Variation in palatability and biochemical traits within and among eleven beef muscles[1,2,3,4]

M. S. Rhee[5], T. L. Wheeler[6], S. D. Shackelford, and M. Koohmaraie

ARS, USDA, Roman L. Hruska U.S. Meat Animal Research Center, Clay Center, NE 68933

ABSTRACT: The objective of this study was to determine the extent of variation in, and relationships among, biochemical and palatability traits within and among 11 major beef muscles. Longissimus thoracis et lumborum (LD), psoas major (PM), gluteus medius (GM), semimembranosus (SM), adductor (AD), biceps femoris (BF), semitendinosus (ST), rectus femoris (RF), triceps brachii (TB), infraspinatus (IS), and supraspinatus (SS) from one side of 31 Charolais × MARC III steer carcasses were vacuum-packaged, stored at 2°C until 14 d postmortem, and then frozen at –30°C. The 2.54-cm-thick steaks were obtained from two or three locations within muscles in order to assess biochemical traits and Warner-Bratzler shear force, and from near the center for sensory trait evaluation. The PM was most tender and was followed by IS in both shear force and tenderness rating ($P < 0.05$). The other muscles were not ranked the same by shear force and tenderness rating. The BF had the lowest ($P < 0.05$) tenderness rating. The PM, GM, and LD had lower ($P < 0.05$) collagen concentration (2.7 to 4.5 mg/g muscle) than muscles from the chuck and round (5.9 to 9.0 mg/g), except for the AD (4.9 mg/g). Desmin proteolysis was highest ($P < 0.05$) for BF and LD (60.7 and 60.1% degraded), and was lowest ($P < 0.05$) for PM (20.2%). The PM, TB, IS, RF, and ST had relatively long sarcomere lengths (>2.1 μm), whereas the GM had the shortest ($P < 0.05$) sarcomere length (1.7 μm). Cooking loss was lowest ($P < 0.05$) for BF (18.7%) and was followed by LD and IS (20.7%); it was highest ($P < 0.05$) for ST (27.4%). Across all muscles, tenderness rating was highly correlated ($r > 0.60$) with shear force, connective tissue rating, sarcomere length, and collagen content. Within a muscle, correlations among all traits were generally highest in LD and lowest in AD. Within muscle, location effects were detected ($P < 0.05$) for shear force (PM, ST, BF, SM, and RF), sarcomere length (PM, ST, BF, LD, SS, IS, SM, and RF), collagen concentration (PM, BF, SS, IS, SM. AD, TB, and RF), desmin degradation (PM, GM, BF, SM, AD, and, RF), and cooking loss (all muscles except SS and AD). There is a large amount of variation within and among muscles for tenderness traits and tenderness-related biochemical traits. These results increase our understanding of the sources of variation in tenderness in different muscles and provide a basis for the development of muscle-specific strategies for improving the quality and value of muscles.

Key Words: Beef, Collagen, Muscles, Proteolysis, Sarcomere Length, Tenderness

 J. Anim. Sci. 2004. 82:534–550

Introduction

It appears that there is a segment of consumers that is willing to pay a premium for guaranteed tender beef (Boleman et al., 1997; Lusk et al., 2001; Shackelford et al., 2001). However, inconsistency in meat tenderness has been identified as one of the major problems facing the beef industry (Morgan et al., 1991; Boleman et al., 1998). Certain cuts of beef have been identified as needing improvement in tenderness relative to consumer expectations (Morgan et al., 1991; Neely et al., 1998; Brooks et al., 2000). These lower quality cuts

[1]This work was supported, in part, by the USDA, National Research Initiative Competitive Grants Program (Grant No. 99-35503-8437).

[2]Names are necessary to report factually on available data; however, the USDA neither guarantees nor warrants the standard of the product, and the use of the name by USDA implies no approval of the product to the exclusion of others that may also be suitable.

[3]Anti-desmin (clone D3) was developed by D. A. Fischman and was obtained from the Developmental Studies Hybridoma Bank maintained by Univ. of Iowa, Dept. of Biol. Sci., Iowa City 52242, under contract N01-HD-7-3263 from the NICHD.

[4]The authors express their gratitude to P. Beska, P. Ekeren, K. Mihm, P. Tammen, and I. Hwang for technical assistance, and to M. Bierman for secretarial assistance.

[5]Present address: Division of Food Science, College of Life and Environmental Sciences, Korea University, 5-ka Anam-dong, Sungbuk-ku, Seoul, 136-701, South Korea.

[6]Correspondence: P. O. Box 166 (phone: 402-762-4229; fax: 402-762-4149; e-mail: wheeler@email.marc.usda.gov).

Received March 31, 2003.

Accepted October 16, 2003.

make up a majority of the carcass and have been declining in value relative to loin cuts (Cattle Fax, 1998).

Extensive knowledge of meat tenderness variation and meat palatability has been developed for the longissimus. Relative to most muscles, the longissimus has low variation in sensory-detectable connective tissue and sarcomere length; thus, most of the variation in tenderness results from variation in the extent of proteolysis of myofibrillar and cytoskeletal proteins (Koohmaraie, 1992; 1994). Tenderness of other major beef muscles is lowly to moderately related to the tenderness of the longissimus (Slanger et al., 1985; Shackelford et al., 1995; Wheeler et al., 2000a) because these muscles vary considerably in sarcomere length and collagen content (Herring et al., 1965; McKeith et al., 1985; Wheeler et al., 2000b) and likely vary in the extent of proteolysis (Wheeler et al., 2000b). However, most results include only a few muscles, and very little is known about variation in proteolysis among beef muscles. Furthermore, information on amount and sources of variation in meat tenderness among locations within beef muscles is very limited. Therefore, the objective of this study was to determine the extent of variation in and relationships among biochemical and palatability traits within and among 11 major beef muscles.

Materials and Methods

Samples

The Roman L. Hruska U.S. Meat Animal Research Center (MARC) Animal Care and Use Committee approved the use and treatment of animals in this experiment according to guidelines established by the USDA. Thirty-one Charolais × MARC III steers were slaughtered using humane procedures at 14 to 16 mo of age at a commercial processing plant in five groups spanning 70 d. Carcasses were chilled conventionally for 36 h at 0°C. Right carcass sides were ribbed (USDA, 1997) between 12th and 13th ribs, and USDA quality and yield grade factors were measured by trained MARC personnel (USDA, 1997). Right sides were transported to the MARC meat laboratory. At 72 h postmortem, the following muscles were dissected from one side of each carcass, vacuum-packaged, stored at 2°C until 14 d postmortem, and then frozen at –30°C: longissimus thoracis et lumborum (**LD**), psoas major (**PM**), gluteus medius (**GM**), semimembranosus (**SM**), adductor (**AD**), biceps femoris (**BF**), semitendinosus (**ST**), rectus femoris (**RF**), triceps brachii (**TB**), infraspinatus (**IS**), and supraspinatus (**SS**). These frozen muscles were cut into 2.54-cm-thick steaks with a band saw. Steaks of each muscle were assigned to trained sensory panel evaluation (from near the center) and Warner-Bratzler shear force (two or three locations) as illustrated in Figure 1.

