Improving the sensory and nutritional quality of fresh meat

Edited by
Joseph P. Kerry and David Ledward

CRC Press
Boca Raton Boston New York Washington, DC

WOODHEAD PUBLISHING LIMITED
Cambridge New Delhi

3

Fresh meat texture and tenderness

D. A. King, T. L. Wheeler, S. D. Shackelford and M. Koohmaraie, US Meat Animal Research Center, USA

Abstract: Strategies to consistently produce tender meat products should help maintain and build consumer confidence. Numerous antemortem and postmortem factors can impact upon tenderness, both positively and negatively. Generally, these effects are mediated through alteration of sarcomere length, postmortem proteolysis, or connective tissue integrity. The interaction of these component traits is complex and muscle dependent. Therefore, antemortem and postmortem management decisions must be made carefully, possibly on a muscle-by-muscle basis. This chapter discusses antemortem and postmortem management strategies that can be used to influence meat tenderness attributes. Additionally, tenderness assessment and prediction are addressed.

Key words: genetic markers, management, meat tenderness, prediction.

3.1 Introduction

Consumers have certain expectations regarding the quality of the meat they purchase. Eating satisfaction is determined by the perceived value delivered by three palatability traits: tenderness, juiciness, and flavor. Each of these traits is important and deficiency in any one of them could result in consumer dissatisfaction. However, the majority of meat palatability research has emphasized tenderness because of its importance in consumer perceptions of muscle foods. The importance of tenderness is evidenced by consumers' ability to discern differences in tenderness and willingness to pay premiums for guaranteed tender products (Boleman *et al.*, 1997; Lusk *et al.*, 2001; Shackelford *et al.*, 2001). Additional evidence comes from consumer survey results indicating that, of the three palatability traits, tenderness is the most important contributor to their eating satisfaction (Miller *et al.*, 1995). Certain cuts of beef have been reported to be inconsistent with regard to tenderness and need improvement relative to consumer

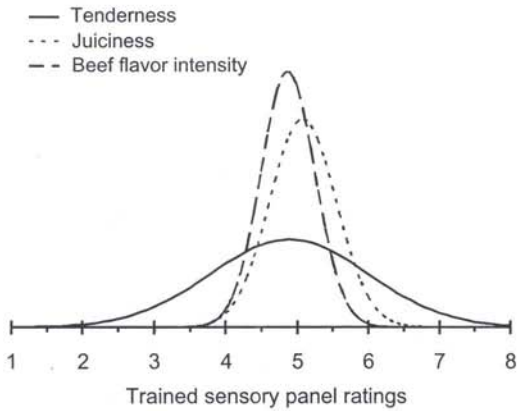

Fig. 3.1 Variation in tenderness, flavor, and juiciness ratings for beef *longissimus* steaks from young, grain-fed steers. Adapted from Wheeler *et al.* (2001a).

expectations (Neely *et al.*, 1998; Savell *et al.*, 1999; Brooks *et al.*, 2000; Behrends *et al.*, 2005).

Tenderness is the most variable of the three palatability traits (Fig. 3.1). In large studies comparing animals of diverse genetic backgrounds reared in a calf-fed, corn–corn silage based production system, animal-to-animal variation in tenderness traits is more than double the variation observed in flavor intensity and juiciness (Wheeler *et al.*, 1996a, 2001a). Furthermore, tenderness differences across muscles within carcasses have been reported to be larger than differences in flavor or juiciness (Carmack *et al.*, 1995; Shackelford *et al.*, 1995; Rhee *et al.*, 2004). Additionally, Rhee *et al.* (2004) and Searls *et al.* (2005) reported substantial differences in Warner–Bratzler shear force values across locations within some muscles.

3.2 Muscle constituents and structure contributing to tenderness variation

Physical and chemical properties of muscle interact to determine the tenderness of the resulting meat products. Therefore, it is important to understand the muscle constituents and structures that contribute to the variation in tenderness. For a review of the macroscopic and microscopic structure of muscle, muscle contraction, and the conversion of muscle to meat, the reader is referred to Aberle *et al.* (2001). Numerous sources contribute to the variation in tenderness of meat; however, these effects ultimately are asserted by altering one or more of three component traits: connective tissue amount and quality, sarcomere length, and the rate and extent of postmortem proteolysis of key structural proteins are considered to be the primary component traits contributing to explainable tenderness variation.

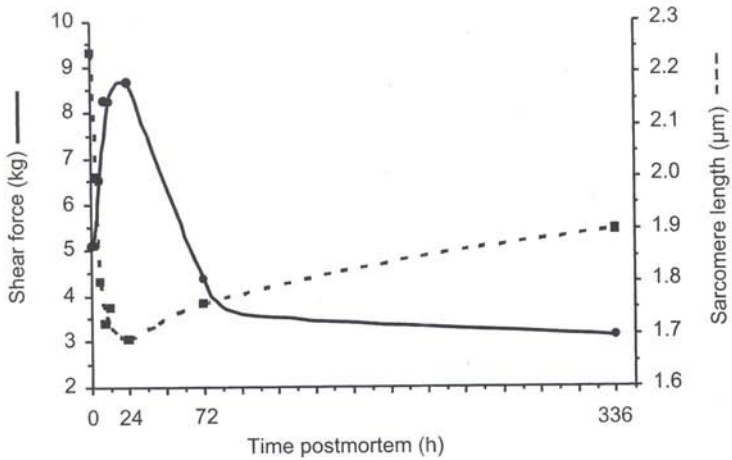

Fig. 3.2 Changes in Warner–Bratzler shear force and sarcomere length in lamb *longissimus* muscle during chilling and postmortem storage. Adapted from Wheeler and Koohmaraie (1994).

The connective tissue fraction of meat, predominantly comprised of collagen, provides structural support to muscles and transfers force generated during contraction to the skeleton. The contribution of collagen to meat tenderness is determined by a number of factors, such as total collagen concentration, types of collagen present, and cross-linking of the collagen matrix. The effects of connective tissue on tenderness is often referred to as 'background toughness' (Marsh, 1977) and are thought to be a minor source of animal-to-animal variation in *longissimus* tenderness of young animals. However, as animals mature, intermolecular cross-linking stabilizes the collagen matrix (Avery *et al.*, 1996). The stabilized collagen is more resistant to solubilization by heating, which increases meat toughness (Goll *et al.*, 1964; Shorthose and Harris, 1990).

Total collagen content varies between muscles depending on their skeletal location and function in the live animal, and partially explains tenderness differences between muscles (McKeith *et al.*, 1985; Wheeler *et al.*, 2000b; Rhee *et al.*, 2004). For example, muscles located in the limbs of the animal, which are used for locomotion, generally have greater collagen concentrations than support muscles located in the epaxial regions.

The contractile state of muscle is a key contributor to the myofibrillar tenderness of meat. The increased overlap of the thick and thin filaments associated with contracted muscle (i.e. shorter sarcomeres) is associated with greater toughness (Locker and Hagyard, 1963; Marsh and Leet, 1966). Wheeler and Koohmaraie (1994) measured the effects of rigor and early postmortem storage on sarcomere length of lamb *longissimus* and the consequential effects on tenderness (Fig. 3.2). Sarcomere length was longest at death and was reduced to a minimum at 24 h.

Warner–Bratzler shear force increased to a maximum at 24 h and improved dramatically during 14 d of ageing. When sarcomere shortening during rigor was prevented, the increase in Warner–Bratzler shear force during the first hours postmortem was not observed (Koohmaraie *et al.*, 1996a). However, tenderization still occurred. Collectively, these results indicate that lamb *longissimus* is intermediate in tenderness at death and rigor shortening causes a reduction in tenderness during the first 24 h. At some point after death, degradation of structural proteins is initiated and results in tenderization. Veiseth *et al.* (2004) reported that calpain degradation of key structural proteins began within a few hours postmortem. Therefore, in muscles with low to intermediate collagen concentrations, the ultimate tenderness of the muscle is dictated by the extent of sarcomere shortening that is allowed to occur and how much postmortem protein degradation occurs.

After death, tenderization begins and will continue at varying rates and for varying periods of time postmortem. For detailed reviews of the tenderization process, the reader is referred to Koohmaraie (1992a, 1995, 1996). Postmortem changes that are observed during refrigerated storage include loss of Z-disk and sarcomere integrity resulting from proteolytic degradation of numerous cytoskeletal proteins such as troponin-T, titin, nebulin, desmin, vinculin, filamin, synemin, and dystrophin (Taylor *et al.*, 1995; Koohmaraie, 1992a, 1996). The proteins observed to be degraded in postmortem meat function to provide muscle integrity through involvement in inter- (e.g. desmin and vinculin) and intra-myofibril (e.g. titin, nebulin, and possibly troponin-T) linkages and the attachment of muscle cells to the basal lamina (e.g. laminin, and fibronectin) (Price, 1991; Robson *et al.*, 1997). Therefore, it is evident that degrading these proteins results in a weakening of the myofibril structure, resulting in tenderization. However, it is notable that the major contractile proteins, actin and myosin, are unaffected during postmortem storage.

Numerous investigations have been conducted to deduce the proteolytic system responsible for these changes. Lysosomal proteases (e.g. cathepsins; Goll *et al.*, 1983; Ouali and Valin, 1980; Zeece *et al.*, 1992), multicatalytic proteinase complex (Goll, 1991; Koohmaraie, 1992c, 1994) and the calpain system (Ouali and Talmant, 1990; Koohmaraie *et al.*, 1992b, 1995, 1996) have all been examined as potentially causing the tenderization observed during postmortem storage. Of these, only the calpain system has been found to produce the changes normally seen in postmortem muscle (Koohmaraie, 1996). Calpain mediated proteolysis of cytoskeletal proteins begins soon after death (Veiseth *et al.*, 2004) and continues for some period of time, depending on species.

Collectively, connective tissue content, sarcomere length, and the extent of postmortem proteolysis of myofibrillar proteins can explain the majority of the variations in tenderness. However, their interaction is complex and is muscle dependent. For example, psoas major is very tender due to long sarcomere lengths and low collagen content, despite a very low amount of postmortem proteolysis. Biceps femoris is relatively tough due to high collagen concentration and medium sarcomere length, despite having as much or more proteolysis as all other muscles (Rhee *et al.*, 2004).

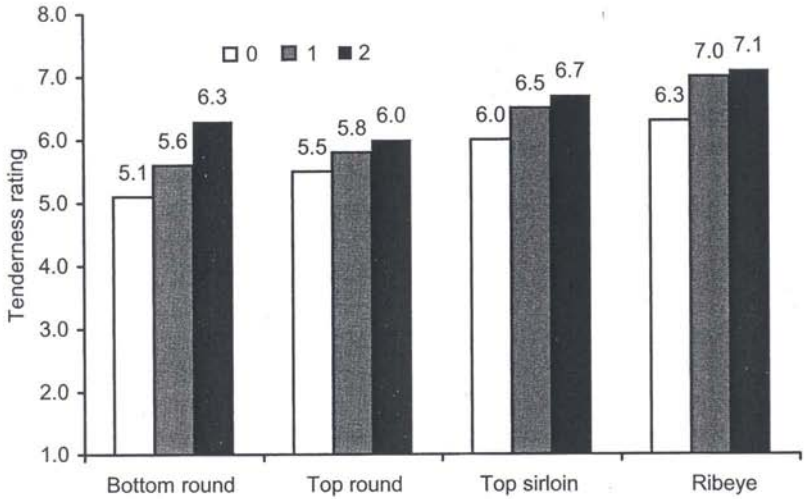

Fig. 3.3 Trained sensory panel tenderness ratings for four beef muscles from Piedmontese cross cattle with 0, 1, or 2 copies of the inactive myostatin allele. Adapted from Wheeler *et al.* (2001b).

