. 80:3315-3327.
[203] Thompson, J. 2002. Managing meat tenderness. Proc. 48th Intl. Cong. Meat Sci. and Technol. 48:17-27.

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Funded by the Beef Checkoff