Cooking

Steaks were thawed (5°C) and cooked on a Magigrill belt grill (MagiKitch'n, Inc., Quakertown, PA) as described by Wheeler et al. (1998) with the following exceptions. The preheat platen on the belt grill was set at 149°C, rather than disconnected, and the change required that cooking time be reduced to 5.5 min, rather than 5.7 min. Percentage cooking loss was calculated as the total of percentage thawing loss and percentage cooking loss, and the cooking loss data presented are the average of cooking loss from sensory and shear force steaks.

Warner-Bratzler Shear Force

Warner-Bratzler shear force was conducted as described by Wheeler et al. (1998). One of the two halves from each sheared core was used for sarcomere length determination. The other half of each core was trimmed to remove the crusted cooked surface and then diced and powdered in liquid nitrogen for the determination of collagen concentration and desmin proteolysis.

Sarcomere length

Sarcomere length was measured on the cores used to determine Warner-Bratzler shear force. Samples were fixed according to Koolmees et al. (1986). The helium-neon laser diffraction method described by Cross et al. (1981) was used on cooked sample (36 total measurements per observation) as described by Wheeler et al. (2002).

Collagen Concentration

Collagen concentration was determined on the cores used to determine Warner-Bratzler shear force. Sample preparation, separation of hydroxyproline by HPLC, and quantification of collagen were conducted as described by Wheeler et al. (2000b).

Immunoblotting

Protein extraction, electrophoresis, Western blotting, and quantification of desmin were determined on the cores used to determine Warner-Bratzler shear force as described by Wheeler and Koohmaraie (1999) and Wheeler et al. (2002). Samples for reference standards were obtained from the same 11 muscles of two beef carcasses within 1 h postmortem. At-death samples from the two carcasses were pooled to create a single reference standard for each muscle. Muscle-specific reference standards were used because at-death samples varied among muscles in the amount of desmin. There also is animal-to-animal variation in the amount of desmin in a given muscle (unpublished data); thus, some values for percentage degradation were negative (more desmin in the 14-d sample than

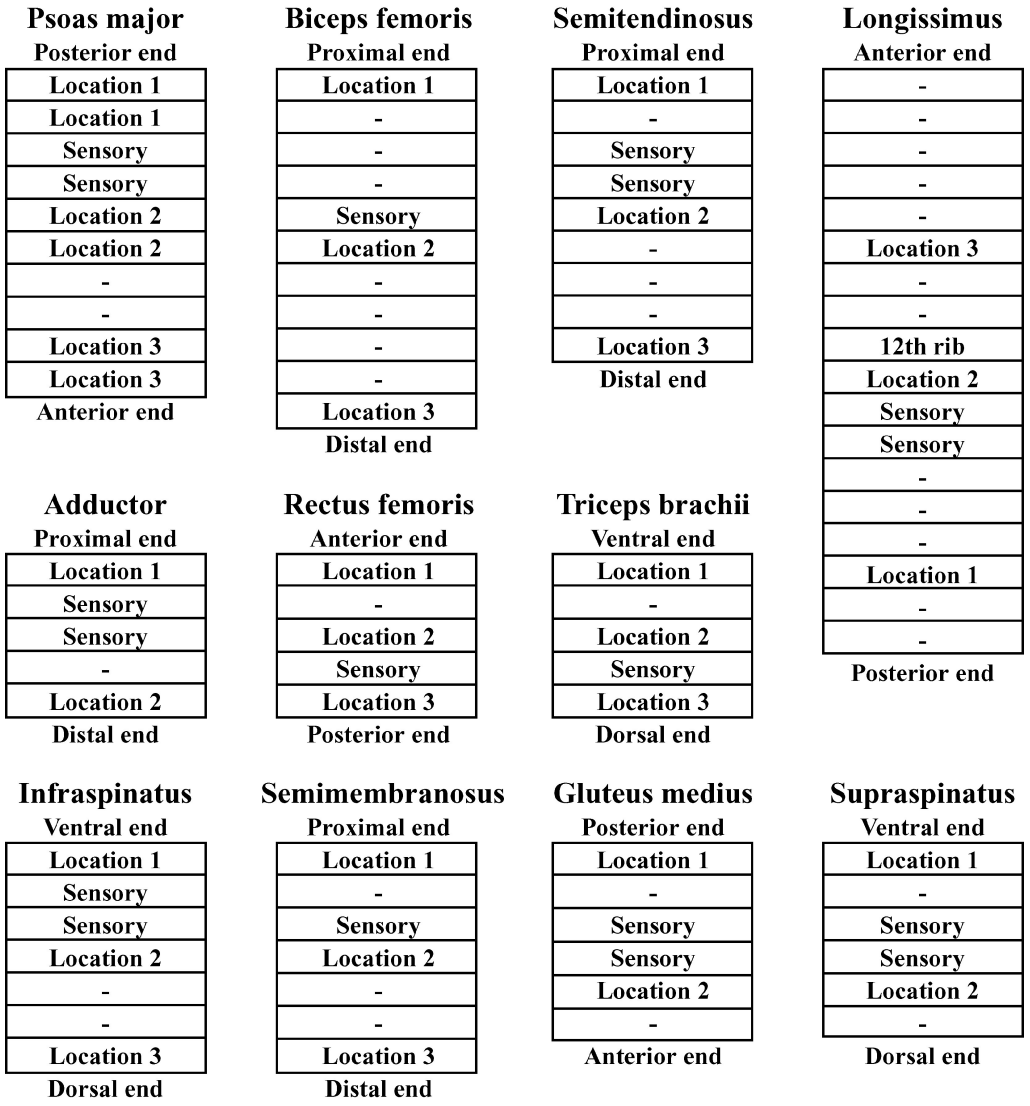

Figure 1. Sampling locations for Warner-Bratzler shear force and biochemical traits, and trained sensory evaluation of 11 beef muscles (proximal = nearest the vertebral column). Each horizontal section represents a 2.54-cm-thick steak. Locations 1, 2, and 3 were used for Warner-Bratzler shear force and biochemical traits.

in the at-death standard). Within a blot, the lowest negative value was set to zero and all other values from that blot were adjusted proportionately. Data were expressed as the percentage of the at-death desmin that was degraded.

Trained Sensory Evaluation

Steaks were evaluated immediately after cooking by an eight-member trained descriptive attribute sensory panel as described by Wheeler et al. (1998). Panelists scored each sample for tenderness, amount of connective tissue, juiciness, and beef flavor intensity on 8-point scales (8 = extremely tender, none, extremely juicy, and extremely intense to 1 = extremely tough, abundant, extremely dry, and extremely bland, respectively) and off-flavor on a 4-point scale (4 = none to 1 = intense).

Statistical Analyses

Data were analyzed by analysis of variance using the GLM procedure of SAS (SAS Inst. Inc., Cary, NC) for a completely randomized design. The model included the main effect of muscle (AD, BF, GM, IS, LD, PM, RF, SM, SS, ST, and TB). A split-plot design was used to analyze location within muscle (Locations 1, 2, and 3). When the main effect was significant ($P < 0.05$), least squares means separation was accomplished by the PDIFF option (a pairwise t-test). Simple correlations were obtained from the PROC CORR procedure of SAS. Sampling multiple locations provided replications that were used to calculate the proportion of variance due to animal and location from the PROC VARCOMP procedure. Variance components (σ^2_{animal}, $\sigma^2_{\text{location}}$, and σ^2_{error}) were estimated, and proportions due to animal and location were calculated with these

equations: proportion due to animal = $\sigma^2_{animal}/(\sigma^2_{animal} + \sigma^2_{location} + \sigma^2_{error})$ and proportion due to location = $\sigma^2_{location}/(\sigma^2_{animal} + \sigma^2_{location} + \sigma^2_{error})$.