3.3 Antemortem factors affecting meat tenderness

3.3.1 Genetic conditions affecting tenderness

Meat tenderness is affected by complex interactions of multiple antemortem and postmortem factors. Genetics determine an animal's potential for producing tender meat, and the interaction of genetics with ante- and postmortem environment and management will determine the ultimate tenderness of the meat from an animal. A mutation in the myostatin gene has been associated with the condition in cattle known as 'double muscling' (Grobet *et al.*, 1997; Kambadur *et al.*, 1997; McPherron and Lee, 1997; Smith *et al.*, 1997). This syndrome is characterized by embryonic hyperplasia caused by inactive myostatin, which normally inhibits cell-proliferation. Carcasses of double-muscled cattle yield a greater percentage of retail product than carcasses of normal cattle (Arthur, 1995; Wheeler *et al.*, 1997a). Additionally, meat from these animals is more tender, primarily due to reduced collagen concentration (Wheeler, unpublished data). Animals with one or two inactive myostatin alleles produced ribeye, top sirloin, bottom round, and top round steaks that received greater trained sensory panel tenderness ratings than animals with two normal alleles at the myostatin locus (Fig. 3.3; Wheeler *et al.*, 2001b). In addition, bottom round steaks from animals with two inactive myostatin allele received higher tenderness ratings than steaks from animals with one inactive allele. In all muscles evaluated, increasing the number of inactive myostatin

alleles decreased collagen concentration (Wheeler, unpublished data). This trend was more pronounced in the bottom round, which had the highest collagen content of the four muscles evaluated.

Cattle with *Bos indicus* inheritance are commonly used in tropical and subtropical environments. The heat tolerance and insect resistance possessed by these breeds, coupled with their maternal characteristics, have made them a valuable part of beef production in these regions. However, *Bos indicus* cattle, especially Brahman, have been repeatedly reported to produce tougher meat than *Bos taurus* cattle (Koch *et al.*, 1982; Peacock *et al.*, 1982; Crouse *et al.*, 1989; Wheeler *et al.*, 1990a,b, 1996a, 2001a). Increased toughness of meat produced by *Bos indicus* cattle has been demonstrated to be due to increased calpastatin levels (Wheeler *et al.*, 1990b; Whipple *et al.*, 1990b; Pringle *et al.*, 1997), resulting in less proteolytic degradation (Whipple *et al.*, 1990b) and slower improvements in tenderness with ageing (Wheeler *et al.*, 1990a,b; O'Connor *et al.*, 1997) in meat from *Bos indicus*-influenced carcasses. Breeding programs utilizing *Bos taurus* × *Bos indicus* matings are commonly used to capitalize on heterosis and the positive traits possessed by *Bos indicus* breeds. Crouse *et al.* (1989) reported that increasing the proportion of Brahman inheritance from 0 to 100% resulted in progressive decreases in trained sensory panel tenderness ratings. This effect was even more pronounced as percentage of Sahiwal inheritance increased from 0 to 100%. Additionally, the variation in tenderness within a breed group increased as the percentage of *Bos indicus* inheritance increased. In partial agreement, Johnson *et al.* (1990) reported that increasing Brahman influence reduced tenderness scores and inhibited improvements in Warner–Bratzler shear force after 5 or 10 d of ageing. However, Johnson *et al.* (1990) reported no difference in tenderness or ageing response between Angus and ¼ Brahman steers. The use of composite breeds comprised of 3/8 *Bos indicus* inheritance and 5/8 *Bos taurus* inheritance is commonly used by beef producers to incorporate the positive attributes of *Bos indicus* cattle. Bidner *et al.* (2002) reported that calves sired by bulls of Brahman derivative breeds (3/8 Brahman) were less tender after 10 d of ageing than calves sired by Angus bulls. This is in agreement with the results of O'Connor *et al.* (1997) which found that *longissimus* steaks from 3/8 *Bos indicus* steers produced higher shear force values when compared to *Bos taurus* steers after ageing up to 35 d postmortem, regardless of the source of the *Bos taurus* germplasm.

A muscle hypertrophy condition in lamb that causes dramatic toughening of the resulting meat is called callipyge (Cockett *et al.*, 1994, 2005; Koohmaraie *et al.*, 1995; Carpenter *et al.*, 1996; Freking *et al.*, 1998). The hypertrophy is caused by decreased protein degradation, and is associated with increased calpastatin activity in the hypertrophied muscles (Koohmaraie *et al.*, 1995; Lorenzen *et al.*, 2000). The response of various muscles to the callipyge condition is proportional to the increase in calpastatin activity within the muscle (Koohmaraie *et al.*, 1995). The meat from callipyge lamb is less tender than normal lamb because the higher calpastatin activity inhibits the rate and extent of postmortem proteolysis by μ-calpain (Koohmaraie *et al.*, 1995).

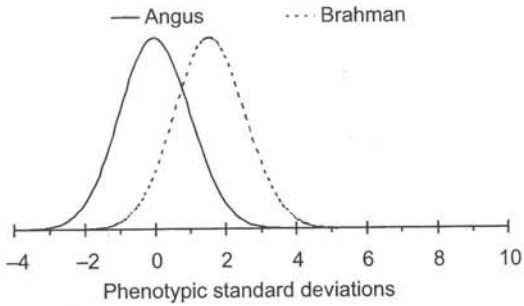

Fig. 3.4 Phenotypic variation in *longissimus* tenderness of Angus- (most tender breed represented) and Brahman- (toughest breed represented) sired progeny. Adapted from Wheeler *et al.* (2001a).

3.3.2 Genomic approaches to meat tenderness

Measures of tenderness have been reported to be moderately heritable, with estimates ranging from 0.30 to 0.53 (Shackelford *et al.*, 1994; Wheeler *et al.*, 1996a, 2001a, 2004a, 2005; Dikeman *et al.*, 2005). Smith *et al.* (2003) estimated that 46% of the variation in tenderness is genetic and 54% is environmental. This indicates that improving tenderness via genetic selection is possible. Palatability trait differences have been characterized among cattle breeds (Koch *et al.*, 1982; Wheeler *et al.*, 1996a, 2001a, 2004a, 2005) and are considered in cross-breeding programs. However, substantial variation in tenderness exists within breeds and the opportunity for improving tenderness by selecting seedstock within a breed may be as great, or greater, than by changing breeds (Fig. 3.4; Wheeler, *et al.*, 1996a, 2001a).

Several quantitative trait loci (QTL) associated with tenderness have been identified (Smith *et al.*, 2003). Of these, two have been found that correspond to the genes responsible for μ-calpain (CAPN1) and its inhibitor calpastatin (CAST). Two SNP markers with significant utility for marker-assisted selection have been identified for the CAPN1 gene (Page *et al.*, 2002; White *et al.*, 2005). The allele associated with improved tenderness in one of these markers (CAPN1 316) is present at low to intermediate frequencies in *Bos taurus* populations (Table 3.1; Page *et al.*, 2004), but segregate less appreciably in *Bos indicus* populations (Casas *et al.*, 2005). A second marker (CAPN1 4751) was reported by White *et al.* (2005) to segregate in both *Bos taurus* and *Bos indicus* populations. These authors suggested that simultaneous analysis of the CAPN1 316 and 4751 markers would provide optimal information in marker assisted selection for tenderness at the μ-calpain locus. Several markers flanking the CAST gene have been demonstrated to be associated with tenderness (Casas *et al.*, 2006; Schenkel *et al.*, 2006). The favorable allele of one of these markers has been reported to have a frequency of approximately 60% in commercial cattle (Table 3.1.; Schenkel *et al.*, 2006). Casas *et al.* (2006) reported that the effects of the CAPN1 and CAST loci appear to be

Table 3.1 Frequencies of favorable alleles and effects of unfavorable alleles of SNP markers for Warner–Bratzler shear force values measured at 14 d postmortem

Population	Favorable allele	Frequency (%)	Effect of unfavorable allele 14 d WBSF (kg)		Source
			Heterozygous unfavorable	Homozygous unfavorable	
CAST					
Bos taurus	T	79	0.29	0.31	Casas *et al.* (2006)
Bos indicus	T	72	0.28	0.48	Casas *et al.* (2006)
Bos taurus × *Bos indicus*	T	83	0.05	0.47	Casas *et al.* (2006)
$CAST_{RsaI}$					
Bos taurus	C	63	0.16	0.21	Schenkel *et al.* (2006)
$CAPN1_{316}$					
Bos taurus	C	32	0.16	0.29	Page *et al.* (2004)
Bos indicus	C	1	–	–	Casas *et al.* (2005)
Bos taurus × *Bos indicus*	C	41	0.18	0.55	White *et al.* (2005)
$CAPN1_{4751}$					
Bos taurus	C	58	–0.014	0.27	White *et al.* (2005)
Bos indicus	C	10	0.40	–	White *et al.* (2005)
Bos taurus × *Bos indicus*	C	64	0.28	0.44	White *et al.* (2005)

additive and do not interact. Therefore, it appears that markers for both of these genes can be used simultaneously in breeding programs to improve tenderness. Markers for both genes are available in commercial tests. The effects of these markers on tenderness are relatively small (Table 3.1), but indicate significant opportunity to improve the tenderness of the beef population.

Continuing efforts are needed to validate the effectiveness of these markers on independent resource populations as well as samples of commercial cattle. Additionally, it is likely that additional markers will be identified and developed as new populations become available. Furthermore, understanding how the genes identified by these markers interact with one another and with environmental factors to affect tenderness is needed. Knowledge of those interactions would allow the development of expected progeny differences (EPDs) that are adjusted based on genetic marker information (Smith *et al.*, 2003). Finally, research on the interaction between genotype and management strategies will allow a whole-system approach to improving tenderness.

3.3.3 Grain feeding effects on tenderness

In the U.S. and other countries, market animals are commonly placed in feed lots and given *ad libitum* access to concentrate-based rations to produce rapid, efficient

growth and to ensure that animals reach slaughter weights at young ages. This practice has been reported to produce heavier, fatter, and more muscular carcasses compared to forage feeding (Bowling *et al.*, 1977; Aberle *et al.*, 1981). Concentrate-fed animals also produced steaks that were more tender than forage-fed animals. Increased mass and fat thickness in grain-fed carcasses slows chilling and, consequently, reduces sarcomere shortening during the onset of rigor (Tatum, 1981). Bowling *et al.* (1977) compared the tenderness of meat from grain-fed steer carcasses and slowly or conventionally chilled forage-fed carcasses. Sarcomere lengths were longest in grain-fed carcasses, shortest in conventionally chilled, forage-fed carcasses, and intermediate in slowly chilled, forage-fed carcasses. Trained sensory panel tenderness ratings were highest for meat from grain-fed carcasses and did not differ across chilling rates.

