

**BEEF QUALITY: FACTORS AFFECTING TENDERNESS
AND MARBLING****Marija Špehar, D. Vincek, S. Žgur****Summary**

Tenderness is, undoubtedly, the most important single meat quality trait. Variation in meat tenderness is the main factor for consumer dissatisfaction; hence this trait must be controlled in order to improve customer satisfaction and decision to repurchase. Variation in beef tenderness may be attributed to breed (genetic status), carcass composition, and environmental factors (chronological age, time on feed, implants and ante-mortem stress). Many post-mortem treatments like ageing, electrical stimulation, chilling rate, and post-mortem tenderization technologies also affect tenderness. Carcass fat proportion, especially intramuscular fat (marbling), plays an important role in the meat sensory characteristics, since it contributes directly to its sensory properties. Expedite methodologies to predict meat tenderness on the live animal or at slaughterhouses level have been developed to satisfy the consumer demands. Variation in meat tenderness is also greatly affected by the selection. Among different breeds, genetic evaluation programs are being developed, and the current research is focused on genes with major effects on meat tenderness and marbling.

Key words: beef quality, tenderness, marbling

Introduction

The most important aspect of meat quality is its eating quality or overall eating satisfaction (Fergusson, 2004), being a function of the combined effects of tenderness, juiciness, and flavour (Tatum et al., 1999; Thompson, 2004). Other important aspect of meat quality is meat appearance when purchased and some of these characteristics, such as colour, can be measured instrumentally. However, other aspects require a subjective approach, and the best ways to evaluate meat quality are scores of trained taste panellists who evaluate different components of meat eating quality.

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Meat with good sensory properties is what consumers desire, so beef industry must supply meat with these attributes on a consistent and uniform basis.

Carcass fat proportion, especially intramuscular fat (marbling), plays an important role in the meat sensory characteristics (Fergusson, 2004), since it contributes directly to its sensory properties. Based on this observation, marbling score has been used by the US beef industry as the primary predictor of beef meat quality (USDA, 1997). Marbling has no direct effect on meat tenderness (Wheeler et al., 1994), however some indirect effects, resulting from the association between marbling and carcass overall fatness degree may have a substantial effect on meat quality (Berry, 1993; Fergusson, 2004). In spite of marbling effect on meat eating properties Miller et al. (1995) found that consumers preferred meat of higher tenderness, concluding that the United States (US) consumers considered tenderness the first component of satisfaction/dissatisfaction. If the consumers are satisfied with meat tenderness, then they will be concerned with flavour where marbling plays an important role.

The inconsistency in meat tenderness has been identified as one of the major problems facing the US beef industry (Morgan et al., 1991), and the US Meat Animal Research Center (MARC) considers that research efforts should be focused on meat tenderness because: 1) it presents large variation among animals, carcasses, muscles, and cuts of meat (Searls et al., 2005); 2) consumers can discern between tenderness levels and are prepared to pay a premium for tender meat (Boleman et al., 1997); 3) consumers consider tenderness to be the single most important component of meat quality (Miller et al., 1995). Therefore, the problem of consumer dissatisfaction will be minimized if beef industry can solve the problem of meat tenderness variability/inconsistency. The development of expedite methodologies to predict meat tenderness on the live animal or at slaughterhouses level have been developed to satisfy the consumer demands. Tenderness is, undoubtedly, the most important meat quality trait to improve in beef meat. Another important way to improve this meat quality trait is by selection. Among different breeds, genetic evaluation programs are being developed, and the current research is focused on genes with major effects on meat tenderness and marbling. Genetic evaluation progress can have an important effect on the improvement of beef sensory characteristics, as well as on uniformity and consistency.

Tenderness variation factors

Sources of tenderness variation in beef may be attributed to carcass composition (marbling), breed/genetic and environmental factors (chronological age, time on feed, implants and ante-mortem stress). Many post-mortem treatments also affect tenderness like ageing, electrical stimulation, chilling rate, post-mortem tenderization technologies (CaCl₂-injection, blade tenderization, etc).

Breed/genetic differences

The effect of genetics on meat tenderness is clearly observed when meat of *Bos taurus* is compared with meat of *Bos indicus*. The latter type presents tougher meat (Wheeler et al., 2004, 2005), due to lower proteolysis of myofibrillar proteins, as a result of the higher activity of calcium-dependent protease inhibitor (Shackelford et al., 1991). Within breeds estimates indicate that genetics controls about 30 to 50% of the variation in beef tenderness (Shackelford et al., 1994), representing the heritability or additive gene effects of tenderness.