Results and Discussion

Muscle Effects

Muscles varied considerably in overall sensory tenderness ratings (Table 1). The PM received the highest ($P < 0.05$) tenderness rating, followed by IS and then by LD, TB, RF, and GM. The BF received the lowest ($P < 0.05$) tenderness rating. These results are in general agreement with previous reports (McKeith et al., 1985; Carmack et al., 1995; Shackelford et al., 1995). Although the IS was the second most tender muscle, it was not as tender relative to the PM as previously reported (Shackelford et al., 1995), but the relative tenderness of the IS agreed with other results (McKeith et al., 1985; Carmack et al., 1995). Tenderness ratings among muscles were similar to those of Carmack et al. (1995) except, for no apparent reason, they reported a relatively lower tenderness rating for SM. In 1-d postmortem beef, McKeith et al. (1985) found differences in tenderness among muscles similar to the differences we found, except that ST and BF were rated higher in tenderness relative to other muscles in their study. Shackelford et al. (1995) reported higher tenderness ratings for ST, SS, and BF, and lower ratings for SM relative to our results (Table 1). Morgan et al. (1991) also reported higher tenderness ratings for SS and lower ratings for SM relative to our results. In 1-d-postmortem pork, Wheeler et al. (2000b) reported higher tenderness ratings for ST and TB than for LD.

The PM had the highest ($P < 0.05$) sensory ratings for amount of connective tissue (least connective tissue), followed by LD and then IS and TB, and BF received the lowest ($P < 0.05$) ratings (Table 1). These results are consistent with previous reports (McKeith et al., 1985; Morgan et al., 1991; Shackelford et al., 1995). Consistent with the higher tenderness rating for ST in pork, ST also had less sensory-detectable connective tissue than four other muscles, including the LD (Wheeler et al., 2000b). Muscle rankings for tenderness and amount of connective tissue ratings were very similar and reflect the impact of connective tissue amount on differences in tenderness among muscles, but they also may be partly due to autocorrelation among sensory ratings.

Although there were differences ($P < 0.01$) among muscles in sensory juiciness ratings (Table 1), beef flavor intensity, and off-flavor (Table 1), variation within and among muscles for these traits was much lower than for tenderness rating. Muscle rankings for juiciness rating were generally similar to their tenderness ranking, except for BF. Although ranked lowest in tenderness among muscles, the BF was tied for highest juiciness ranking with IS and PM. Our juiciness results do not agree with previous findings for the BF (Carmack, et al., 1995; Shackelford et al., 1995; Wheeler et al., 2000b) or PM (McKeith et al., 1985; Shackelford et al., 1995), possibly due to the belt grill method of cooking. However, McKeith et al. (1985) also reported that BF was among the juiciest muscles.

Sensory beef flavor intensity rating was highest ($P < 0.05$) for LD and lowest ($P < 0.05$) for PM, although differences among muscles were relatively small (Table 1). Off-flavor rating was highest ($P < 0.05$) for LD (least off-flavors) and lowest ($P < 0.05$) for PM and IS. These results are in agreement with those of Shackelford et al. (1995) but are not consistent with Carmack et al. (1995), who reported that the PM had the highest beef flavor intensity.

The range in muscle means for Warner-Bratzler shear force was 2 kg compared to 3.7 sensory tenderness rating units (Table 2). The PM had the lowest ($P < 0.05$) shear force, followed by IS, and AD and SS had the highest ($P < 0.05$) shear force. Warner-Bratzler shear force muscle rankings generally agreed with tenderness ratings, except that BF moved from 11th to 4th most tender, and the ST moved from 10th to 7th most tender. More accurate differentiation among muscles for tenderness by Warner-Bratzler shear force, relative to sensory tenderness rating, was achieved than in previous results (Shackelford et al., 1995). Our current results for Warner-Bratzler shear force are consistent with those of McKeith et al. (1985) and Brooks et al. (2000), except that both these studies reported Warner-Bratzler shear force for BF that ranked it among the least tender. In the study of Shackelford et al. (1995), there were no differences in Warner-Bratzler shear force between TB, LD, ST, GM, SS, BF, and SM. It has been proposed (Harris and Shorthose, 1988; Shackelford et al., 1995) that Warner-Bratzler shear force does not properly measure tenderness differences among muscles. This conclusion still appears to be correct, particularly for some round muscles, although to a lesser extent overall. However, this fact does not affect the usefulness of Warner-Bratzler shear force to study differences in tenderness within muscles (e.g., location effects).

In agreement with Shackelford et al. (1995), the LD was the most variable in Warner-Bratzler shear force, followed by SM. Variability in shear force was lowest in PM. Inconsistent findings have been reported for the longissimus tenderness relative to other muscles. Zinn et al. (1970) and Koohmaraie et al. (1988) observed that LD was the toughest muscle among three bovine muscles, whereas Shorthose and Harris (1990) and Brooks et al. (2000) reported that LD was one of the tenderest muscles. These discrepancies are likely due to the fact that because the LD is more variable in tenderness (among experiments) than other muscles, in any given experiment, if the LD is relatively tender it will be one of the most tender muscles and if it is relatively tough, it will be one of the least tender muscles. This could be particularly true for experi-