These data suggest that increased tenderness associated with grain feeding is not solely due to reduced sarcomere shortening. The improved tenderness of grain-fed animals is likely attributable to increased growth rate, which has been associated with increased protein turnover (Koohmaraie *et al.*, 2002), postmortem proteolysis (Aberle *et al.*, 1981; Purchas *et al.*, 2002), and collagen solubility (Aberle *et al.*, 1981). Aberle *et al.* (1981) reported that increasing time on a high-energy diet to 70 d increased tenderness ratings, myofibril fragmentation index (a measure of proteolytic degradation), and collagen solubility. These authors attributed these differences to rapid growth in grain-fed animals. These findings are consistent with those of May *et al.* (1992), who found that sensory panel tenderness ratings were optimized at 84 d on feed. Tatum *et al.* (1980) found no improvements in tenderness associated with feeding steers longer than 100 d. Short *et al.* (1999) reported that tenderness increased with increasing time on feed, but steers placed on feed at 18 mo of age showed no further improvement after 90 d on feed while steers placed on feed at 6 mo of age displayed slight improvements through 270 d on feed. These findings suggest that grain feeding cattle for 90 to 100 d should optimize tenderness.

3.3.4 Effects of growth promotants on meat tenderness

Improving the rate and efficiency of growth in market animals is an important economic consideration to livestock producers. Therefore, the administration of agents that partition nutrients towards muscle deposition is a common practice. Though numerous metabolic modifiers have been utilized in meat production, the most commonly used include anabolic steroids and beta adrenergic agonists (BAA). Despite substantial evidence demonstrating the efficacy and safety of using growth promotants, their use is prohibited in some countries, particularly the European Union.

The vast majority of cattle fed in the U.S. receive anabolic steroid implants, which can be broadly classified according to the chemical nature of their active ingredients (estrogens, progestins, androgens, and combination) and the concentration of each (mild or strong; Montgomery *et al.*, 2001). Of single ingredient implants, estrogenic implants are considered most effective in steers while andro-

genic implants are considered most effective in heifers (Dikeman, 2003). Combination implants containing both estrogens and androgens generally provide greater growth responses than single ingredient implants and are, therefore, considered to be most 'aggressive' (Montgomery *et al.*, 2001; Dikeman, 2003). Animals may be implanted at multiple stages of production and may receive multiple implants during the finishing phase. Endless combinations of compounds, dosages, and timing that might be utilized in an implant strategy make discerning the effects of implants extremely complex. However, anabolic implants are generally reported to have neutral or negative effects on meat tenderness compared to non-implanted controls (Morgan, 1997; Montgomery *et al.*, 2001; Dikeman, 2003). In a review of available literature, Morgan (1997) estimated that meat from implanted animals has a Warner–Bratzler shear force value 0.5 kg higher than meat from non-implanted animals. These effects are largely dependent on the implanting strategy used. As implanting strategies increase in aggressiveness (use of androgenic, combination and/or multiple implants), the negative effects on tenderness are amplified (Morgan, 1997; Platter *et al.*, 2003). Schneider *et al.* (2007) reported that Warner–Bratzler shear force values increased linearly as the cumulative dose of estradiol 17-β plus trenbalone acetate (1:10 ratio) increased in two sequential implants. Samber *et al.* (1996) studied several implant protocols and reported that using a mild implanting strategy at the beginning of the feeding period was less detrimental to tenderness than strategies using aggressive implants at the beginning of the feeding period. Platter *et al.* (2003) studied the effects of various lifetime implanting protocols (from approximately 2 mo of age through finishing) and found that Warner–Bratzler shear force values increased as the number of lifetime implants increased from zero to two and from two to three. Steers implanted four or five times had shear force values intermediate to the shear force values of steers implanted two or three times. Dikeman (2003) concluded that cattle should not be implanted within 70 d of slaughter.

Interest in the use of BAA (e.g., Cimaterol, $L_{644,969}$, ractopamine, zilpaterol) in meat animals has increased because of the dramatic increases in lean growth associated with their use. Numerous reports indicate that BAA negatively affects meat tenderness (Dikeman, 2003). The toughening effect is thought to be due to reduced proteolysis resulting from increased calpastatin activity (Koohmaraie *et al.*, 1991, 1996b). In the U.S., BAA have recently been approved for use in swine (ractopamine) and beef cattle (ractopamine and zilpaterol). The compounds also are approved for cattle in some other countries. Feeding pigs either 10 or 20 ppm ractopamine resulted in higher Warner–Bratzler shear force values, but did not affect tenderness scores compared to non-supplemented pigs (Carr *et al.*, 2005). This is in agreement with the findings of Uttaro *et al.* (1993), who reported that 20 ppm ractopamine increased Warner–Bratzler shear force values and decreased myofibril fragmentation in loin chops of supplemented pigs compared with those of non-supplemented pigs. Gruber *et al.* (2007) reported that cattle fed 200 mg/steer/d ractopamine produced steaks that were less tender than non-supplemented control through 21 d of postmortem ageing. In their study, the effect of ractopamine on tenderness was larger in Brahman crossbred steers than in

Continental or British crossbred cattle (0.5, 0.3, 0.2 kg Warner–Bratzler shear force, respectively). Avendaño-Reyes *et al.* (2006) compared cattle fed ractopamine and zilpaterol to non-supplemented controls and found that both compounds increased Warner–Bratzler shear force values of *longissimus* steaks by 10 and 16%, respectively. Strydom and Nel (1999) fed zilpaterol (0.15 mg/kg live weight/d) to steers for the final 30 or 50 days on feed and reported that both zilpaterol treatments reduced sensory panel tenderness ratings by 0.8 units (8 point scale) compared to controls. In comparison, Casey *et al.* (1997) reported even greater increases in Warner–Bratzler shear force due to zilpaterol fed to steers that had been either implanted with 24 mg estradiol and 120 mg trenbalone acetate (1.5 kg) or not implanted (2 kg). Available information indicates that feeding currently available BAA would have detrimental effects on tenderness.

3.4 Postmortem technologies affecting meat tenderness

Once an animal has been harvested, postmortem management strategies can be employed to optimize the tenderness of the resulting meat. These strategies either manipulate the inherent biochemical processes that are active in postmortem muscle, or physically or chemically alter the myofibrillar or connective tissue structures of the muscle. When applied appropriately, postmortem technologies can improve the overall palatability and consistency of meat being produced.

3.4.1 Postmortem ageing

Soon after slaughter, the calpain enzyme system begins degrading cytoskeletal proteins (Koohmaraie, 1996; Veiseth *et al.*, 2004). The rate and extent of the ageing response is influenced by numerous factors such as the calpastatin activity in the muscle, muscle pH, and storage temperature. Though tenderization with ageing is well established, identifying optimum ageing time is difficult. Koohmaraie (1996) recommended that beef, lamb, and pork *longissimus* be stored for 10–14 d, 7–10 d, and 5 d, respectively, to ensure adequate tenderization. It is important to note the results of muscle profiling studies (e.g. Rhee *et al.*, 2004; Von Seggern *et al.*, 2005) suggest that the contribution of component traits driving tenderness differences are muscle dependent. Therefore, the ageing time needed to optimize tenderness is likely to differ across muscles. Gruber *et al.* (2006) reported that 17 muscles differed in ageing response (2 to 28 d of storage) with the decrease in Warner–Bratzler shear force ranging from 0.5 kg in US Choice biceps femoris to 2.5 kg in US Select *longissimus lumborum*. Mies *et al.* (1999) reviewed literature pertaining to different subprimal cuts of beef and recommended ageing times of 12, 11, 11–15, 14, 21, 12, and 15 d for chuck roll (longissimus thoracis and complexus), shoulder clod (triceps brachii and infraspinatus), ribeye roll (longissimus thoracis), strip loin (longissimus lumborum), top sirloin (gluteus medius), bottom round (biceps femoris), and top round (semimembranosus and adductor)

subprimals, respectively. The identification of optimum ageing times for various muscles is further complicated by differing reports on the magnitude of tenderness improvements due to ageing. These inconsistencies in the literature may be partially due to meat that is inherently tender requiring less ageing time to reach a point where no further increases are detectable. Additionally, in some studies, ageing treatments may be confounded with intramuscular differences in tenderness (Rhee *et al.*, 2004) which may potentially mask the effects of ageing on tenderness. King *et al.* (2007) attempted to mitigate the confounding effects of location within the muscle in an investigation of ageing effects on gluteus medius and triceps brachii tenderness by evaluating 50 muscles of each at six ageing times (7 to 42 d postmortem) and sampling a single location in each muscle for tenderness evaluations. In that experiment, slice shear force values decreased by 24 and 21% in gluteus medius and triceps brachii, respectively. However, most of the improvement in slice shear force values (18%) had been achieved by 28 d postmortem in both muscles.

3.4.2 Electrical stimulation

Electrical stimulation applied to pre-rigor carcasses causes muscle contraction and, consequently, rapid depletion of glycogen stores in muscle before chilling. Electrical stimulation has been reported to enhance the tenderness of beef (Cross *et al.*, 1979, 1984; Savell *et al.*, 1981). The improvement in tenderness is generally attributed to the prevention of cold-induced toughening (Cross *et al.*, 1984), activation of endogenous proteases (Bowling *et al.*, 1978; Cross, 1979), and physical disruption of muscle fibers (Savell *et al.*, 1978). Hopkinson *et al.*, (1985) reported that Warner–Bratzler shear force values of *longissimus* steaks from electrically stimulated steer carcasses at 2 d postmortem were similar to *longissimus* steaks from non-stimulated carcasses aged for 14 d (6.41 and 6.35, respectively). This is in agreement with the results of Savell *et al.* (1981), who reported that the improvement in Warner–Bratzler shear force values due to electrical stimulation at 1 d postmortem (25.8%) was similar to the improvement due to 8 d of postmortem ageing (25.1%). Savell *et al.* (1981) also reported that the improvement in tenderness due to electrical stimulation was greater in carcasses that were initially tough than in those carcasses that were inherently tender. Electrical stimulation effects on tenderness are highly dependent on the parameters used in electrical stimulation application. Generally, high voltage is required to elicit a significant tenderization response. The extensive literature regarding electrical stimulation should be consulted for additional information.

3.4.3 Chilling effects on tenderness

During the first 24 h postmortem, anaerobic glycolysis depletes muscle glycogen causing the accumulation of lactate. As a result, muscle pH declines from 7.4 to approximately 5.5. As ATP stores are depleted, actomyosin bonds are fixed. During this process, sarcomere shortening occurs, causing toughening (Wheeler

and Koohmaraie, 1994). At lower temperatures, the sarcoplasmic reticulum's ability to sequester calcium is reduced (Whiting, 1980). As a result, low temperatures (below 10 °C) in early postmortem muscle possessing adequate ATP stores to cause contraction result in sarcomere shortening (Locker and Hagyard, 1963), which causes toughening (Marsh and Leet, 1966; Marsh *et al.*, 1968). This condition is termed 'cold shortening'. Marsh and Leet (1966) suggested that cold shortening could be minimized by not allowing muscle temperatures to fall below 10 °C until muscle pH had declined below 6.2.

Additionally, the rate of temperature decline can have profound effects on proteolytic degradation of muscle proteins. Extremely rapid chilling of longissimus and triceps brachii muscles resulted in less desmin degradation (10 percentage points) during the first 24 h postmortem (King *et al.*, 2003). Rates of desmin degradation were similar in rapidly chilled and conventionally chilled muscles during the next 13 d of ageing. In contrast, Whipple *et al.* (1990a) compared conventional chilling to holding carcasses at ambient temperatures for 6 h before chilling. Delayed chilling provided a more favorable environment for proteolysis, resulting in higher myofibril fragmentation index values at 3, 7, and 14 d postmortem and lower shear force values at 1 d postmortem in carcasses subjected to delayed chilling. However, Warner–Bratzler shear force values were not affected by delayed chilling at 14 d postmortem. Though high-temperature conditioning is effective in improving tenderness, this practice is not recommended due to food safety concerns.