Among breeds, approximately 50% of the variation in meat tenderness is controlled by genetic effects (Wheeler et al., 1996; Wheeler et al., 2001, 2004, 2005). However, differences in meat tenderness among breeds are often lower than the variation found among animals within breeds, and are overridden by larger differences between muscles or cuts (Wheeler et al., 1996). The amounts and distribution of connective tissue among muscles seems to be dependent on muscle development, growth, and especially the function (Purslow, 2005). This author reports that these sources of variability can affect the manipulation of this trait to achieve more tender meat.

Chronological age

Normally, beef is slaughtered between 9 and 30 months of age, within this age range a large variation on tenderness can be observed. As animals increase in chronological age, tenderness decreases (Purslow, 2005), and sensory panel scores for tenderness decrease (Shackelford et al., 1995; Žgur, 1996). The main reason for tougher meat in older animals is a change in collagen characteristics as noted by Harper (1999). Collagen content in meat does not change much, but its solubility diminishes with increased animal age. The amount of total insoluble collagen in meat increases with animal age and

effects meat tenderness. Animal age is an important criterion in beef grading (USDA, 1997), however, age alone does not determine beef toughness (Harper, 1999).

Marbling

Modern meat is occasionally criticized for its lack of juiciness, and this is attributed to low levels of intramuscular fat. Inter-fascicular or intramuscular adipose tissue is a unique fat depot; being the last fat tissue to be deposited, and the first to be utilized by the animal as an energy source. The selection for leaner carcasses leads to lower intramuscular fat. However, marbling greatly affects meat flavour (Thompson, 2004) and a minimum amount 2.0–2.5 % is necessary for a desirable eating quality. Human perceptions of tenderness and juiciness appear to be interrelated, and juicy meat may be perceived as more tender compared to a similar less juicy sample.

Several studies (Berry, 1993; Žgur, 1996; Killinger et al., 2004) have shown that tenderness, measured by shear force, increases when better marbling is attained. The connective tissue rigidity is weakened with increased marbling accumulation resulting in tender meat. A recent study by Nishimura et al. (1999) seems to confirm this theory, since the development of intramuscular fat in the longissimus dorsi muscle appears to disorganize the structure of connective tissue, leading to the tenderization of highly marbled beef of Wagyu breed.

Time on feed

Generally, fat deposition increases with the increasing time on feed, and an improvement in meat tenderness can be observed. Therefore, increasing the time on feed can improve beef tenderness, due to the effect on marbling score, and on carcass protection during cooling. Several authors (Xie et al., 1996; Sami et al., 2004) reported positive effects of longer time on feed on tenderness, marbling and sensory characteristics of beef. However, animals that are finished on concentrate feed tend to reach a given slaughter weight sooner than animals that are finished on the pasture. Thus, concentrate-fed animals usually are slightly tenderer because they are slaughtered at younger age. The influence of growth rate on meat tenderness seems to depend mainly on changes of muscle protein turnover. If higher growth rate is related to higher muscle protein synthesis and degradation rate, increased meat tenderness can be expected and vice versa. Muscle protein turnover is highly correlated with post

mortem protein degradation rate and so with ageing and meat tenderness (Žgur et al., 2003).

Stress – Pre-slaughter handling

What constitutes stress depends on the individual animal, its previous experience, and its temperament. However, both psychological stressors (restraint, novelty, and handling) and physiological stressors (hunger, thirst, fatigue, injury, and thermal exposure) have been identified as contributors to meat toughness (Harper, 1999). The way that animals are handled pre-slaughter (Lensink et al., 2000), and animal temperament (King et al., 2006) may have a marked affect on meat quality. During the conversion of muscle to meat an acidification of the tissue occurs, resulting in a pH fall from about 7.0 to 5.5 in normal meat. Pre-slaughtering handling can cause an unusually high rate of pH fall or a limited pH fall, resulting in PSE (pale, soft and exudative) and DFD (dark, firm and dry) meat, respectively. The PSE condition is usually attributed to acute stress in the immediately pre-slaughter period, while DFD is usually associated with chronic (long term) stress or prolonged feed withdrawal.

Conditions such as fasting or fighting between animals can deplete glycogen levels pre-slaughter, thus, limiting the extent of acidification and resulting in meat of high ultimate pH (≥ 6.0). In fact, stressing an animal before slaughter causes a number of biochemical effects on muscle, shortening the muscle fibres (sarcomeres) leading to meat toughness (Hwang et al., 2004). Stressed animals before slaughter present increased Warner-Bratzler shear force values, and produce tougher beef as demonstrated by Hwang et al. (2004). Paradoxically, meat with pH higher than 6.2 can be relatively tender (Beltrán et al., 1997), although meat does not appeal to the customer due to its dark colour (Viljoen et al., 2002).