Table 1. Descriptive statistics for trained sensory panel traits among muscles

Trait and muscle	Mean	SD	Minimum	Maximum	CV
Overall tenderness[a]					
Psoas major	7.4[f]	0.27	7.0	8.0	3.6
Infraspinatus	5.9[g]	0.62	4.8	6.9	10.4
Longissimus	5.7[h]	0.84	3.4	7.1	14.9
Triceps brachii	5.2[i]	0.53	4.1	6.4	10.1
Rectus femoris	4.9[j]	0.51	3.8	5.8	10.3
Gluteus medius	4.7[k]	0.64	3.6	6.5	13.8
Adductor	4.3[l]	0.54	3.4	5.3	12.5
Semimembranosus	4.2[l]	0.69	2.7	5.3	16.5
Supraspinatus	4.1[l]	0.61	2.8	5.3	14.7
Semitendinosus	4.1[l]	0.60	2.1	5.1	14.7
Biceps femoris	3.7[m]	0.53	2.5	4.8	14.2
Amount of connective tissue[b]					
Psoas major	7.7[f]	0.27	7.0	8.0	2.1
Longissimus	6.9[g]	0.53	5.1	7.6	7.7
Infraspinatus	6.7[h]	0.52	5.1	7.4	7.8
Triceps brachii	6.5[h]	0.36	5.8	7.3	5.5
Rectus femoris	6.2[i]	0.42	5.3	6.9	6.7
Gluteus medius	6.2[i]	0.51	5.1	7.1	8.2
Adductor	5.7[j]	0.55	4.5	6.9	9.7
Semitendinosus	5.6[j]	0.43	4.6	6.5	7.7
Supraspinatus	5.5[j]	0.57	4.3	7.0	10.4
Semimembranosus	5.4[j]	0.64	4.2	6.6	11.9
Biceps femoris	4.6[k]	0.55	3.5	5.4	12.0
Juiciness[c]					
Biceps femoris	5.3[f]	0.24	4.9	5.7	4.5
Infraspinatus	5.3[fg]	0.27	4.8	5.8	5.2
Psoas major	5.2[fgh]	0.34	4.4	5.9	6.7
Triceps brachii	5.2[ghi]	0.25	4.4	5.7	4.9
Rectus femoris	5.2[ghi]	0.23	4.8	5.7	4.4
Longissimus	5.1[hij]	0.26	4.6	5.6	5.0
Gluteus medius	5.1[ij]	0.25	4.4	5.5	5.0
Semimembranosus	5.0[j]	0.20	4.6	5.4	4.1
Adductor	4.9[k]	0.25	4.3	5.3	5.2
Supraspinatus	4.9[k]	0.23	4.4	5.4	4.7
Semitendinosus	4.8[k]	0.28	4.0	5.3	5.9
Beef flavor intensity[d]					
Longissimus	4.4[f]	0.19	4.1	4.8	4.2
Biceps femoris	4.3[g]	0.23	3.8	4.7	5.3
Semimembranosus	4.2[gh]	0.20	3.8	4.6	4.7
Triceps brachii	4.2[ghi]	0.19	3.8	4.6	4.5
Rectus femoris	4.1[hij]	0.22	3.8	4.7	5.3
Semitendinosus	4.1[ij]	0.22	3.6	4.4	5.3
Supraspinatus	4.1[ij]	0.25	3.5	4.5	6.1
Gluteus medius	4.1[ij]	0.20	3.7	4.6	4.9
Adductor	4.1[j]	0.26	3.4	4.4	6.3
Infraspinatus	4.0[j]	0.24	3.6	4.5	5.9
Psoas major	3.9[k]	0.23	3.3	4.3	5.9
Off-flavor[e]					
Psoas major	2.2[j]	0.16	1.9	2.6	7.1
Infraspinatus	2.3[j]	0.19	1.8	2.6	8.6
Adductor	2.3[ij]	0.18	2.0	2.8	7.7
Supraspinatus	2.4[hi]	0.17	2.0	2.6	7.0
Gluteus medius	2.4[gh]	0.17	1.9	2.8	7.1
Rectus femoris	2.4[gh]	0.20	2.0	2.8	8.3
Semitendinosus	2.4[gh]	0.18	2.1	2.8	7.3
Biceps femoris	2.4[gh]	0.16	2.1	2.8	6.5
Triceps brachii	2.5[gh]	0.16	2.2	3.0	6.4
Semimembranosus	2.5[g]	0.18	2.1	2.9	7.3
Longissimus	2.7[f]	0.16	2.4	3.0	6.0

[a]1 = extremely tough, 2 = very tough, 3 = moderately tough, 4 = slightly tough, 5 = slightly tender, 6 = moderately tender, 7 = very tender, and 8 = extremely tender.

[b]1 = abundant, 2 = moderately abundant, 3 = slightly abundant, 4 = moderate, 5 = slight, 6 = traces, 7 = practically none, and 8 = none.

[c]1 = extremely dry, 2 = very dry, 3 = moderately dry, 4 = slightly dry, 5 = slightly juicy, 6 = moderately juicy, 7 = very juicy, and 8 = extremely juicy.

[d]1 = extremely bland, 2 = very bland, 3 = moderately bland, 4 = slightly bland, 5 = slightly intense, 6 = moderately intense, 7 = very intense, and 8 = extremely intense.

[e]1 = intense, 2 = moderate, 3 = slight, and 4 = none.

[f,g,h,i,j,k,l,m]Means in a column within a trait that do not have a common superscript differ ($P < 0.05$).

Table 2. Descriptive statistics for Warner-Bratzler shear force (WBSF), sarcomere length, collagen concentration, desmin proteolysis, and cooking loss

Trait and muscle	Mean[a]	SD	Minimum	Maximum	CV
WBSF, kg					
Psoas major	2.95[i]	0.26	2.40	3.45	8.8
Infraspinatus	3.27[h]	0.44	2.42	4.09	13.6
Rectus femoris	3.86[g]	0.38	3.26	4.69	10.0
Biceps femoris	3.87[g]	0.36	3.25	4.55	9.4
Triceps brachii	3.98[g]	0.34	3.14	4.72	8.5
Longissimus	3.99[g]	0.86	2.45	6.26	21.5
Semitendinosus	4.29[f]	0.35	3.36	5.24	8.2
Gluteus medius	4.44[ef]	0.45	3.14	5.03	10.2
Semimembranosus	4.64[de]	0.62	3.55	6.01	13.4
Adductor	4.73[cd]	0.62	3.70	6.48	13.1
Supraspinatus	4.95[c]	0.83	3.36	6.65	16.7
Sarcomere length, μm					
Psoas major	2.94[c]	0.08	2.77	3.08	2.8
Triceps brachii	2.41[d]	0.10	2.23	2.58	3.9
Infraspinatus	2.25[e]	0.10	2.04	2.43	4.6
Rectus femoris	2.19[f]	0.06	2.07	2.32	2.9
Semitendinosus	2.12[g]	0.04	2.02	2.22	1.9
Supraspinatus	1.94[h]	0.09	1.77	2.12	4.7
Adductor	1.90[i]	0.07	1.81	2.11	3.4
Biceps femoris	1.81[j]	0.04	1.71	1.86	2.0
Longissimus	1.80[j]	0.06	1.62	1.89	3.1
Semimembranosus	1.80[j]	0.03	1.74	1.86	1.8
Gluteus medius	1.66[k]	0.06	1.53	1.77	3.4
Collagen concentration, mg/g					
Psoas major	2.67[h]	0.46	1.80	3.65	17.2
Gluteus medius	4.28[g]	0.62	3.19	5.61	14.5
Longissimus	4.52[fg]	0.66	3.51	6.38	14.5
Adductor	4.87[f]	0.55	3.92	6.03	11.4
Rectus femoris	5.90[e]	0.71	4.80	8.00	12.1
Triceps brachii	6.29[e]	0.77	4.82	7.58	12.2
Infraspinatus	7.58[d]	1.19	6.00	11.35	15.7
Semimembranosus	7.68[d]	0.89	5.91	10.05	11.6
Biceps femoris	8.74[c]	1.12	6.43	11.24	12.9
Semitendinosus	8.76[c]	0.86	7.35	10.58	9.8
Supraspinatus	9.04[c]	0.95	7.25	11.17	10.5
Desmin proteolysis, % degraded					
Biceps femoris	60.7[c]	13.7	18.6	80.7	22.6
Longissimus	60.1[c]	15.8	10.8	78.7	26.2
Semimembranosus	46.9[d]	15.3	15.9	72.6	32.6
Gluteus medius	38.8[e]	15.3	13.2	73.4	39.5
Semitendinosus	38.5[e]	13.7	10.3	74.7	35.5
Triceps brachii	34.8[ef]	18.4	2.4	84.3	52.9
Adductor	29.7[fg]	11.1	7.3	52.4	37.3
Rectus femoris	29.1[fg]	10.7	11.5	52.4	36.6
Infraspinatus	25.2[gh]	14.9	8.2	58.2	59.1
Supraspinatus	24.4[gh]	14.4	0.6	64.5	59.1
Psoas major	20.2[h]	10.8	6.2	48.7	53.2
Cooking loss, %[b]					
Biceps femoris	18.7[i]	1.2	16.6	20.7	6.1
Longissimus	20.7[h]	1.3	18.6	23.6	6.5
Infraspinatus	20.7[h]	1.4	18.4	23.8	6.8
Triceps brachii	22.0[g]	1.2	20.2	24.2	5.4
Psoas major	23.6[f]	1.1	21.7	25.7	4.7
Gluteus medius	23.6[f]	1.9	18.6	28.3	8.2
Rectus femoris	24.4[e]	1.0	22.4	26.7	4.1
Semimembranosus	25.6[d]	1.4	22.6	29.3	5.4
Adductor	26.9[c]	1.1	25.2	29.1	4.2
Supraspinatus	27.3[c]	1.5	24.9	30.4	5.6
Semitendinosus	27.4[c]	1.4	24.0	30.1	5.2