3.4.4 Pre-rigor alterations in carcass position

The extent of sarcomere shortening during the onset of rigor mortis in an intact carcass is limited by skeletal restraint. Herring *et al.* (1965a,b) and Hostetler *et al.* (1970) found that hanging carcasses by the achilles tendon stretches some muscles while allowing others to contract, which impacted tenderness. Several investigators have examined the use of alternative methods of hanging or altering carcasses to increase the tension on valuable muscles. In a method called 'tenderstretch', Hostetler *et al.* (1970 and 1972) hung carcasses by the obturator foramen to stretch the *longissimus* and other valuable muscles. This method is used by some processors in Europe. Carcasses in Australia can be tenderstretched to qualify for a higher quality grade. This strategy is not currently used in the U.S., primarily because tenderstretched carcasses require more space in the chilling cooler, and the shape of muscles from tenderstretched carcasses are not conducive to traditional fabrication methods. However, with the advent of marketing individual muscles, this strategy might merit reconsideration by U.S. processors. Another procedure termed 'tender cut' involves severing the bones and connective tissue at the 12th thoracic vertebrae and in the pelvic girdle to stretch the *longissimus* and round muscles (Wang *et al.*, 1994, 1996; Ludwig *et al.*, 1997). This process places the weight of the carcass on the muscle rather than the skeleton, thereby lengthening sarcomeres and improving tenderness in economically important muscles.

3.4.5 Enhancement strategies to improve tenderness

Processing strategies can be applied to post-rigor muscle to improve palatability. Blade tenderization is commonly applied to cuts destined for food service establishments. In this process, thin, needle-like blades are used to disrupt muscle fibers and connective tissue. George-Evins *et al.* (2004) reported that blade tenderization improved the tenderness of gluteus medius steaks without negative effects on other palatability traits. Savell *et al.* (1977) evaluated the use of blade tenderization on four beef muscles and noted that a single pass through a blade tenderizer decreased shear force values of gluteus medius, semimembranosus, and longissimus steaks, but did not affect biceps femoris steaks relative to non-tenderized controls. A second application of blade tenderization further reduced Warner–Bratzler shear force values of semimembranosus and also improved biceps femoris steaks. Additionally, after a single application of blade tenderization, longissimus steaks received higher sensory panel ratings for overall and myofibrillar tenderness, and perceivable connective tissue (less connective tissue), but were also rated as less juicy. Another approach to muscle enhancement is to use injection of marinades containing non-meat ingredients to increase palatability traits (Miller, 1998). Marinades commonly contain salts (e.g. sodium chloride), water-binders (e.g. sodium phosphates), exogenous enzymes (e.g. papain, bromelain, and ficin), and/or antioxidants (e.g. rosemary). The effects of these solutions on tenderness are mediated through the dilution of myofibrillar proteins, the degradation of myofibrillar or connective tissue proteins by exogenous enzymes or the activation of endogenous enzymes by calcium chloride (Koohmaraie *et al.*, 1989; Wheeler *et al.*, 1992, 1993). Vote *et al.* (2000) found that injecting beef strip loins with distilled water or 0.25% sodium tripolyphosphate solution decreased tenderness relative to untreated controls, but injecting with 0.25% sodium tripolyphosphate, 2.5% sodium lactate, 0.5% sodium chloride solution improved tenderness. Additionally, Vote *et al.* (2000) reported that increasing the level of injection from 7.5 to 15% of green weight provided incremental increases in tenderness. Mueller *et al.* (2006) reported that beef round muscles injected (12% pickup) with a 5% sodium chloride and 2.95% sodium tripolyphosphate solution received higher consumer ratings for tenderness, juiciness, and flavor than blade tenderized or non-injected muscles. Calcium chloride has been used to activate the calpain system and increase tenderization in beef longissimus, semimembranosus, and triceps brachii compared to non-injected or water-injected controls, regardless of injection level, calcium chloride concentration, or time of injection (Wheeler *et al.*, 1993; 1997b); however, no commercial implementation of calcium chloride marinades has occurred to our knowledge.

3.5 Laboratory tenderness assessment

The evaluation of strategies intended to improve tenderness requires that tenderness assessments be accurate and repeatable. AMSA (1995) provides a set of guidelines for tenderness assessment by trained sensory panels and shear force

measurements. Regardless of the method used, care must be exercised to collect accurate and repeatable tenderness data.

3.5.1 Trained sensory panel

The gold standard for tenderness assessment is a trained sensory panel comprised of highly trained individuals. There are numerous ways to use a trained sensory panel, depending on the question to be addressed. One of the most common is a trained descriptive attribute panel for detecting differences in traits such as tenderness, juiciness, and flavor intensity. Some considerations for the selection and training of panel members include availability, motivation, skill, and consistency (Wheeler *et al.*, 1997d). Panelists should be identified, screened to assure their ability to discern differences, and trained as described by Cross *et al.* (1978) and AMSA (1995). Samples presented to the panel must be of sufficient quantity to allow all panel members to evaluate the sample adequately and representative of the inferences to be made. Constant evaluation of the panel and periodic refresher training of the panelists is necessary to prevent drift and to maintain accuracy and precision. In addition, a well trained sensory panel is expensive for a laboratory to maintain.

3.5.2 Untrained/consumer panel

Consumer evaluations of meat products provide excellent information regarding acceptability of products. In-home tests provide important information about consumer acceptance and preferences when actually using the product (e.g. Neely *et al.*, 1998; Savell *et al.*, 1999). However, these studies are complicated by lack of control over sample preparation, consumers failing to complete the study, and the potential for incomplete or incorrect recording of data. Central location consumer panels provide the opportunity to collect consumer impressions while controlling sample presentation and provide a data collection environment that may improve accuracy (e.g. Hoover *et al.*, 1995; Carr *et al.*, 2004). Wheeler *et al.* (2004b) evaluated untrained laboratory consumer panels in relation to slice shear force and noted that consumer panels were able to detect differences in tenderness categories with as few as four panelists, although the correlation of mean panel ratings to slice shear force values increased as the number of panelists increased to 16 ($r = -0.68$ and -0.92 for panels consisting of 4 and 16 panelists, respectively). The repeatability of mean panel scores of duplicate samples was 0.80, although accuracy and repeatability varied widely among individual panelists. These data suggest that, depending on the samples of interest, untrained laboratory consumer panels may be a valuable tool in evaluating meat tenderness.

3.5.3 Warner–Bratzler shear force

Sensory panel data collection is a slow, cumbersome process. The need to collect data on a large number of samples in a narrow time frame has led to the widespread

use of instrumental measures of tenderness. The most common instrumental objective tenderness measurement is Warner–Bratzler shear force. Warner–Bratzler shear force involves shearing 1.27 cm-diameter cores (removed from cooked steaks parallel to the muscle fiber orientation) with a V-notch blade (1.016 mm-thick with a half-round bevel) attached to a load cell on a Warner–Bratzler shear machine or a universal testing machine. Though collection of shear force data is viewed as routine, differences in accuracy and repeatability exist between individual laboratories conducting tests (Wheeler *et al.*, 1997c). Obtaining accurate and repeatable Warner–Bratzler shear force data requires investigators to be vigilant with regard to numerous factors such as cooking methodology, core removal, and shearing of cores (Wheeler *et al.*,1996b, 1998). For detailed discussions of standardizing protocols, the reader is referred to Savell *et al.* (1994) and Wheeler *et al.* (1997d).

3.5.4 Slice shear force

Efforts to develop a rapid tenderness measurement to be used in on-line tenderness classification programs resulted in the advent of slice shear force (Shackelford *et al.*, 1999). Slice shear force involves the shearing of a 1 cm thick × 5 cm long slice removed parallel to the muscle fiber orientation with a flat, blunt-ended blade. The thickness and bevel of the slice shear force blade is the same as those used for the Warner–Bratzler V-notch blade. Slice shear force values are highly repeatable ($r = 0.91$) and more strongly related to trained sensory panel ratings than Warner–Bratzler shear force values ($r = -0.82$ and -0.77, respectively; Shackelford *et al.*, 1999). Additionally, removing 'good' slices for slice shear force is easier than acquiring 'good' cores for Warner–Bratzler shear force. Finally, since slice shear force can be measured on hot steaks and is measured on one slice rather than 6 or more cores, lab throughput is increased relative to Warner–Bratzler shear force.

Other instrumental measures of tenderness have been used, depending on the type of information desired by the investigator. These include compression tests, Allo–Kramer shear, the MIRINZ tenderometer, as well as various modifications of shear tests. Regardless of the type of shear force measured, investigators should be cognizant of the limitations of shear force data. It is common to attempt to identify thresholds for consumer acceptance. However, the inherent differences between labs and varying consumer acuity and perceptions for tenderness make these attempts dubious (Wheeler *et al.*, 1997c,d). A level of tenderness that is perfectly acceptable to one consumer may be completely unacceptable to another. In general, inferences made using shear force data should be limited to relative treatment differences within an experiment. Finally, Warner–Bratzler and slice shear force values do not accurately reflect differences in tenderness between muscles (Harris and Shorthose, 1988). Shackelford *et al.* (1995) reported that Warner–Bratzler shear force values identified few differences among 10 beef muscles, but trained sensory panel ratings stratified these muscles into four tenderness groups. This is likely because shear force measures do not accurately represent the contribution of connective tissue to tenderness differences between

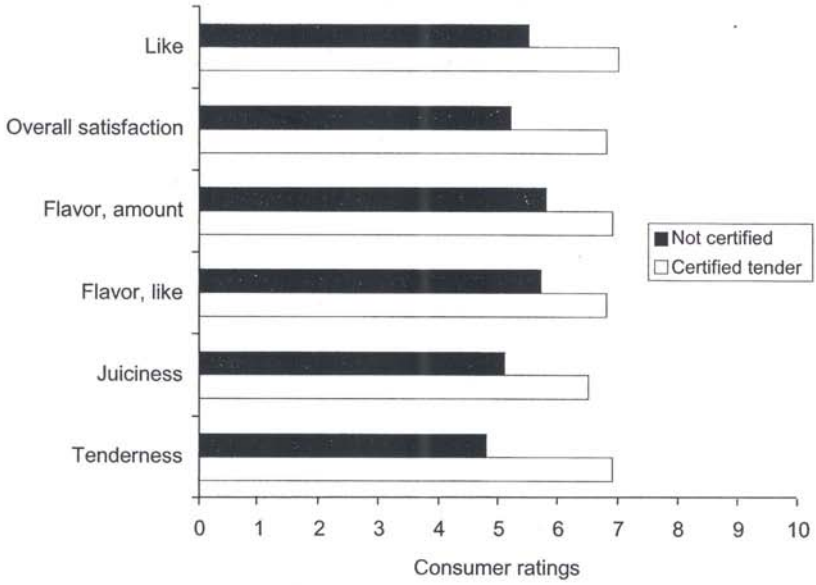

Fig. 3.5 Consumer ratings of sensory traits of steaks certified tender or not-certified by a slice shear force tenderness classification system. Adapted from Shackelford *et al.* (2001).

muscles (Bouton *et al.*, 1978). Those conclusions were confirmed by the results of Rhee *et al.* (2004).