Mounier et al. (2006) research on stress during transport has shown that periodically resting and feeding animals can overcome some negative consequences for meat toughness. For animals that require long distance transport between farms and slaughterhouses, addressing their nutritional and physiological needs during transport can reduce variation in meat toughness.

Ageing

Variation in meat tenderness is also created during post-mortem storage, under a process known as ageing. At slaughter, a muscle has an intermediate

shear force, and during the first 12 to 24 hours after slaughter there is a large decrease in sarcomere length, i.e., rigor mortis development; which is associated with a large increase in toughness (Strydom et al., 2005). An opposite phenomenon (i.e., tenderization) also begins either at slaughter or shortly after slaughter, resulting from the weakening of the myofibrils caused by the proteolysis of structural proteins, which are responsible for maintaining structural integrity of myofibrils (Huff-Lonergan et al., 1996; Strydom et al., 2005). This process is called post-mortem proteolysis, and is responsible for meat ageing.

The enzymatic system involved in meat ageing is the calpain proteolytic system, being a calcium-dependent system. This system presents three components: a low-calcium-requiring enzyme (u-calpain), a high-calcium-requiring enzyme (m-calpain), and an inhibitor (calpastatin) which specifically inhibits the activity of the two calpain enzymes. To improve the consistency of beef tenderness, carcasses should be aged under refrigerated conditions (1-3°C); this practice will eliminate a large portion of the variation in meat tenderness. The tenderization during ageing occurs regardless of the size of the cut (carcass, steaks, roasts, etc.), and will be faster at higher temperatures, but will not occur at all in frozen meat.

Chilling rate

After slaughter carcasses need to be refrigerated in order to prevent spoilage due to micro organisms' growth (Savell et al., 2005). If carcasses are chilled too rapidly, the result is "cold shortening" and subsequent meat toughness. Cold shortening occurs when the muscle is chilled under 15°C before the completion of rigor (Savell et al., 2005). Even under normal chilling conditions, carcasses with less than 1.6 cm of subcutaneous fat over the rib eye presents reduced tenderness because of cold shortening (Savell et al., 2005). Ageing a carcass affected by cold shortening will not alleviate the detrimental effects on tenderness. To ensure more tender meat, carcasses must be protected from very rapid cooling during the first 6-12 hours after slaughter.

Post-mortem tenderization technologies

Conditions in post-mortem muscle are not always optimal to maximize meat tenderness, however, several techniques may be used post-mortem to increase tenderness (White et al., 2006). The calpains enzymatic system activation requires the availability of calcium. When calcium availability is low,

the ageing process will be difficult. However, exogenous calcium can be added to meat, thus activating calpains, inducing more rapid, and extensive tenderization (Lawrence et al., 2003). The process, known as calcium-activated tenderization (CAT), consists of injecting meat cuts (either pre-rigor or post-rigor) with 5% (by weight) of a solution (2.2%) of food-grade calcium chloride. Following injection, cuts are vacuum-packaged and stored for seven days prior to consumption. This process is more effective if applied in pre-rigor meat (the first 3 hours after slaughter), but can be applied up to 14 days post-mortem. At the recommended levels of calcium chloride, this process has little effect on other meat quality traits. The CAT has been tested under commercial conditions in large beef processing facilities, and presents an enormous potential to help beef industry in its effort to reduce variation in beef tenderness.

Beef carcasses subjected to high voltage electrical current presents higher tenderness (Strydom et al., 2005). The effect is equal on all meat cuts (White et al., 2006). The electrical stimulation effect is thought to be interfered primarily through prevention of structural damage of the tissues due to severe contractions. Proper application of high-voltage electrical stimulation will prevent the cold-shortening in leaner carcasses, and consequently improve meat tenderness (Strydom et al., 2005). Electrical stimulation speeds up the post-mortem conversion of muscle to meat (rigor mortis) and thus reduces the ageing time (Strydom et al., 2005).

Genetic improvement of tenderness

Several studies (Shackelford et al., 1991; Shackelford et al., 1994) have shown that there is also individual variation in meat tenderness. Carcass quality traits are under genetic control and highly heritable (Bertrand et al., 2001). The design of appropriate breeding programs to improve beef tenderness need genetic information, such as, heritability, phenotypic and genetic correlations among traits (Table 1). Heritability measures the proportion of variation in a trait due to additive genetic effects of the genes.