[a]Mean of two or three locations except for cooking loss.
[b]Mean of three or four replications (two or three from Warner-Bratzler shear and one from sensory evaluation).
[c,d,e,f,g,h,i,j,k]Means in a column within a trait that do not have a common superscript differ ($P < 0.05$).

ments with small numbers of observations. This happens because other muscles do not change as much in tenderness when the LD changes. Certainly, some of the differences in the tenderness rank of muscles among experiments may be due to differences in cooking methodology, aging time, and sample location. Our samples were aged 14 d and rapidly cooked on a belt grill. The Warner-Bratzler shear force and biochemical trait results in Table 2 constitute the mean of two or three locations.

The range in muscle means for sarcomere length was 1.3 μm (Table 2). The PM had the longest ($P < 0.05$) sarcomere length, followed by TB, IS, RF, and ST—all with sarcomere lengths greater than 2.0 μm. The BF, LD, and SM had relatively short sarcomere lengths and the GM was the shortest ($P < 0.05$). These results were in general agreement with previous reports (Herring et al., 1965; Hostetler et al, 1972; McKeith et al., 1985), although the sarcomere length of GM was shorter than reported by Herring et al. (1965) and McKeith et al. (1985). However, we have found a high degree of variation in sarcomere length both among and within GM steaks (unpublished data). The ST was the most variable in sarcomere length in this study.

A wide range in collagen concentration was observed among the 11 muscle means (Table 2). The PM had the lowest ($P < 0.05$) collagen concentrations, followed by GM and LD, and the BF, ST, and SS had the highest ($P < 0.05$) collagen concentration. Muscles from the loin and rib had a lower ($P < 0.05$) collagen concentration than chuck and round muscles, except for AD. The high variability in tenderness of the GM has been attributed to connective tissue (Harris et al., 1992); however, our results indicate that sarcomere length may contribute more than connective tissue to that variability. In comparison, our collagen concentration values were generally lower than the results of Cross et al. (1973) and Seideman et al. (1989). Collagen concentration for most muscles was similar to that found by McKeith et al. (1985), with the exception of four muscles (GM, TB, RF, and IS) that they reported to be much higher in collagen. These differences are likely due primarily to two factors. Our method for measuring collagen and our approach for sampling the muscle were different from the other experiments. We used the Warner-Bratzler shear force cores for samples which, by design, do not include any large pieces of connective tissue (e.g., the connective tissue seam in the center of the IS would not be included in any sample). Also our samples were cooked whereas other data have been collected on raw muscle. Our objective was to relate variation in collagen to variation in measurements of tenderness; thus, the sample is the same as that used for Warner-Bratzler shear force determination and may not have the same collagen concentration as it would have if the entire muscle was sampled.

There was a wide range among muscles in the mean percentage of desmin that was degraded (Table 2). Desmin degradation was greatest ($P < 0.05$) for the BF and LD and was lowest ($P < 0.05$) for the PM and SS. The IS, AD, and RF also had less than 30% desmin degradation. Extensive data have been published on calpain system activities and postmortem proteolysis in the longissimus (for review, see Koohmaraie, 1992; 1994). However, very little data have been published on postmortem proteolysis in other major muscles. Recently, Wheeler et al. (2000b) reported that variation in desmin degradation among five pork muscles at 1 d postmortem ranged from 0 to 39%, with the LD having the most degradation. Wheeler and Koohmaraie (1999) reported that, in 10-d-postmortem lamb, desmin was 80% degraded in the LD and 60% degraded in the PM. The differences among muscles in postmortem proteolysis are in general agreement among studies, but any differences within the same muscle among studies could be due to species differences, differences in the methodology used to detect the extent of protein degradation, or estimates made on too small a number of observations for a highly variable trait.

Reduced desmin proteolysis in the SS is consistent with a report that SS has more than twice as much calpastatin as the LD (Koohmaraie et al., 1995), which could partially explain the reduced amount of proteolysis in the SS. In addition, PM has a higher proportion (50%) of red fibers relative to most muscles (Hunt and Hedrick, 1977), and Cassens et al. (1967) reported that muscles with high proportions of red fibers had three- to fourfold higher concentration of Zn^{++}, which also inhibits calpains (Guroff, 1964; Koohmaraie, 1990) and could partially explain the low amount of desmin proteolysis in the PM.

It has been documented that degradation of desmin is associated with meat tenderness (Koohmaraie et al., 1991; Robson et al., 1991; Ho et al., 1996). In earlier work (Koohmaraie et al., 1988; Seideman et al., 1989), little tenderization during aging in the PM has been reported. However, Fritz and Greaser (1991) found almost complete nebulin degradation after postmortem storage of bovine PM for 48 h at 4°C. Also, Wheeler and Koohmaraie (1999) observed 35.1% of desmin degradation in lamb PM at 10 d postmortem. There is little doubt that the PM is tender due to long sarcomere length and low collagen content. That the PM is the tenderest muscle despite the fact that limited postmortem proteolysis is consistent with previous results indicating muscles with long sarcomeres can be very tender without extensive proteolysis (Wheeler et al., 2000b). In addition, Koohmaraie et al. (1996) demonstrated that the impact of proteolysis on tenderness was minimal, when rigor shortening was prevented. Thus, these results indicate that the relative contribution of sarcomere length, postmortem proteolysis, and collagen concentration to the tenderness of each muscle may vary considerably.