3.6 On-line tenderness prediction

Many investigators have attempted to apply technologies such as Tendertec (George *et al.*, 1997; Belk *et al.*, 2001), connective tissue probe (Swatland, 1995; Swatland and Findlay, 1997; Swatland *et al.*, 1998), elastography (Berg *et al.*, 1999), near-infrared spectroscopy (Hildrum *et al.*, 1994; Park *et al.*, 1998), ultrasound (Park and Whittaker, 1991; Park *et al.*, 1994), image analysis (Li *et al.*, 1999, 2001), lean color attributes (Wulf *et al.*, 1997), image analysis traits using prototype Beef Cam modules (Belk *et al.*, 2000), and a combination of colorimetric, marbling, and hump height traits (Wulf and Page, 2000), for the purpose of tenderness classification of meat, with little success. In the early 1990s, scientists at USMARC concluded that a direct measure of tenderness was required to obtain an accurate enough measurement to create a useful tenderness classification system, if the tenderness assessment could be made at normal processing speeds. To this end, slice shear force was developed and incorporated into a rapid process for cooking and obtaining a slice shear force value of the longissimus muscle as carcasses were presented for grading (Shackelford *et al.* 1998, 1999). Consumers gave higher ratings for all sensory traits to U.S. Select beef classified as tender by slice shear force compared to beef not classified as tender (Fig. 3.5; Shackelford *et al.*, 2001).

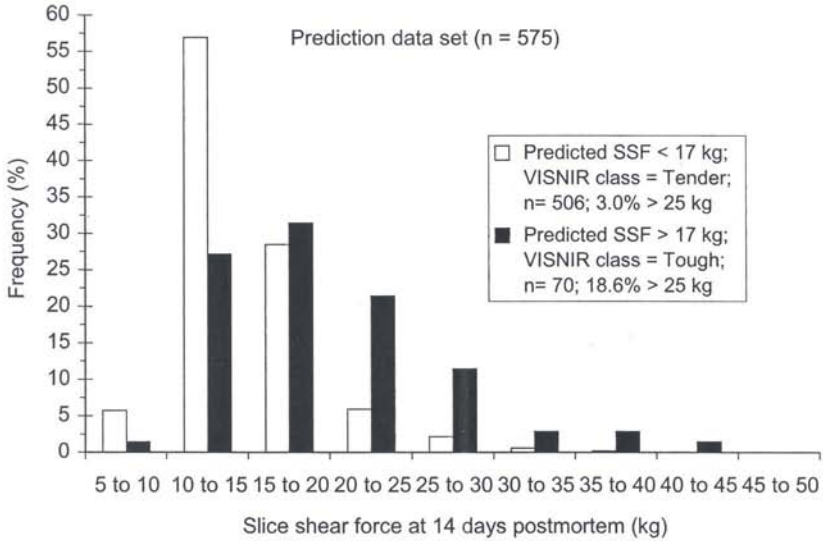

Fig. 3.6 Distribution of slice shear force values of *longissimus* steaks predicted as tough or tender by VISNIR spectroscopy. Adapted from Shackelford *et al.* (2005).

To date, one large beef processor is using the slice shear force technology in cooperation with a large retailer to produce a guaranteed-tender product line. Anticipating that the majority of the industry would deem it to be too invasive and costly for implementation, simultaneous efforts were focused on developing a non-invasive approach. Visible and near-infrared-reflectance (VISNIR) spectroscopy technology appeared to have the most potential to classify beef carcasses according to tenderness (Shackelford *et al.*, 2005). Early application of VISNIR tenderness classification was focused on US Select carcasses because these carcasses are discounted relative to US Choice carcasses, even though the vast majority of US Select carcasses are acceptably tender. Shackelford *et al.*, (2005) reported that VISNIR spectroscopy was effective in identifying carcasses that produced tender meat after ageing. In the validation data set reported in that study, carcasses predicted to be tender had higher sensory panel tenderness ratings compared to those not predicted to be tender (5.6 versus 5.1, respectively). Furthermore, only 5.5 percent of carcasses predicted to be tender had slice shear force values greater than 25 kg compared to 30.1% of those not predicted to be tender (Fig. 3.6). Future research objectives related to tenderness prediction include the application of this technology to carcasses of all quality grades, muscles other than the *longissimus*, and other species.

3.7 Conclusions

Tenderness is critical to the consumer acceptance of meat products. Numerous

antemortem and postmortem factors can impact tenderness, both positively and negatively. Therefore, antemortem and postmortem management decisions must be made carefully. Recent advances in the development of genetic markers for use in selection decisions are encouraging. Meanwhile, antemortem management should strive to optimize efficiency and palatability traits. Tenderness prediction technology can be used to segregate carcasses into product lines. Additionally, postmortem strategies can be used singularly or in concert to further ensure the eating quality of muscle foods.

3.8 Sources of further information and advice

Muscle structure, contraction, and conversion of muscle to meat

Aberle, E.D., Forrest, J.C., Gerrard, D.E., and Mills, E.W. (2001), Principles of Meat Science, Dubuque, IA, USA, Kendall/Hunt Publishing

Postmortem tenderization

Koohmaraie, M. (1994), Muscle proteinases and meat ageing. *Meat Sci.*, **36**, 93–104.

Koohmaraie, M. (1995), The biological basis of meat tenderness and potential genetic approaches for its control and prediction. *Proc. Recip. Meat Conf.*, **48**, 69–75.

Koohmaraie, M. (1996), Biochemical factors regulating the toughening and tenderization process of meat. *Meat Sci.*, **43**, S193–S201

Growth promotants

Dikeman, M.E. (2003), Metablolic modifiers and genetics: Effects on carcass traits and meat quality. *Intl. Cong. Meat Sci. Technol.*, **49**, 1–38.

Montgomery, T.H., Dew, P.F. and Brown, M.S. (2001), Optimizing carcass value and the use of anabolic implants in beef cattle. *J. Anim. Sci.*, **79** (E-Suppl), E296–306.

Morgan, J.B., (1997), Implant programs effects on USDA beef carcass quality grade traits and meat tenderness. Proc. Impact of implants on performance and carcass value of beef cattle, Okla. Agric. Exp. Statn,, Stillwater, P-957:147–154.

Tenderness measurement

AMSA (1995), Research Guidelines for Cookery, Sensory Evaluation, and Instrumental Tenderness Measurements of Fresh Meat. Savoy, IL, American Meat Sci. Assoc.

Cross, H.R., Moen R. and Stanfield, M.S. (1978), Training and testing of judges for sensory analysis of meat quality. *Food Technol.*, **37**, 48.

Savell, J. W., Miller, R. K, Wheeler, T., Koohmaraie, M., Shackelford, S., Morgan, B., Calkins, C., Miller, M., Dikeman, M., McKeith, F., Dolezal, G., Henning, B., Busboom, J., West, R., Parrish, F., and Williams, S. (1994), Standardized Warner–Bratzler shear force procedures for genetic evaluation. Available: http://meat.tamu.edu/shear.pdf Accessed: 30 May, 2007.

Wheeler, T.L., Shackelford, S.D. and Koohmaraie, M. (1997d), Standardizing collection and interpretation of Warner–Bratzler shear force and sensory tenderness data. *Proc. Recip. Meat Conf.*, 50, 68–77.

3.9 References

Aberle, E.D., Forrest, J.C., Gerrard, D.E., and Mills, E.W. (2001), Principles of Meat Science, Dubuque, IA, Kendall/Hunt Publishing.

Aberle, E.D., Reeves, E.S., Judge, M.D., Hunsley, R.E., and Perry, T.W. (1981), Palatability and muscle characteristics of cattle with controlled weight gain: Time on a high energy diet. *J. Anim. Sci.*, 52, 757–763.

AMSA (1995), Research Guidelines for Cookery, Sensory Evaluation, and Instrumental Tenderness Measurements of Fresh Meat. Savoy, IL, Am. Meat Sci. Assoc..

Arthur, P.F. (1995), Double muscling in cattle: A review. *Aust. J. Agric. Res.*, 46, 1493–1515.

Avendano-Reyes, L., Torres-Rodriguez, V., Meraz-Murillo, F.J., Perez-Linares, C., Figueroa-Saavedra, F., and Robinson, P.H. (2006), Effects of two {beta}-adrenergic agonists on finishing performance, carcass characteristics, and meat quality of feedlot steers. *J. Anim Sci.*, 84, 3259–3265.

Avery, N.C., Sims, T.J., Warkup, C., and Bailey, A.J. (1996), Collagen cross-linking in porcine m. longissimus lumborum: Absence of a relationship with variation in texture at pork weight. *Meat Sci.*, 42 (3), 355–369.

Behrends, J.M., Goodson, K.J., Koohmaraie, M., Shackelford, S.D., Wheeler, T.L., Morgan, W.W., Reagan, J.O., Gwartney, B.L., Wise, J.W., and Savell, J.W. (2005), Beef customer satisfaction: Factors affecting consumer evaluations of calcium chloride-injected top sirloin steaks when given instructions for preparation. *J. Anim. Sci.*, 83 (12), 2869–2875.

Belk, K.E., Scanga, J.A., Wyle, A.M., Wulf, D.M., Tatum, J.D., Reagan, J.O., and Smith, G.C. (2000), The use of video image analysis and instrumentation to predict beef palatability. *Proc. Recip. Meat Conf.*, 53, 10–15.

Belk, K.E., George, M.H., Tatum, J.D., Hilton, G.G., Miller, R.K., Koohmaraie, M., Reagan, J.O., and Smith, G.C. (2001), Evaluation of the Tendertec beef grading instrument to predict the tenderness of steaks from beef carcasses. *J. Anim. Sci.*, 79 (3), 688–697.

Berg, E.P., Kallel, F., Hussain, F., Miller, R.K., Ophir, J., and Kehtarnavaz, N. (1999), The use of elastography to measure quality characteristics of pork semimembranosus muscle. *Meat Sci.*, 53 (1), 31–35.

Bidner, T.D., Wyatt, W.E., Humes, P.E., Franke, D.E., and Blouin, D.C. (2002), Influence of Brahman-derivative breeds and Angus on carcass traits, physical composition, and palatability. *J. Anim. Sci.*, 80, 2126–2133.

Boleman, S.J., Boleman, S.L., Miller, R.K., Taylor, J.F., Cross, H.R., Wheeler, T.L., Koohmaraie, M., Shackelford, S.D., Miller, M.F., West, R.L., Johnson, D.D., and Savell, J.W. (1997), Consumer evaluation of beef of known categories of tenderness. *J. Anim. Sci.*, 75, 1521–1524.

Bouton, P.E., Ford, A.L., Harris, P.V., Shorthose, W.R., Ratcliff, D., and Morgan, J.H.L. (1978), Influence of animal age on the tenderness of beef: Muscle differences. *Meat Sci.*, 2, 301–311.

Bowling, R.A., Smith, G.C., Carpenter, Z.L., Dutson, T.R., and Oliver, W.M. (1977), Comparison of forage-finished and grain-finished beef carcasses. *J. Anim. Sci.*, 45, 209–215.

Bowling, R.A., Smith, G.C., Dutson, T.R., and Carpenter, Z.L. (1978), Effect of prerigor conditioning treatments on lamb muscle shortening, pH, and ATP. *J. Food Sci.*, 43, 502–514.