Table 1 – HERITABILITY (H²) OF BEEF CARCASS TRAITS (MARSHALL, 1999)

Trait*	h ^{2**}	Range***
Lean yield (A)	0.47	0.26-0.76
Lean yield (W)	0.48	
Lean yield (F)		
Longissimus muscle area (A)	0.42	0.06-0.65
Longissimus muscle area (W)	0.41	
Longissimus muscle area (F)		0.38-0.52
Marbling score (A)	0.38	0.19-0.79
Marbling score r (F)	0.65	0.18-0.52
Marbling score (W)	0.36	
Tehnological quality traits		
Intramuscular lipid %	0.26	0.26-0.93
Shear force	0.30	0.02-0.53
Calpastatin activity		0.15-0.65
Myofibrillar fragmentation		0.17-0.58
Ultimate pH	0.26	0.10-0.19
Water loss	0.24	
Sensory panel traits		
Tenderness	0.22	0.03-0.50
Flavour intensity	0.10	0.00-0.43
Flavour desirability	0.01	
Juiciness	0.14	0.00-0.26

*Letter in parentheses indicates that the trait was evaluated at the constant age or days in feedlot (A), carcass weight (W) or fat thickness (F)

Intramuscular fat content (usually evaluated in the longissimus dorsi muscle) is often subjectively evaluated by visual inspection of a cross-section of longissimus muscle (i.e. marbling score), and in some studies has been measured objectively by chemical analysis (i.e. intramuscular lipid percentage). Both measures indicate that intramuscular fat content is highly heritable (Marshall, 1999; Bertrand et al., 2001). Shear force and myofibrillar fragmentation are physical indexes of tenderness, whereas calpastatin activity is a biochemical index; involved in the enzymatic degradation of myofibrillar proteins during post-mortem storage (ageing). These objective indicators of tenderness seem to be more heritable than the subjective tenderness evaluated by sensory panellists (Marshall, 1999).

Genetic correlations are important to consider in multiple-trait selection and in the design of breeding systems, because selection for one trait can cause a response in other traits (Marshall, 1999). Genetic antagonisms tend to slow the rate of improvement or even cause undesirable change in some traits. The genetic relationships of marbling score with fat thickness and lean yield are of

particular interest, because in many markets these variables represent important criteria in the determination of carcass price. Traditionally, it has been assumed that higher marbling scores were genetically associated with increased external fat and decreased lean yield, both within and between breeds, and the average genetic correlations presented by Marshall (1999) and Bertrand et al., (2001) seem to confirm this statement (Table 2).

Table 2 – GENETIC CORRELATIONS (RG) AMONG CARCASS, TECHNOLOGICAL QUALITY AND SENSORY PANEL TRAITS (MARSHALL, 1999)

Trait	Review estimates* (mean r_g)	Recent estimates**	
		Mean	Range
Carcass traits			
Marbling score/Lean yield	-0.25	-0.19	-0.06 to 0.12
Marbling score/Fat thickness	0.35	0.09	-0.12 to 0.44
Marbling score/Carcass weight	0.25	0.09	-0.05 to 0.36
Technological quality traits			
Intramuscular fat/Marbling score	0.81		0.65 to 0.96
Intramuscular fat/Fat thickness	0.26		0.06 to 0.71
Intramuscular fat/Lean yield	-0.47		-0.90 to -0.11
Intramuscular fat/Shear force	-0.64		-0.93 to -0.05
Shear force/Calpastatin activity	0.63		0.35 to >1
Shear force/Lean yield	-0.19		-0.47 to 0.00
Shear force/Ultimate pH	-0.03		
Shear force/Water loss	-0.06		
Subjective sensory panel traits			
Tenderness/Intramuscular fat	0.30		0.06 to 0.50
Tenderness/Lean yield	-0.19		-0.48 to 0.03
Tenderness/Shear force	-0.86		-1 to -0.64
Tenderness/Juiciness	0.79		0.43 to 0.95
Tenderness/Flavour intensity	0.86		0.63 to 1.00

The use of a subjective marbling score as an indicator of intramuscular fat percentage is confirmed by the high (0.65 to 0.96) genetic correlation (Table 2). Fat thickness and lean yield appear to be more closely correlated with the actual intramuscular fat percentage than with the subjective marbling score. It is generally accepted that the use of genetically correlated traits may enhance rates of genetic response in livestock via reduced generation intervals, increased selection differentials, and increased accuracy of selection (Bourdon, 2000). Some of these studies showed that calpastatin activity measured at 24-h post-mortem in Brahman steers is positively associated with muscle shear force, a physical objective measure of meat tenderness. Shackelford et al. (1994)

reported that calpastatin activity was highly heritable (0.65), and confirmed by the literature revision (Bertrand et al., 2001), where an average heritability of 0.54 for calpastatin activity was reported.

Shear force has been widely used as a direct measure of meat tenderness, and genetic correlations superior to 0.30, between calpastatin activity at 24-h postmortem and shear force values have been reported by several studies (Shackelford et al., 1994; Marshall, 1999). High genetic correlations, and moderate phenotypic correlations between calpastatin activity and shear force values, suggest that meat tenderness traits can be used to establish possible relationships between calpastatin activity (phenotypes) and polymorphic regions within the calpastatin gene (genotypes).