Table 3. Effect of location within muscle on Warner-Bratzler shear force, sarcomere length, collagen, desmin proteolysis, cooking loss, and cooking time

Muscle[a]	Location[b]	WBS[c]	SEM	SL[d]	SEM	COL[e]	SEM	DES[f]	SEM	CKL[g]	SEM	CKT[h]	SEM
PM	1	3.08^{i}	0.06	2.90^{j}	0.02	3.20^{i}	0.11	15.0^{j}	2.4	25.2^{i}	0.3	71.3^{k}	0.2
	2	2.77^{j}		2.99^{i}		2.52^{j}		21.1^{ij}		22.8^{j}		72.0^{j}	
	3	3.01^{i}		2.95^{i}		2.30^{j}		24.6^{i}		23.1^{j}		72.8^{i}	
ST	1	4.74^{i}	0.08	1.81^{k}	0.01	8.71	0.22	38.2	2.9	28.4^{i}	0.4	69.9^{j}	0.3
	2	4.03^{j}		2.06^{j}		8.63		40.0		28.1^{i}		70.9^{i}	
	3	4.10^{j}		2.50^{i}		8.94		37.2		25.2^{j}		70.2^{ij}	
GM	1	4.55	0.09	1.64	0.01	4.47	0.14	31.8^{j}	2.9	22.7^{j}	0.5	70.8	0.3
	2	4.31		1.68		4.09		45.7^{i}		24.9^{i}		71.5	
BF	1	3.70^{j}	0.10	1.84^{i}	0.01	9.59^{i}	0.29	70.7^{i}	2.8	20.2^{i}	0.3	70.7	0.3
	2	4.04^{i}		1.80^{j}		9.16^{i}		53.4^{j}		17.2^{j}		70.5	
	3	3.87^{ij}		1.80^{j}		7.46^{j}		58.1^{j}		19.6^{i}		70.3	
LD	1	4.06	0.18	1.76^{j}	0.01	4.72	0.16	57.1	3.2	22.1^{i}	0.3	70.8^{j}	0.2
	2	3.71		1.81^{i}		4.62		61.3		20.0^{j}		71.4^{j}	
	3	4.20		1.82^{i}		4.21		62.0		19.4^{j}		72.2^{i}	
SS	1	4.72	0.17	1.99^{i}	0.02	9.58^{i}	0.21	25.7	2.8	27.4	0.4	71.4^{j}	0.2
	2	5.18		1.89^{j}		8.50^{j}		23.1		27.9		73.2^{i}	
IS	1	3.36	0.10	2.28^{i}	0.03	8.80^{i}	0.28	25.0	3.1	19.4^{k}	0.4	70.9	0.2
	2	3.34		2.27^{i}		7.60^{j}		22.9		21.2^{j}		71.0	
	3	3.10		2.19^{j}		6.33^{k}		27.8		22.4^{i}		70.7	
SM	1	3.69^{k}	0.13	1.83^{i}	0.01	7.43^{j}	0.22	68.2^{i}	3.1	25.1^{k}	0.3	70.4	0.2
	2	4.57^{j}		1.82^{i}		8.51^{i}		41.8^{j}		27.3^{i}		69.8	
	3	5.65^{i}		1.76^{j}		7.10^{j}		30.6^{k}		26.2^{j}		70.3	
AD	1	4.55	0.14	1.90	0.01	5.77^{i}	0.14	46.2^{i}	2.3	27.6	0.3	70.9	0.2
	2	4.92		1.92		3.96^{j}		13.3^{j}		27.8		70.6	
TB	1	3.97	0.07	2.40	0.02	6.91^{k}	0.20	31.6	3.7	22.2^{j}	0.4	70.2	0.2
	2	3.87		2.41		5.65^{j}		36.1		20.6^{k}		70.6	
	3	4.10		2.42		6.31^{i}		36.7		24.1^{i}		70.7	
RF	1	3.62^{j}	0.09	2.24^{i}	0.02	4.46^{k}	0.16	11.7^{k}	2.4	23.3^{j}	0.3	70.6	0.2
	2	3.71^{j}		2.22^{i}		5.66^{j}		22.2^{j}		24.7^{i}		70.6	
	3	4.25^{i}		2.11^{j}		7.58^{i}		53.5^{i}		25.4^{i}		70.8	

[a]PM = psoas major; ST = semitendinosus; GM = gluteus medius; BF = biceps femoris; LD = longissimus thoracis et lumborum; SS = supraspinatus; IS = infraspinatus; SM = semimembranosus; AD = adductor; TB = triceps brachii; and RF = rectus femoris.
[b]Refer to Figure 1 for sampling locations.
[c]WBS = Warner-Bratzler shear force, kg.
[d]SL = sarcomere length, μm.
[e]COL = collagen concentration, mg/g.
[f]DES = desmin, percentage degraded.
[g]CKL = cooking loss, %.
[h]CKT = cooked temperature, °C.
[i,j,k]Within a trait and muscle, location means that do not have a common superscript differ ($P < 0.05$).

Cooking loss of the steaks differed ($P < 0.05$) among muscles. Cooking loss was lowest ($P < 0.05$) for the BF, followed by the LD and IS, and then TB. It was highest ($P < 0.05$) for the ST, SS, and AD. The low cooking loss of the BF was unique among round muscles. Results of Lawrence et al. (2001), also using the belt grill at 163°C, are consistent with the high cooking loss of the ST, but they reported much higher cooking loss for the LD, GM, and BF than we found. Shackelford et al. (1997) reported similar differences in cooking loss for the ST and BF that also were cooked with a belt grill.

Location Effects

For Warner-Bratzler shear force, a location effect was detected ($P < 0.05$) in the PM, ST, BF, SM, and RF (Table 3). The location effect on shear force was greatest in the SM, where shear force increased ($P < 0.05$) from proximal to distal portions of the muscle. The posterior end of the RF and the proximal end of the ST had higher ($P < 0.05$) shear force than the other locations ($P < 0.05$). These results are consistent with those reported by Shackelford et al. (1997), indicating that the ST was less tender at the proximal end. These results also indicate that, in some muscles, sampling location can affect the results of tenderness evaluations and should be considered when designing experiments and interpreting the results.

Sarcomere length of most muscles was affected ($P < 0.05$) by location (Table 3). The location effect on sarcomere length was greatest in the ST, as sarcomere length increased ($P < 0.05$) from the proximal to the distal end. This location effect in ST resulted in the large CV for sarcomere length (Table 2). Herring et al. (1965) proposed that muscles vary in sarcomere

length due to the differences in the amount of tension placed on them in a hanging carcass during chilling and rigor mortis development. Large location differences in sarcomere length of the ST may be due to the differences in tension and/or differences in the extent to which the ST responds to tension along its length due to skeletal restraint, spatial restriction by, and attachment to other muscles. In other muscles, the magnitude of the location effect on sarcomere length was relatively small (<0.13μm). Sarcomere lengths in the dorsal ends of the SS and IS, the distal end of the SM, and the posterior end of the RF were shortest ($P < 0.05$) within each of these muscles. In the LD, the posterior end had a sarcomere length shorter ($P < 0.05$) than the anterior locations. The anterior end of the PM had a slightly shorter ($P < 0.05$) sarcomere length than the remainder of the muscle, and the proximal end of BF had a sarcomere length longer ($P < 0.05$) than the remainder of the muscle.

Variation in sarcomere length and its relationship to meat tenderness have been well documented (Locker, 1960; Herring et al., 1965; Hostetler et al., 1972). It seems that increased sarcomere length up to about 2.0 μm is accompanied by increased tenderness (Bouton et al., 1973; Wheeler et al., 2000b), depending on the contribution of other factors affecting tenderness. Four of the five most tender muscles (excluding the LD) had sarcomere lengths >2.0 μm. In agreement with that conclusion, the proximal location in the ST had 1.81-μm sarcomere length and was significantly less tender than the middle location with a sarcomere length of 2.06 μm, which was not different in tenderness from the distal location even though sarcomere length had increased up to 2.50 μm. Furthermore, Hostetler et al. (1972) did not observe a large effect on shear force of the PM with large treatment-induced variation in sarcomere length (but all were >2.3 μm), and their results indicated that across different muscles increasing the sarcomere length beyond 2.3 μm does not produce concomitant increases in tenderness.