Brooks, J.C., Belew, J.B., Griffin, D.B., Gwartney, B.L., Hale, D.S., Henning, W.R., Johnson, D.D., Morgan, J.B., Parrish, F.C. Jr., Reagan, J.O., and Savell, J.W. (2000), National Beef Tenderness Survey – 1998. *J. Anim. Sci.*, 78, 1852–1860.

Carmack, C.F., Kastner, C.L., Dikeman, M.E., Schwenke, J.R., and Garcia Zepeda, C.M. (1995), Sensory evaluation of beef-flavor intensity, tenderness, and juiciness among major beef muscles. *Meat Sci.*, 39, 143–147.

Carpenter, C.E., Rice, O.D., Cockett, N.E., and Snowder, G.D. (1996), Histology and composition of muscles from normal and callipyge lambs. *J. Anim. Sci.*, 74 (2), 388–393.

Carr, M.A., Crockett, K.L., Ramsey, C.B., and Miller, M.F. (2004), Consumer acceptance of calcium chloride-marinated top loin steaks. *J. Anim Sci.*, 82, 1471–1474.

Carr, S.N., Ivers, D.J., Anderson, D.B., Jones, D.J., Mowrey, D.H., England, M.B., Killefer,

J., Rincker, P.J., and McKeith, F.K. (2005), The effects of ractopamine hydrochloride on lean carcass yields and pork quality characteristics. *J. Anim. Sci.*, 83, 2886–2893.

Casas, E., White, S.N., Riley, D.G., Smith, T.P.L., Brenneman, R.A., Olson, T.A., Johnson, D.D., Coleman, S.W., Bennett, G.L., and Chase, C.C. Jr. (2005), Assessment of single nucleotide polymorphisms in genes residing on chromosomes 14 and 29 for association with carcass composition traits in *Bos indicus* cattle. *J. Anim. Sci.*, 83 (1), 13–19.

Casas, E., White, S.N., Wheeler, T.L., Shackelford, S.D., Koohmaraie, M., Riley, D.G., Chase, C.C. Jr., Johnson, D.D., and Smith, T.P.L. (2006), Effects of calpastatin and {micro}-calpain markers in beef cattle on tenderness traits. *J. Anim. Sci.*, 84 (3), 520–525.

Casey, N.H., Montgomery, T.H., Scheltens, M.L. (1997), The effect of zilpaterol on feedlot performance, carcass quality, USDA carcass grades and meat quality. *Intl. Cong. Meat Sci. and Technol.*, 43, 262–263.

Cockett, N.E., Jackson, S.P., Shay, T.D., Nielsen, D., Moore, S.S., Steele, M.R., Barendse, W., Green, R.D., and Georges, M. (1994), Chromosomal localization of the callipyge gene in sheep (Ovis aries) using bovine DNA markers. *Proc. Natl. Acad. Sci., USA*, 91, 3019–3023.

Cockett, N.E., Smit, M.A., Bidwell, C.A., Segers, K., Hadfield, T.L., Snowder, G.D., Georges, M., and Charlier, C. (2005), The callipyge mutation and other genes that affect muscle hypertrophy in sheep. *Genet. Sel. Evol.*, 37(Suppl. 1), S65–S81.

Cross, H.R. (1979), Effects of electrical stimulation on meat tissue and muscle properties – A review. *J. Food Sci.*, 44, 509–523.

Cross, H.R., Crouse, J.D., and MacNeill, M.D. (1984), Influence of breed, sex, age, and electrical stimulation on carcass and palatability traits of three bovine muscles. *J. Anim. Sci.*, 58, 1358–1365.

Cross, H.R., Moen R., and Stanfield, M.S. (1978), Training and testing of judges for sensory analysis of meat quality. *Food Technol.*, 37, 48

Crouse, J.D., Cundiff, L.V., Koch, R.M., Koohmaraie, M., and Seideman, S.C. (1989), Comparison of *Bos indicus* and *Bos taurus* inheritance for carcass beef characteristics and meat palatability. *J. Anim. Sci.*, 67, 2661–2668.

Dikeman, M.E. (2003), Metablolic modifiers and genetics: Effects on carcass traits and meat quality. *Intl. Cong. Meat Sci. Technol.*, 49, 1–38.

Dikeman, M.E., Pollak, E.J., Zhang, Z., Moser, D.W., Gill, C.A., and Dressler, E.A. (2005), Phenotypic ranges and relationships among carcass and meat palatability traits for fourteen cattle breeds, and heritabilities and expected progeny differences for Warner–Bratzler shear force in three beef cattle breeds. *J. Anim. Sci.*, 83 (10), 2461–2467.

Freking, B.A., Keele, J.W., Nielsen, M.K., and Leymaster, K.A. (1998), Evaluation of the ovine callipyge locus: II. Genotypic effects on growth, slaughter, and carcass traits. *J. Anim. Sci.*, 76 (10), 2549–2559.

George, M.H., Tatum, J.D., Dolezal, H.G., Morgan, J.B., Wise, J.W., Calkins, C.R., Gordon, T., Reagan, J.O., and Smith, G.C. (1997), Comparison of USDA quality grade with Tendertec for the assessment of beef palatability. *J. Anim. Sci.*, 75 (6), 1538–1546.

George-Evins, C.D., Unruh, J.A., Waylan, A.T., and Marsden, J.L. (2004), Influence of quality classification, aging period, blade tenderization, and endpoint cooking temperature on cooking characteristics and tenderness of beef gluteus medius steaks. *J. Anim. Sci.*, 82, 1863–1867.

Goll, D.E. (1991), Role of proteinases and protein turnover in muscle growth and meat quality. *Proc. Recip. Meat Conf.*, 44, 25–36.

Goll, D.E., Bray, R.W., and Hoekstra, W.G. (1964), Age-associated changes in bovine muscle connective tissue. 3. Rate of solubilization at 100 °C. *J. Food Sci.*, 29, 622–628.

Goll, D.E., Otsuka, Y., Nagainis, P.A., Shannon, J.D., Sathe, S.K., and Muguruma, M. (1983), Role of muscle proteinases in maintenance of muscle integrity and mass. *J. Food Biochem.*, 7, 137–177.

Grobet, L., Poncelet, D., Royo, L.J., Brouwers, B., Pirottin, D., Michaux, C., Menissier, F., Zanottie, M., Dunner, S., and Georges, M. (1997), Molecular definition of an allelic series

of mutations disrupting the myostatin function and causing double-muscling in cattle. *Mamm. Genome*, 9, 210–213.

Gruber, S.L., Tatum, J.D., Scanga, J.A., Chapman, P.L., Smith, G.C., and Belk, K.E. (2006), Effects of postmortem aging and USDA quality grade on Warner–Bratzler shear force values of seventeen individual beef muscles. *J. Anim. Sci.*, 84, 3387–3396.

Gruber, S.L., Tatum, J.D., Engle, T.E., Prusa, K.J., Laudert, S.B., Schroeder, A.L., and Platter, W.J. (2007), Effects of ractopamine supplementation and postmortem aging on longissimus muscle palatability of beef steers differing in biological type. *J. Anim. Sci. 2008*, 86, 205–210.

Harris, P.V. and Shorthose, W.R. (1988), 'Meat texure', in Lawrie, R.A., *Developments in Meat Science – 4*. London, Elsevier Applied Science Publishers, 245–286.

Herring, H.K., Cassens, R.G. and Briskey, E.J. (1965a), Further studies on bovine muscle tenderness as influenced by carcass position, sarcomere length, and fiber diameter. *J. Food Sci.*, 30, 1049–1054.

Herring, H.K., Cassens, R.G., and Briskey, E.J. (1965b), Sarcomere length of free and restrained bovine muscles at low temperatures as related to tenderness. *J. Sci. Food Agric.*, 16, 378–384.

Hildrum, K.I., Nilsen, B.N., Mielnik, M., and Naes, T. (1994), Prediction of sensory characteristics of beef by near-infrared spectroscopy. *Meat Sci.*, 38, 67–80.

Hoover, L.C., Cook, K.D., Miller, M.F., Huffman, K.L., Wu, C.K., Lansdell, J.L., and Ramsey, C.B. (1995), Restaurant consumer acceptance of beef loin strip steaks tenderized with calcium chloride. *J. Anim Sci.*, 73, 3633–3638.

Hopkinson, S.F., Ringkob, T.P., and Bailey, C.M. (1985), Cutability and the effect of electrical stimulation and aging on tenderness of beef from young intact males and castrates. *J. Anim. Sci.*, 60, 675–681.

Hostetler, R.L., Landmann, W.A., Link, B.A., and Fitzhugh, H.A. Jr. (1970), Influence of carcass position during rigor mortis on tenderness of beef muscles: Comparison of two treatments. *J. Anim. Sci.*, 73, 1064–1073.

Hostetler, R.L., Link, B.A., Landmann, W.A., and Fitzhugh, H.A. (1972), Effect of carcass suspension on sarcomere length and shear force of some major bovine muscles. *J. Food Sci.*, 37, 132–135.

Johnson, D.D., Huffman, R.D., Williams, S.E., and Hargrove, D.D. (1990), Effects of percentage Brahman and Angus breeding, age-season of feeding, and slaughter end point on meat palatability and carcass characteristics. *J. Anim. Sci.*, 68, 1980–1986.

Kambadur, R., Sharma, M., Smith, T.P.L., and Bass, J.J. (1997), Mutations in myostatin (GDF8) in double-muscled Belgian Blue and Piedmontese cattle. *Genome Res.*, 7, 910–915.

King, D.A., Dikeman, M.E., Wheeler, T.L., Kastner, C.L., and Koohmaraie, M. (2003), Chilling and cooking rate effects on some myofibrillar determinants of tenderness of beef. *J. Anim. Sci.*, 81, 1473–1481.

King, D.A., Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (2007), Comparison of palatability characteristics of beef gluteus medius and triceps brachii muscles. *J. Anim. Sci.*, (in press).

Koch, R.M., Dikeman, M.E., and Crouse, J.D. (1982), Characterization of biological types of cattle (Cycle III). I. Carcass composition, quality and palatability. *J. Anim. Sci.*, 54, 35–45.

Koohmaraie, M. (1992a), The role of Ca(2+)-dependent proteases (calpains) in post mortem proteolysis and meat tenderness. *Biochimie*, 74, 239–45.

Koohmaraie, M. (1992b), Effect of pH, temperature, and inhibitors on autolysis and catalytic activity of bovine skeletal muscle mu-calpain. *J. Anim. Sci.*, 70, 3071–3080.

Koohmaraie, M. (1992c), Ovine skeletal muscle multicatalytic proteinase complex (proteasome): Purification, characterization, and comparison of its effects on myofibrils with mu-calpains. *J. Anim. Sci.*, 70, 3697–3708.