Effects of selection for increased intramuscular fat content or improved shear force values on meat technological quality could range from slightly antagonistic to moderately favourable (Marshall, 1999). Tenderness, flavour intensity and juiciness are the most commonly studied sensory traits of beef, and are highly genetically correlated among them (Table 2), and selection for leanness could be slightly antagonistic to tenderness and juiciness. Genetic correlations of intramuscular fatness and tenderness have ranged from slightly negative to moderately or highly positive. Shear force values appear to be highly genetically correlated to sensory quality, and seem to be the best indicator of genetic potential for sensory quality among all carcass composition or technological quality traits of beef that have been evaluated to date. A selection on marbling score may provide a correlated improvement of tenderness ($r_g = -0.90$ to -0.11), however, marbling is positively correlated to the carcass fatness (Table 2), and the indirect improvement of tenderness through a selection on intramuscular lipid content or marbling score will have counterproductive effects on carcass quality (Marshall, 1999).

Quantitative trait loci

Most traits of economic importance including beef palatability are considered as quantitative traits (i.e. controlled by many genes). However, in some traits a large amount of variation may be accounted for individual genes action. The development of genetic markers and linkage maps in bovine has made the identification of genetic regions possible where loci, known as quantitative trait loci (QTL), influence economically important traits (Casas et al., 2001; Casas, 2002; Casas et al., 2003a; Casas et al., 2003b). A genetic marker is a known DNA sequence that is believed to be physically located near a QTL. Examples of genetic markers include restriction fragment

length polymorphisms (RFLP), randomly amplified polymorphic DNA (RAPD), mini-satellites, micro-satellites, and SNP (Single Nucleotide Polymorphism). Each marker has a specific location in the genetic material (Casas, 2002). Marker assisted selection (MAS) uses information about these regions in livestock selection programs to identify individuals with favourable combinations of QTLs (Casas, 2002).

Tenderness quantitative trait loci

Quantitative trait loci for carcass traits have been detected on different chromosomes (Table 3). Several studies independently identified a QTL on BTA29 affecting tenderness, either in crosses between *Bos taurus* and *Bos indicus* or in crosses between *Bos taurus* breeds (Casas et al., 2005). Other QTL with the impact on beef tenderness traits were identified on BTA4, 5, 9, 11, 15, and 20, but have not been confirmed in independent studies. There is also a lack of evidence for a gene within the QTL region that could be considered as a strong candidate. On the contrary, polymorphisms in two genes, CAST (calpastatin) and LOX (Lysyl oxidase), both located on BTA7, where no QTL for tenderness has been reported, have been associated with an effect on the beef tenderness trait (Barendse, 1997, 2002). The calpastatin gene has been proposed as a candidate locus for marker assisted selection by Killefer and Koochmarai (2004), because of the role calpastatin plays in ageing as an inhibitory regulator of the calpain system.

Table 3 – QUANTITATIVE TRAIT LOCI IDENTIFIED FOR TENDERNESS (DAVIS, 2007)

Chromosome	Family	Candidate gene
4 [§]	BM	-
5 [£]	PA	-
7	CB	calpastatin
15	BH	-
29 [§]	PA	μ-calpain
29 [£]	PA	μ-calpain

BM = Belgian blue X MARC III; PA = Piedmontese X Angus; BH = Brahman X Hereford; CB = Charolais-Brahman X Belmont Red; § - Shear force at 3 d post-mortem (kg); £ - Shear force at 14 d post-mortem (kg).

Marbling quantitative trait loci

Several QTLs for marbling were reported with location on BTA2, BTA3 and BTA27 (Casas, 2002). Interestingly, the myostatin gene lies on BTA2 where the QTL was detected (Casas et al., 1998; Casas, 2002). However, it seems unlikely that this gene is involved in the variation found in all studies because some do not include breeds known to be the carriers of double muscling. Other QTLs on BTA5, 8, 9, 10, 14, 16, 17, 23, and 29 were also reported but have not yet been confirmed. Genetic markers associated with intramuscular fat deposition or marbling have been reported, and are located on chromosomes BTA5 and BTA14, where QTL for these traits have been suggested elsewhere. On BTA5, the polymorphic micro-satellite loci CSSM34 and ETH10, which are 20 cM apart, are associated with marbling scores in the Angus, Shorthorn, and Wagyu breeds (Barendse, 1997, 2002). In the mitochondrial transcription factor A (TFAM) single nucleotide polymorphisms has been found and correlated with marbling and subcutaneous fat depth in Wagyu x Limousin crosses (Jiang et al., 2005).