A location effect on collagen concentration was detected ($P < 0.05$) in the PM, BF, SS, IS, SM, AD, TB, and RF (Table 3). The location effect on collagen was greatest ($P < 0.05$) in the RF, and the collagen concentration of the RF increased ($P < 0.05$) from the anterior end to the posterior end, whereas the collagen content of the IS decreased ($P < 0.05$) from the ventral to the dorsal locations. The middle location of the TB was lowest ($P < 0.05$), and the center of the SM was highest ($P < 0.05$), in collagen concentration within each muscle. Within the BF and AD muscles, the lowest ($P < 0.05$) collagen concentration was in the distal location. Within the SS, the lowest ($P < 0.05$) collagen concentration was at the dorsal end. The PM had location effects on collagen ($P < 0.05$) despite the low collagen concentration. A location with a lower concentration of collagen was not necessarily consistent with an improvement in tenderness in that location. The only muscle to show a trend toward higher shear force with a higher concentration of collagen was the RF. These results indicate the high degree of interaction among sarcomere length, collagen concentration, and proteolysis within and among muscles affects meat tenderness of individual muscles.

Desmin degradation of many muscles (PM, GM, BF, SM, AD, and RF) was affected ($P < 0.05$) by location (Table 3). Especially large location differences were detected in the SM, RF, and AD. Desmin degradation of the SM decreased ($P < 0.05$) from the proximal to the distal end, and was over twice as much at the proximal end as was detected at the distal end of the SM. In the RF, desmin degradation increased ($P < 0.05$) to over four times as much from anterior to posterior locations. In the SM, location effects on desmin degradation were closely associated with location differences in Warner-Bratzler shear force. However, in the RF, despite the higher ($P < 0.05$) desmin degradation, Location 3 was less tender than Locations 1 and 2. This may be due to higher collagen content and shorter sarcomere length of Location 3 compared with those of Location 1 and 2. The proximal location of the AD had much more ($P < 0.05$) desmin degradation than the distal location. The anterior location of the GM and the proximal location of the BF had higher ($P < 0.05$) desmin degradation than the other locations within those muscles. Despite minimal desmin degradation in the PM, location effects were detected ($P < 0.05$).

All muscles, except the SS and AD, had location effects for percentage cooking loss (Table 3). Cooking loss of the IS, SM, and TB was different ($P < 0.05$) among all three locations. The center of the BF and TB had the lowest ($P < 0.05$) cooking loss within each muscle, and the center of the SM had the highest ($P < 0.05$) cooking loss. The anterior end of the GM, posterior end of the LD, and the dorsal ends of the TB and IS had the highest ($P < 0.05$) cooking loss, and the distal end of the ST had the lowest ($P < 0.05$) cooking loss within each muscle, respectively. For the ST and BF, our results for location effects on cooking loss were consistent with the results of Shackelford et al. (1997), and they also reported that percentage cooking loss of the ST and BF was moderately repeatable (0.61 and 0.59, respectively).

Cooked temperatures of the PM, LD, and SS were higher ($P < 0.05$) than the targeted temperature of 70°C (Table 3). Differences among locations for cooked temperature were found in the PM, ST, LD, and SS; however, cooking loss did not necessarily increase as cooked temperature increased. Locations differed in cooked temperature by, at most, 1.8°C (SS). It is unlikely that the small differences in cooked temperature among locations or among muscles would impact any of the other traits.

Variances

Repeated measures of several traits at two or three locations within muscles made it possible to evaluate

Table 4. Proportion of total variance attributable to animal and location from multiple measurements of Warner-Bratzler (WBS) shear force and various biochemical traits from different locations within muscles[a]

Muscle/No. of locations	WBS shear force		Sarcomere length		Collagen		Desmin		Cooking loss	
	Animal	Location	Animal	Location	Animal	Location	Animal	Location	Animal	Location
Psoas major/3	0.39	0.19	0.47	0.18	0.21	0.35	0.40	0.10	0.21	0.37
Infraspinatus/3	0.42	0.05	0.30	0.10	0.26	0.39	0.62	0.01	0.13	0.32
Longissimus/3	0.62	0.05	0.26	0.12	0.34	0.07	0.69	0.01	0.15	0.36
Triceps brachii/3	0.45	0.05	0.44	0.01	0.17	0.23	0.70	0.01	0.01	0.41
Rectus femoris/3	0.29	0.32	0.14	0.36	0.11	0.75	0.13	0.73	0.15	0.28
Gluteus medius/2	0.53	0.09	0.45	0.10	0.28	0.09	0.59	0.27	0.42	0.26
Adductor/2	0.22	0.08	0.31	0.04	0.00	0.73	0.11	0.76	0.17	0.02
Semimembranosus/3	0.21	0.64	0.13	0.38	0.24	0.26	0.30	0.55	0.35	0.25
Supraspinatus/2	0.54	0.10	0.21	0.24	0.24	0.29	0.66	0.00	0.43	0.03
Semitendinosus/3	0.23	0.42	0.00	0.95	0.21	0.01	0.56	0.01	0.24	0.42
Biceps femoris/3	0.18	0.07	0.14	0.13	0.15	0.31	0.51	0.24	0.14	0.51

[a]Refer to Figure 1 for sampling locations.

the proportion of the total variance that could be attributed to animal-to-animal variation and the proportion that was due to location effects (Table 4). In previous experiments, we have sometimes used repeated measures on consecutive steaks as a measure of the repeatability of that trait because we assume that the consecutive steaks should be the same for most traits. However, in the current experiment, the repeated measures were made at different locations within the muscle, not on consecutive steaks; thus, they provide information about sources of variation but not about the repeatability of the measurements. As discussed above, many muscles had significant location effects for several traits. As would be expected, generally those muscle/trait combinations that had significant location effects also had a greater proportion of their variance attributed to location relative to animal than if location effects were not significant (Table 4). For some muscle/trait combinations, animal variation explained a large proportion of the variance, and, for some combinations, neither animal nor location could account for a majority of the variance. These results are in agreement with previous findings that have indicated there is little repeatable animal variation in tenderness of ST and BF (Shackelford et al., 1997), and results from the present study expand those findings to include the SM, AD, RF, and PM.

These results also provide previously unavailable estimates of the degree of animal and location variation among major beef muscles for the tenderness-related traits of sarcomere length, collagen concentration, desmin degradation, and cooking loss. Only the PM and GM had more than 40% of the variation in sarcomere length explained by animal differences (Table 4). None of the muscles had a high proportion of the variation in collagen attributable to animal variance. Only the SM, AD, and RF had less than 40% of the variation in desmin degradation explained by animals, and only the GM and SS had more than 40% of the variation in cooking loss explained by animal differences.

Correlations Among Muscles

The LD, RF, and SM were significantly ($P < 0.05$) correlated with seven or eight other muscles for sensory tenderness rating (Table 5). The AD, BF, GM, IS, and PM were correlated with five or six other muscles. On the contrary, ST was moderately correlated only with SS. The TB and SS were correlated with three or four other muscles, respectively. The highest correlation among muscles was between GM and LD, and the second highest correlation was between GM and SM. The LD was moderately to highly correlated with 7 of 10 other muscles. These results agree with Wheeler et al. (2000a), who reported the correlations among four beef muscles (LD, GM, BF, and SM) for tenderness rating, except that there was no correlation between SM and BF in the present study.