Koohmaraie, M. (1995), The biological basis of meat tenderness and potential

genetic approaches for its control and prediction. *Proc. Recip. Meat Conf.*, 48, 69–75.
Koohmaraie, M. (1996), Biochemical factors regulating the toughening and tenderization process of meat. *Meat Sci.*, 43, S193–S201.
Koohmaraie, M., Crouse, J.D., and Mersmann, H.J. (1989), Acceleration of postmortem tenderization in ovine carcasses through infusion of calcium chloride: Effect of concentration and ionic strength. *J. Anim. Sci.*, 67, 934–942.
Koohmaraie, M., Doumit, M.E., and Wheeler, T.L. (1996a), Meat toughening does not occur when rigor shortening is prevented. *J. Anim. Sci.*, 74, 2935–2942.
Koohmaraie, M., Kent, M.P., Shackelford, S.D., Veiseth, E., and Wheeler, T.L. (2002), Meat tenderness and muscle growth: Is there any relationship? *Meat Sci.*, 62, 345–352.
Koohmaraie, M., Shackelford, S.D., Muggli-Cockett, N.E., and Stone, R.T. (1991), Effect of the beta-adrenergic agonist L644,969 on muscle growth, endogenous proteinase activities, and postmortem proteolysis in wether lambs. *J. Anim. Sci.*, 69, 4823–4835.
Koohmaraie, M., Shackelford, S.D., and Wheeler, T.L. (1996b), Effects of a beta-adrenergic agonist (L-644,969) and male sex condition on muscle growth and meat quality of callipyge lambs. *J. Anim. Sci.*, 74, 70–79.
Koohmaraie, M., Shackelford, S.D., Wheeler, T.L., Lonergan, S.M., and Doumit, M.E. (1995), A muscle hypertrophy condition in lamb (Callipyge): Characterization of effects on muscle growth and meat quality traits. *J. Anim. Sci.*, 73, 3596–3607.
Li, J., Tan, J., Martz, F.A., and Heymann, H. (1999), Image texture features as indicators of beef tenderness. *Meat Sci.*, 53, 17–22.
Li, J., Tan, J., and Shatadal, P. (2001), Classification of tough and tender beef by image texture analysis. *Meat Sci.*, 57, 341–346.
Locker, R.H. and Hagyard, C.J. (1963), A cold shortening effect in beef muscles. *J. Food Sci. Agric.*, 14, 787–793.
Lorenzen, C.L., Koohmaraie, M., Shackelford, S.D., Jahoor, F., Freetly, H.C., Wheeler, T.L., Savell, J.W., and Fiorotto, M.L. (2000), Protein kinetics in callipyge lambs. *J. Anim. Sci.*, 78, 78–87.
Ludwig, C.J., Claus, J.R., Marriott, N.G., Johnson, J., and Wang, H. (1997), Skeletal alteration to improve beef longissimus muscle tenderness. *J. Anim. Sci.*, 75, 2404–2410.
Lusk, J.L., Fox, J.A., Schroeder, T.C., Mintert, J., and Koohmaraie, M. (2001), In-store valuation of steak tenderness. *Am. J. Agric. Econ.*, 83, 539–550.
Marsh, B.B. (1977), The nature of tenderness. *Proc Recip. Meat Conf.*, 30, 69–74.
Marsh, B.B. and Leet, N.G. (1966), Studies in meat tenderness. III. The effects of cold shortening on tenderness. *J. Food Sci.*, 31, 450–459.
Marsh, B.B., Woodhams, P.R., and Leet, N.G. (1968), Studies in meat tenderness. 5. The effects on tenderness of carcass cooling and freezing before the completion of rigor mortis. *J. Food Sci.*, 33, 12–18.
May, S.G., Dolezal, H.G., Gill, D.R., Ray, F.K., and Buchanan, D.S. (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.
McKeith, F.K., De Vol, D.L., Miles, R.S., Bechtel, P.J., and Carr, T.R. (1985), Chemical and sensory properties of thirteen major beef muscles. *J. Food. Sci.*, 50, 869–872.
McPherron, A.C. and Lee, S.J. (1997), Double muscling in cattle due to mutations in the myostatin gene. *Proc. Natl. Acad. Sci., USA*. 94, 12457–12561.
Mies, P.D., Belk, K.E., Tatum, J.D., and Smith, G. C.. (1999), Effects of postmortem aging on beef tenderness and aging guidelines to maximize tenderness of different beef subprimal cuts. Available: http://ansci.colostate.edu/files/meat_science/mies.pdf Accessed: May 31, 2007.
Miller, M.F., Huffman, K.L., Gilbert, S.Y., Hamman, L.L., and Ramsey, C.B. (1995), Retail consumer acceptance of beef tenderized with calcium chloride. *J. Anim. Sci.*, 73, 2308–2314.
Miller, R. K. (1998), Functionality of non-meat ingredients used in enhanced pork. Available: http://www.meatscience.org/Pubs/porkfact.asp Accessed April 5, 2007.

Montgomery, T.H., Dew, P.F., and Brown, M.S. (2001), Optimizing carcass value and the use of anabolic implants in beef cattle. *J. Anim. Sci.*, 79 (E-Suppl), E296–306.

Morgan, J.B. (1997), Implant programs effects on USDA beef carcass quality grade traits and meat tenderness. Proc. Impact of implants on performance and carcass value of beef cattle, Okla. Agric. Exp. Statn,, Stillwater, P-957, 147–154.

Mueller, S.L., King, D.A., Baird, B.E., McKenna, D.R., Osburn, W.N., and Savell, J.W. (2006), In-home consumer evaluations of individual muscles from beef rounds subjected to tenderization treatments. *Meat Sci.*, 74 (2), 272–280.

Neely, T.R., Lorenzen, C.L., Miller, R.K., Tatum, J.D., Wise, J.W., Taylor, J.F., Buyck, M.J., Reagan, J.O., and Savell, J.W. (1998), Beef customer satisfaction: Role of cut, USDA quality grade, and city on in-home consumer ratings. *J. Anim. Sci.*, 76, 1027–1033.

O'Connor, S.F., Tatum, J.D., Wulf, D.M., Green, R.D., and Smith, G.C. (1997), Genetic effects on beef tenderness in *Bos indicus* composite and *Bos taurus* cattle. *J. Anim. Sci.*, 75, 1822–1830.

Ouali, A. and Talmant A. (1990), Calpains and calpastatin distribution in bovine, porcine, and ovine skeletal muscles. *Meat Sci.*, 28, 331–348.

Ouali, A. and Valin, C. (1980), Effect of muscle lysosomal enzymes and calcium activated nuetral proteinase on myofibrillar ATPase activity: Relationship with ageing changes. *Meat Sci.*, 5, 233–245.

Page, B.T., Casas, E., Heaton, M.P., Cullen, N.G., Hyndman, D.L., Morris, C.A., Crawford, A.M., Wheeler, T.L., Koohmaraie, M., Keele, J.W. and Smith, T.P.L. (2002), Evaluation of single-nucleotide polymorphisms in CAPN1 for association with meat tenderness in cattle. *J. Anim. Sci.*, 80, 3077–3085.

Page, B.T., Casas, E., Quaas, R.L., Thallman, R.M., Wheeler, T.L., Shackelford, S.D., Koohmaraie, M., White, S.N., Bennett, G.L., Keele, J.W., Dikeman, M.E. and Smith, T.P.L. (2004), Association of markers in the bovine CAPN1 gene with meat tenderness in large crossbred populations that sample influential industry sires. *J. Anim. Sci.*, 82, 3474–3481.

Park, B., Chen, Y.R., Hruschka, W.R., Shackelford, S.D., and Koohmaraie, M. (1998), Near-infrared reflectance analysis for predicting beef longissimus tenderness. *J. Anim. Sci.*, 76, 2115–2120.

Park, B. and Whittaker, A.D. (1991), Non-intrusive measurement of meat tenderness. *ASAE (Am. Soc. Ag. Eng.)* St. Joseph, MO. pp 1–13.

Park, B., Whittaker, A.D., Miller, R.K., and Hale, D.S. (1994), Ultrasonic spectral analysis for beef sensory analysis. *J. Food Sci.*, 59, 697–724.

Peacock, F.M., Koger, M., Palmer, A.Z., Carpenter, J.W., and Olson, T.A. (1982), Additive breed and heterosis effects for individual and maternal influences on feedlot gain and carcass traits of Angus, Brahman, Charolais, and crossbred steers. *J. Anim. Sci.*, 55, 797–803.

Platter, W.J., Tatum, J.D., Belk, K.E., Scanga, J.A., and Smith, G.C. (2003), Effects of repetitive use of hormonal implants on beef carcass quality, tenderness, and consumer ratings of beef palatability. *J. Anim Sci.*, 81, 984–996.

Price, M.G. (1991), Striated muscle endosarcomeric and exosarcomeric lattices. *Advances in Structural Biology*, 1, 175–207.

Pringle, T.D., Williams, S.E., Lamb, B.S., Johnson, D.D., and West, R.L. (1997), Carcass characteristics, the calpain proteinase system, and aged tenderness of Angus and Brahman crossbred steers. *J. Anim. Sci.*, 75, 2955–2961.

Purchas, R.W., Burnham, D.L., and Morris, S.T. (2002), Effects of growth potential and growth path on tenderness of beef longissimus muscle from bulls and steers. *J. Anim. Sci.*, 80, 3211–3221.

Rhee, M.S., Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (2004), Variation in palatability and biochemical traits within and among eleven beef muscles. *J. Anim. Sci.*, 82, 534–550.

Robson, R. M., Huff-Lonergan, E., Parrish, F. C. Jr., Ho, C.-Y., Stromer, M. H., Huiatt, T.

W., Bellin, R. M., and Sernett, S. W. (1997), Postmortem changes in myofibrillar and other cytoskeletal proteins in muscle. *Proc. Recip. Meat Conf.*, 50, 43–52.

Samber, J.A., Tatum, J.D., Wray, M.I., Nichols, W.T., Morgan, J.B., and Smith, G.C. (1996), Implant program effects on performance and carcass quality of steer calves finished for 212 days. *J. Anim. Sci.*, 74, 1470–1476.

Savell, J.W., Dutson, T.R., Smith, G.C., and Carpenter, Z.L. (1978), A research note: Structural changes in electrically stimulated beef muscle. *J. Food Sci.*, 43, 1606–1609.

Savell, J.W., Lorenzen, C.L., Neely, T.R., Miller, R.K., Tatum, J.D., Wise, J.W., Taylor, J.F., Buyck, M.J., and Reagan, J.O. (1999), Beef customer satisfaction: Cooking method and degree of doneness effects on the top sirloin steak. *J. Anim. Sci.*, 77, 645–652.

Savell, J. W., Miller, R. K, Wheeler, T., Koohmaraie, M., Shackelford, S., Morgan, B., Calkins, C., Miller, M., Dikeman, M., McKeith, F., Dolezal, G., Henning, B., Busboom, J., West, R., Parrish, F., and Williams, S. (1994), Standardized Warner–Bratzler shear force procedures for genetic evaluation. Available: http://meat.tamu.edu/shear.pdf Accessed: May 30, 2007.

Savell, J.W., McKeith, F.K., and Smith, G.C. (1981), Reducing postmortem aging time of beef with electrical stimulation. *J. Food Sci.*, 46, 1777–1781.

Savell, J.W., Smith, G.C., and Carpenter, Z.L. (1977), Blade tenderization of four muscles from three weight-grade groups of beef. *J. Food Sci.*, 42, 866–870.

Schenkel, F.S., Miller, S.P., Jiang, Z., Mandell, I.B., Ye, X., Li, H., and Wilton, J.W. (2006), Association of a single nucleotide polymorphism in the calpastatin gene with carcass and meat quality traits of beef cattle. *J. Anim. Sci.*, 84, 291–299.

Schneider, B.A., Tatum, J.D., Engle, T.E., and Bryant, T.C. (2007), Effects of heifer finishing implants on beef carcass traits and longissimus tenderness. *J. Anim. Sci.*, 85, 2019–2030.

Searls, G.A., Maddock, R.J., and Wulf, D.M. (2005), Intramuscular tenderness variation within four muscles of the beef chuck. *J. Anim. Sci.*, 83, 2835–2842.