Conclusion

Variation in meat tenderness is the principal responsible factor for consumer dissatisfaction, and must be as such, controlled in order to improve customer satisfaction. However, variation in this trait is under genetic and environment control; the knowledge of genetics combined with the control of environmental sources of variation may enable beef industry to consistently produce tender beef.

The use of molecular markers offers a great potential to improve efficiency of animal breeding for meat quality traits. Location of these markers affecting beef tenderness in the cattle genome will allow maximizing genetic improvement of beef tenderness; and the presence of these genes will allow producers to sort animals prior to slaughter into groups according to the expected tenderness.

The genomics will undoubtedly increase our knowledge of the genes involved in determining beef quality. The major outcomes are the development of DNA tests to improve beef quality by genetic selection, and the identification of molecular markers to predict the ability of animals to produce beef with desirable quality traits.

REFERENCES

1. Barendse, W. 1997. Assessing lipid metabolism. Patent No: WO9923248. ep.espacenet.com (30. Sept. 2006).
2. Barendse, W. 2002. DNA markers for beef tenderness. Patent No: WO02064820. ep.espacenet.com (30. Sept. 2006).
3. Beltrán, J.A., Jaime, I., Santolaria, P., Sañudo, C., Albertí, P., Rocalés, P. 1997. Effect of stress-induced high post-mortem pH on protease activity and tenderness of beef. *Meat Science*, 45: 201-207.
4. Berry, B.W. 1993. Tenderness of beef loin steaks as influenced by marbling level, removal of subcutaneous fat, and cooking method. *Journal of Animal Science*, 71: 2412-2419.
5. Bertrand, J.K., Green, R.D., Herring, W.O., Moser, D.W. 2001. Genetic evaluation for beef carcass traits. *Journal of Animal Science*, 79(E. Suppl.): E190-E200.
6. 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., Savell, J.W. 1997. Consumer evaluation of beef of known categories of tenderness. *Journal of Animal Science*, 75: 1521-1524.
7. Bourdon, R.M. 2000. Understanding animal breeding. Second Edition ed. Prentice Hall International, London.
8. Casas, E., White, S.N., Riley, D.G., Smith, T.P.L., Breneman, R.A., Olson, T.A., Johnson, D.D., Coleman, S.W., L., B.G., Chase, C.C. 2005. Assessment of single nucleotide polymorphisms in genes residing on chromosomes 14 and 29 for association with carcass composition traits in *Bos indicus* cattle. *Journal of Animal Science*, 83: 13-19.
9. Casas, E., Keele, J.W., Shackelford, S.D., Koohmaraie, M., Stone, R.T. 2003a. Identification of quantitative trait loci for growth and carcass composition in cattle. *Animal Genetics*, 35: 2-6.
10. Casas, E., Shackelford, S.D., Keele, J.W., Koohmaraie, M., Smith, T.P.L., Stone, R.T. 2003b. Detection of quantitative trait loci for growth and carcass composition in cattle. *Journal of Animal Science*, 81: 2976-2983.
11. Casas, E. 2002. Identification of quantitative trait loci in beef cattle. *Journal of Animal Science*, 10: 54-61.
12. Casas, E., Stone, R.T., Keele, J.W., Shackelford, S.D., Kappes, S.M., Koohmaraie, M. 2001. A comprehensive search for quantitative trait loci affecting growth and carcass composition of cattle segregating alternative forms of the myostatin gene. *Journal of Animal Science*, 79: 854-860.
13. Casas, E., Keele, J.W., Shackelford, S.D., M., K., Sonstegard, T.S., Smith, T.P.L., Kappes, S.M., Stone, R.T. 1998. Association of the muscle hypertrophy locus with carcass traits in beef cattle. *Journal of Animal Science*, 76: 468-473.

14. Davis, G.P., Moore, S.S., Drinkwater, R.D., Shorthose, W.R., Loxton, I.D., Barendse, W., Hetzel, D.J.S. 2007. QTL for meat tenderness in the *M. longissimus lumborum* of cattle. *Animal Genetics*, 39:40-45
15. Fergusson, D.M. 2004. Objective on-line assessment of marbling: a brief review. *Australian Journal of Experimental Agriculture*, 44: 681-685.
16. Harper, G.S. 1999. Trends in skeletal muscle and the understanding in beef. *Australian Journal of Agricultural Research*, 50: 1105-1129.
17. Huff-Lonergan, E., Mitsuhashi, T., Beekman, D.D., Parrish, F.C., Olson, D.G., Robson, R.M. 1996. Proteolysis of specific muscle structural proteins by μ -calpain at low pH and temperature is similar to degradation in postmortem bovine muscle. *Journal of Animal Science*, 74: 993-1008.
18. Hwang, I.H., Park, B.Y., Cho, S.H., Lee, J.M. 2004. Effects on muscle shortening and proteolysis on Warner-Bratzler shear force in beef longissimus and semitendinosus. *Meat Science*, 68: 497-505.
19. Jiang, Z., Kunej, T., Michal, J.J., Gaskins, C.T., Reeves, J.J., Busboom, J.R., Dovic, P., Wright Jr., R.W. 2005. Significant associations of the mitochondrial transcription factor A promoter polymorphisms with marbling and subcutaneous fat depth in Wagyu x Limousin F2 crosses. *Biochemical and Biophysical Research Communications*, 334: 516-523.
20. Killefer, J., Koohmaraie, M. 2004. Bovine skeletal muscle calpastatin: cloning, sequence analysis, and steady-state mRNA expression. *Journal of Animal Science*, 72: 606-614.
21. Killinger, K.M., Calkins, C.R., Umberger, W.J., Feuz, D.M., Eskridge, K.M. 2004. Consumer sensory acceptance and value for beef steaks of similar tenderness, but differing in marbling level. *Journal of Animal Science*, 82: 3294-3301.
22. King, D.A., Pfeiffer, S.C.E., Randel, R.D., Welsh, T.H., Oliphint, R.A., Baird, B.E., Curley Jr, K.O., Vann, R.C., Hale, D.C., Savell, J.W. 2006. Influence of animal temperament and stress responsiveness on the carcass quality and beef tenderness of feedlot cattle. *Meat Science*, 74: 546-556.
23. Lawrence, T.E., Dikerman, M.E., Stephens, J.W., Obuz, E., Davis, J.R. 2003. In situ investigation of the calcium-induced proteolytic and salting - in mechanisms causing tenderization in calcium-enhanced muscle. *Meat Science*, 66: 69-75.
24. Lensink, B.J., Fernandez, X., Boivin, X., Pradel, P., Le Neindre, P., Veissier, I. 2000. The impact of gentle contacts on ease of handling, welfare, and growth of cows and on quality of veal meat. *Journal of Animal Science*, 78: 1219-1226.
25. Marshall, D.M. 1999. Genetics of meat quality. In: C.B. Ramsey and A. Ruvinsky (eds.) *The genetics of cattle*. p 605-636. CAB International, London.
26. Miller, M.F., Huffman, K.L., Gilbert, S.Y., Hamman, L.L., Ramsey, C.B. 1995. Retail consumer acceptance of beef tenderized with calcium chloride. *Journal of Animal Science*, 73: 2308-2314.
27. Morgan, J.B., Savell, J.W., Hale, D.S., Miller, R.K., Griffin, D.B., Cross, H.R., Shackelford, S.D. 1991. National beef tenderness survey. *Journal of Animal Science*, 69: 3274-3283.

28. Mounier, L., Dubroeuq, H., Andanson, S., Veissier, I. 2006. Variations in meat pH of beef bulls in relation to conditions of transfer to slaughter and previous history of the animals. *Journal of Animal Science*, 84: 1567-1576.
29. Nishimura, T., Hattori, A., Takahashi, K. 1999. Structural changes in intramuscular connective tissue during the fattening of Japanese black cattle: Effect of marbling on beef tenderization. *Journal of Animal Science*, 77: 93-104.
30. Purslow, P.P. 2005. Intramuscular connective tissue and its role in meat quality. *Meat Science*, 70: 435-447.
31. Sami, A.S., Augustini, C., Schwarz, F.J. 2004. Effects of feeding intensity and time on feed on performance, carcass characteristics and meat quality of simmental bulls. *Meat Science*, 67: 195-201.
32. Savell, J.W., Mueller, S.L., Baird, B.E. 2005. The chilling of carcasses. *Meat Science*, 70: 449-459.
33. Searls, G.A., Maddock, R.J., Wulf, D.M. 2005. Intramuscular tenderness variation within four muscles of the beef chuck. *Journal of Animal Science*, 83: 2835-2842.
34. Shackelford, S.D., Koohmaraie, M., Wheeler, T.L. 1995. Effects of slaughter age on meat tenderness and USDA carcass maturity scores of beef females. *Journal of Animal Science*, 73: 3304-3309.
35. Shackelford, S.D., Koohmaraie, M., Cundiff, L.V., Gregory, K.E., Rohrer, G.A., 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. *Journal of Animal Science*, 72: 857-863.
36. Shackelford, S.D., Koohmaraie, M., Miller, M.F., Crouse, J.D., Reagan, J.O. 1991. An evaluation of tenderness of the longissimus muscle of angus by hereford versus brahman crossbred heifers. *Journal of Animal Science*, 69: 171-177.
37. Strydom, P.E., Frylinck, L., Smith, M.F. 2005. Should electrical stimulation be applied when cold shortening is not a risk? *Meat Science*, 70: 733-742.
38. Tatum, J.D., Smith, G.C., Belk, K.E. 1999. New approaches for improving tenderness, quality, and consistency of beef. In: *Proceedings of the American Society of Animal Science*, Indianapolis, Indiana. p 1-10.
39. Thompson, J.M. 2004. The effects of marbling on flavour and juiciness scores of cooked beef, after adjusting to a constant tenderness. *Australian Journal of Experimental Agriculture*, 44: 645-652.
40. USDA. 1997. United states standard for grades of carcass beef. In: USDA (ed.).
41. Viljoen, H.F., De Kock, H.L., Webb, E.C. 2002. Consumer acceptability of dark, firm and dry (DFD) and normal pH beef steaks. *Meat Science*, 61: 181-185.
42. Wheeler, T.L., Cundiff, L.V., Shackelford, S.D., Koohmaraie, M. 2005. Characterization of biological types of cattle (Cycle VII): Carcass, yield, and longissimus palatability traits. *Journal of Animal Science*, 83: 196-207.
43. Wheeler, T.L., Cundiff, L.V., Shackelford, S.D., Koohmaraie, M. 2004. Characterization of biological types of cattle (Cycle VI): Carcass, yield, and longissimus palatability traits. *Journal of Animal Science*, 82: 1177-1189.