Shackelford, S.D., Koohmaraie, M., Cundiff, L.V., Gregory, K.E., Rohrer, G.A., and Savell, J.W. (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.

Shackelford, S.D., Wheeler, T.L., and Koohmaraie, M. (1995), Relationship between shear force and trained sensory panel tenderness ratings of 10 major muscles from *Bos indicus* and *Bos taurus* cattle. *J. Anim. Sci.*, 73, 3333–3340.

Shackelford, S.D., Wheeler, T.L., and Koohmaraie, M. (1998), Coupling of image analysis and tenderness classification to simultaneously evaluate carcass cutability, longissimus area, subprimal cut weights, and tenderness of beef. *J. Anim. Sci.*, 76, 2631–2640.

Shackelford, S.D., Wheeler, T.L., and Koohmaraie, M. (1999), Evaluation of slice shear force as an objective method of assessing beef longissimus tenderness. *J. Anim. Sci.*, 77, 2693–2699.

Shackelford, S.D., Wheeler, T.L., and Koohmaraie, M. (2005), On-line classification of US Select beef carcasses for longissimus tenderness using visible and near-infrared reflectance spectroscopy. *Meat Sci.*, 69, 409–415.

Shackelford, S.D., Wheeler, T.L., Meade, M.K., Reagan, J.O., Byrnes, B.L., and Koohmaraie, M. (2001), Consumer impressions of Tender Select beef. *J. Anim. Sci.*, 79, 2605–2614.

Short, R.E., Grings, E.E., MacNeil, M.D., Heitschmidt, R.K., Williams, C.B., and Bennett, G.L. (1999), Effects of sire growth potential, growing–finishing strategy, and time on feed on performance, composition, and efficiency of steers. *J. Anim. Sci.*, 77, 2406–2417.

Shorthose, W.R. and Harris, P.V. (1990), Effect of animal age on the tenderness of selected beef muscles. *J. Food Sci.*, 55, 1–8,14.

Smith, T.P.L., Lopez-Corrales, N.L., Kappes, S.M., and Sonstegard, T.S. (1997), Myostatin maps to the interval containing the bovin mh locus. *Mamm. Genome*, 8, 742–744.

Smith, T.P.L., Thallman R.M., Casas, E., Shackelfod, S.D., Wheeler, T.L., and Koohmaraie, M. (2003), Theory and application of genome-based approaches to improve the quality and value of beef. *Outlook on Agriculture*, 32, 253–265.

Strydom, P.E. and Nel, E. (1999), The effect of supplementation period of beta-agonist (zilpaterol), electrical stimulation and ageing period on meat quality characteristics. *Intl. Cong. Meat Sci. Technol.*, 45, 474–475.

Swatland, H.J. (1995), *On-line Evaluation of Meat*. pp. 229–258. Technomic Publishing Co, Inc.

Swatland, H.J., Brooks, J.C., and Miller, M.F. (1998), Possibilities for predicting taste and tenderness of broiled beef steaks using an optical–electromechanical probe. *Meat Sci.*, 50, 1–12.

Swatland, H.J. and Findlay, C.J. (1997), On-line probe prediction of beef toughness, correlating sensory evaluation with fluorescence detection of connective tissue and dynamic analysis of overall toughness. *Food Qual. Pref.*, 8, 233–239.

Tatum, J.D. (1981), Is tenderness nutritionally controlled? *Proc. Recip. Meat Conf.*, 34, 65–67.

Tatum, J.D., Smith, G.C., Berry, B.W., Murphey, C.E., Williams, F.L., and Carpenter, Z.L. (1980), Carcass characteristics, time on feed and cooked beef palatability attributes. *J. Anim. Sci.*, 50, 833–840.

Taylor, R.C., Geesink, G.H., Thompson, V.F., Koohmaraie, M., and Goll, D.E. (1995), Is Z-disk degradation responsible for postmortem tenderization? *J. Anim. Sci.*, 73, 1351–1367.

Uttaro, B.E., Ball, R.O., Dick, P., Rae, W., Vessie, G., and Jeremiah, L.E. (1993), Effect of ractopamine and sex on growth, carcass characteristics, processing yield, and meat quality characteristics of crossbred swine. *J. Anim. Sci.*, 71, 2439–2449.

Veiseth, E., Shackelford, S.D., Wheeler, T.L., and Koohmaraie, M. (2004), Indicators of tenderization are detectable by 12 h postmortem in ovine longissimus. *J. Anim. Sci.*, 82, 1428–1436.

Von Seggern, D.D., Calkins, C.R., Johnson, D.D., Brickler, J.E., and Gwartney, B.L. (2005), Muscle profiling: Characterizing the muscles of the beef chuck and round: 51st International Congress of Meat Science and Technology (ICoMST). *Meat Sci.*, 71, 39–51.

Vote, D.J., Platter, W.J., Tatum, J.D., Schmidt, G.R., Belk, K.E., Smith, G.C., and Speer, N.C. (2000), Injection of beef strip loins with solutions containing sodium tripolyphosphate, sodium lactate, and sodium chloride to enhance palatability. *J. Anim. Sci.*, 78, 952–957.

Wang, H., Claus, J.R., and Marriot, N.G. (1994), Selected skeletal alterations to improve tenderness of beef round muscles. *J. Musc. Foods*, 5, 137–147.

Wang, H., Claus, J.R. and Marriot, N.G. (1996), Prerigor treatment and endpoint temperature effects on U.S. Choice beef tenderness. *J. Musc. Foods*, 7, 45–54.

Wheeler, T.L., Crouse, J.D. and Koohmaraie, M. (1992), The effect of postmortem time of injection and freezing on the effectiveness of calcium chloride for improving beef tenderness. *J. Anim. Sci.*, 70, 3451–3457.

Wheeler, T.L., Cundiff, L.V., Koch, R.M., and Crouse, J.D. (1996a), Characterization of biological types of cattle (Cycle IV): Carcass traits and longissimus palatability. *J. Anim. Sci.*, 74, 1023–1035.

Wheeler, T.L., Cundiff, L.V., Koch, R.M., Dikeman, M.E. and Crouse, J.D. (1997a), Characterization of different biological types of steers (Cycle IV): Wholesale, subprimal, and retail product yields. *J. Anim. Sci.*, 75, 2389–2403.

Wheeler, T.L., Cundiff, L.V., Shackelford, S.D., and Koohmaraie, M. (2001a), Characterization of biological types of cattle (Cycle V): Carcass traits and longissimus palatability. *J. Anim. Sci.*, 79, 1209–1222.

Wheeler, T.L., Cundiff, L.V., Shackelford, S.D., and Koohmaraie, M. (2004a), Characterization of biological types of cattle (Cycle VI): Carcass, yield, and longissimus palatability traits. *J. Anim. Sci.*, 82, 1177–1189.

Wheeler, T.L., Cundiff, L.V., Shackelford, S.D., and Koohmaraie, M. (2005), Characteri-

zation of biological types of cattle (Cycle VII): Carcass, yield, and longissimus palatability traits. *J. Anim. Sci.*, 83, 196–207.

Wheeler, T.L. and Koohmaraie, M. (1994), Prerigor and postrigor changes in tenderness of ovine longissimus muscle. *J. Anim. Sci.*, 72, 1232–1238.

Wheeler, T.L., Koohmaraie, M., Lansdell, J.L., Siragusa, G.R., and Miller, M.F. (1993), Effects of postmortem injection time, injection level, and concentration of calcium chloride on beef quality traits. *J. Anim. Sci.*, 71, 2965–2974.

Wheeler, T.L., Koohmaraie, M., and Shackelford, S.D. (1997b), Effect of postmortem injection time and postinjection aging time on the calcium-activated tenderization process in beef. *J. Anim. Sci.*, 75, 2652–2660.

Wheeler, T.L., Savell, J.W., Cross, H.R., Lunt, D.K., and Smith, S.B. (1990a), Effect of postmortem treatments on the tenderness of meat from Hereford, Brahman, and Brahman cross beef cattle. *J. Anim. Sci.*, 68, 3677–3686.

Wheeler, T.L., Savell, J.W., Cross, H.R., Lunt, D.K., and Smith, S.B. (1990b), Mechanisms associated with the variation in tenderness of meat from Brahman and Hereford cattle. *J. Anim. Sci.*, 68, 4206–4220.

Wheeler, T.L., Shackelford, S.D., Casas, E., Cundiff, L.V., and Koohmaraie, M. (2001b), 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.

Wheeler, T.L., Shackelford, S.D., Johnson, L.P., Miller, M.F., Miller, R.K., and Koohmaraie, M. (1997c), A comparison of Warner–Bratzler shear force assessment within and among institutions. *J. Anim. Sci.*, 75, 2423–2432.

Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (1996b), Sampling, cooking, and coring effects on Warner–Bratzler shear force values in beef. *J. Anim. Sci.*, 74, 1553–1562.

Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (1997d), Standardizing collection and interpretation of Warner–Bratzler shear force and sensory tenderness data. *Proc. Recip. Meat Conf.*, 50, 68–77.

Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (2000a), Relationship of beef longissimus tenderness classes to tenderness of gluteus medius, semimembranosus, and biceps femoris. *J. Anim. Sci.*, 78, 2856–2861.

Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (2000b), Variation in proteolysis, sarcomere length, collagen content, and tenderness among major pork muscles. *J. Anim. Sci.*, 78, 958–965.

Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (2004b), The accuracy and repeatability of untrained laboratory consumer panelists in detecting differences in beef longissimus tenderness. *J. Anim. Sci.*, 82, 557–562.

Wheeler, T.L., Shackelford, S.D., and Koohmaraie, M. (1998), Cooking and palatability traits of beef longissimus steaks cooked with a belt grill or an open hearth electric broiler. *J. Anim. Sci.*, 76, 2805–2810.

Whipple, G., Koohmaraie, M., Dikeman, M.E., and Crouse, J.D. (1990a), Effects of high-temperature conditioning on enzymatic activity and tenderness of *Bos indicus* longissimus muscle. *J. Anim. Sci.*, 68, 3654–3662.

Whipple, G., Koohmaraie, M., Dikeman, M.E., Crouse, J.D., Hunt, M.C., and Kemn, R.D. (1990b), Evaluation of attributes that affect longissimus muscle tenderness in *Bos taurus* and *Bos indicus* cattle. *J. Anim. Sci.*, 65, 597–607.

White, S.N., Casas, E., Wheeler, T.L., Shackelford, S.D., Koohmaraie, M., Riley, D.G., Chase, C.C. Jr., Johnson, D.D., Keele, J.W., and Smith, T.P.L. (2005), A new single nucleotide polymorphism in CAPN1 extends the current tenderness marker test to include cattle of *Bos indicus*, *Bos taurus*, and crossbred descent. *J. Anim. Sci.*, 83, 2001–2008.

Whiting, R.C. (1980), Calcium uptake by bovine muscle mitochondria and sarcoplasmic reticulum. *J. Food Sci.*, 45, 288–292.

Wulf, D.M., O'Connor, S.F., Tatum, J.D., and Smith, G.C. (1997), Using objective measures of muscle color to predict beef longissimus tenderness. *J. Anim. Sci.*, 75, 684–692.

Wulf, D.M. and Page, J.K. (2000), 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.

Zeece, M.G., Woods, T.L., Keen, M.A., and Reville, W.J. (1992), Role of proteinases and inhibitors in postmortem muscle protein degradation. In *Proceedings of the Recip. Meat Conf.*, 45, 51–61.