44. Wheeler, T.L., Cundiff, L.V., Shackelford, S.D., Koohmaraie, M. 2001. Characterization of biological types of cattle (Cycle V): Carcass traits and longissimus palatability. *Journal of Animal Science*, 79: 1209-1222.
45. Wheeler, T.L., Cundiff, L.V., Koch, R.M., Crouse, J.D. 1996. Characterization of biological types of cattle (Cycle IV): Carcass traits and longissimus palatability. *Journal of Animal Science*, 74: 1023-1035.
46. Wheeler, T.L., Vundiff, L.V., Koch, R.M. 1994. Effect of marbling score on beef palatability in *Bos taurus* and *Bos indicus* cattle. *Journal of animal science*, 72: 3145-3151.
47. White, A., O'sullivan, A., Troy, D.J., O'neill, E.E. 2006. Effects of electrical stimulation, chilling temperature and hot-boning on the tenderness of bovine muscles. *Meat Science*, 73: 196-203.
48. Xie, Y.R., Busboom, J.R., Cornforth, D.P., Shenton, H.T., Gaskins, C.T., Johnson, K.A., Reeves, J.J., Wright, R.W., Cronrath, J.D. 1996. Effects of time on feed and post-mortem aging on palatability and lipid composition of crossbred Wagyu beef. *Meat Science*, 43: 157-166.
49. Žgur, S. 1996. Rast in kakovost mesa pri govedu. *Znanost in Praksa v Govedoreji*, 20: 530-534.
50. Žgur, S., Čepon, M., Čepin, S. 2003. Influence of growth rate in two growth periods on intramuscular connective tissue and palatability traits of beef. *Czech Journal of Animal Science*, 48, (3): 113–119

KAKVOĆA GOVEDINE: ČIMBENICI KOJI UTJEČU NA MEKOĆU I MRAMORIRANOST

Sažetak

Mekoća je bez sumnje najvažniji pokazatelj kakvoće goveđeg mesa. Oscilacija mekoće goveđeg mesa glavni je čimbenik nezadovoljstva potrošača. Da bi se poboljšalo zadovoljstvo potrošača, taj se čimbenik mora kontrolirati. Moguće je da do oscilacije mekoće govedine dolazi zbog pasmine/genetike, sastavu trupa (mramoriranosti) i okolišnih čimbenika (kronološka dob, vrijeme hranjenja, implantati i stres prije klanja). Mnogi postupci nakon klanja životinja, kao što su; starenje, elektro-stimulacija, stupanj hladnoće i tehnologije postizanja mekoće, također utječu na mekoću. Udio masnoće u trupu, posebno intramuskularna masnoća (mramoriranost), igra važnu ulogu u senzorskim svojstvima mesa. Razvoj kvalitetnijih metodologija kojima bi se predvidjela mekoća mesa na živoj životinji ili u klaonici, imala bi važnu ulogu u zadovoljstvu potrošača. Drugi, još jedan važni način poboljšanja kakvoće mesa, je selekcija. Među različitim pasminama razvijeni su programi genetskog vrednovanja, a trenutna istraživanja su usredotočena na gene koji najviše utječu na mekoću i mramoriranost mesa.

Key words: kakvoća goveđeg mesa, mekoća, mramoriranost

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