For Warner-Bratzler shear force (Table 6), all muscles, except the PM and IS, were correlated ($P < 0.05$) with seven or more other muscles. On the contrary, there were no correlations between PM and any other muscle. Another tender muscle, the IS, was highly correlated only with the SS. Although correlations among muscles for shear force were generally moderate in magnitude (up to 0.76), they were generally higher correlations than in previous reports (Slanger et al., 1985; Shackelford et al., 1995). It should be recognized that these correlations are among the means of two or three measurements, which could explain why they generally are higher than previously reported. The SM had a high correlation ($r > 0.70$) with the GM, BF, and RF. The LD was correlated with seven other muscles and had the highest correlation with TB among the 10 muscles. Shackelford (1995) also found that LD was most highly correlated ($r = 0.56$) with TB among nine major beef muscles. Correlations among muscles for shear force were similar to

Table 5. Simple correlation coefficients among muscles for tenderness rating

Muscle[a]	AD	BF	GM	IS	PM	RF	SM	SS	ST	TB
LD	0.38*	0.55**	0.73***	0.32	0.54**	0.46**	0.51**	0.32	0.31	0.42*
AD		0.18	0.32	0.38*	0.50**	0.56**	0.47**	0.11	0.06	0.20
BF			0.63***	0.29	0.41*	0.49**	0.30	0.38*	0.33	0.33
GM				0.26	0.44*	0.39*	0.44*	0.26	0.22	0.29
IS					0.32	0.38*	0.47**	0.51**	0.14	0.52**
PM						0.43*	0.53**	0.16	0.04	0.15
RF							0.56**	0.03	0.22	0.37*
SM								0.40*	0.30	0.26
SS									0.43*	0.23
ST										0.25

[a]LD = longissimus thoracis et lumborum; AD = adductor; BF = biceps femoris; GM = gluteus medius; IS = infraspinatus; PM = psoas major; RF = rectus femoris; SM = semimembranosus; SS = supraspinatus; ST = semitendinosus; and TB = triceps brachii.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

those among muscles for tenderness rating, with the exceptions being that SS and ST correlations for shear force were higher and PM correlations were lower than they were for tenderness rating.

Little is known about the relationship among major beef muscles for sarcomere length, collagen content, proteolysis, and cooking loss. Fewer correlations among muscles for sarcomere length (Table 7) occurred than for tenderness rating and shear force. The SS was correlated with the IS, ST, and TB, and the BF was correlated with the IS and ST. The LD was moderately correlated only with the GM, and the AD was correlated with the SM.

For collagen concentration (Table 8), the RF was correlated with all other muscles. The RF was highly ($r > 0.60$) correlated with the BF, SM, SS, and TB, and the SM was highly correlated with the LD, PM, and RF. Other muscles (except AD, IS, and ST) were correlated with seven or more other muscles. These results suggest that selection for cattle with reduced muscle connective tissue would likely benefit most major muscles. However, interestingly, the SS had a negative relationship to all other muscles for collagen concentration.

For desmin proteolysis, the SS was correlated to all 10 other muscles (Table 9). The BF, IS, PM, RF, SM, and ST were correlated with eight or nine other muscles, whereas the GM was correlated only to four other muscles. The LD was moderately to highly correlated ($r > 0.40$) with six other muscles. The BF had high ($r > 0.70$) correlations with the LD and SM, and a relatively high correlation between the LD and SM also was detected for desmin proteolysis. Those muscles (BF, LD, and SM) were ranked highest for desmin proteolysis among the 11 muscles. High correlations ($r \geq 0.60$) between the TB and three muscles (IS, SS, SM), between the PM and two muscles (GM, SS), between the SM and RF, and between the SS and IS also were detected for desmin proteolysis. These results indicate that there is a moderate degree of coordination among muscles for the extent of postmortem proteolysis, and this coordination is as high as would be

Table 6. Simple correlation coefficients among muscles for Warner-Bratzler shear force[a]

Muscle[b]	AD	BF	GM	IS	PM	RF	SM	SS	ST	TB
LD	0.38*	0.57***	0.50**	0.20	0.27	0.48**	0.57***	0.28	0.50**	0.73***
AD		0.53**	0.61***	0.30*	0.16**	0.41*	0.58***	0.49**	0.38*	0.54**
BF			0.60***	0.31	0.06	0.74***	0.76***	0.42*	0.50**	0.58***
GM				0.28	0.31	0.47**	0.76***	0.40*	0.43*	0.56**
IS					0.25	0.35	0.36*	0.73***	0.30	0.41*
PM						0.12	0.16	0.24	–0.05	0.15
RF							0.75***	0.32	0.45*	0.59***
SM								0.42*	0.56***	0.59***
SS									0.39*	0.51**
ST										0.61***

[a]Numbers correlated were the animal means (mean of two or three locations per muscle).

[b]LD = longissimus thoracis et lumborum; AD = adductor; BF = biceps femoris; GM = gluteus medius; IS = infraspinatus; PM = psoas major; RF = rectus femoris; SM = semimembranosus; SS = supraspinatus; ST = semitendinosus; and TB = triceps brachii.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

Table 7. Simple correlation coefficients among muscles for sarcomere length[a]

Muscle[b]	AD	BF	GM	IS	PM	RF	SM	SS	ST	TB
LD	0.32	0.13	0.50**	0.27	–0.01	0.10	0.19	0.26	0.17	0.20
AD		0.17	0.10	0.12	–0.04	0.17	0.38*	–0.12	–0.25	0.28
BF			0.05	0.46*	0.20	0.19	0.24	0.16	0.44*	0.09
GM				0.12	0.23	0.35	0.11	–0.10	0.16	–0.21
IS					–0.16	–0.18	0.02	0.36*	0.34	0.16
PM						0.09	–0.17	–0.11	0.05	–0.21
RF							0.33	–0.08	–0.11	0.12
SM								–0.11	–0.02	0.23
SS									0.39*	0.50**
ST										0.23

[a]Numbers correlated were the animal means (mean of two or three locations per muscle).
[b]LD = longissimus thoracis et lumborum; AD = adductor; BF = biceps femoris; GM = gluteus medius; IS = infraspinatus; PM = psoas major; RF = rectus femoris; SM = semimembranosus; SS = supraspinatus; ST = semitendinosus; and TB = triceps brachii.
*$P < 0.05$.
**$P < 0.01$.

Table 8. Simple correlation coefficients among muscles for collagen concentration[a]

Muscle[b]	AD	BF	GM	IS	PM	RF	SM	SS	ST	TB
LD	0.32	0.44*	0.62***	0.34	0.65***	0.54**	0.60***	–0.53**	0.22	0.47**
AD		0.47**	0.27	0.21	0.54**	0.42*	0.50**	–0.33	0.32	0.38*
BF			0.43*	0.14	0.45	0.61***	0.53**	–0.63***	0.35	0.66***
GM				0.34	0.49**	0.53**	0.56**	–0.52**	0.19	0.45*
IS					0.26	0.45*	0.36*	–0.53**	0.27	0.35
PM						0.57***	0.72***	–0.43*	0.40*	0.43*
RF							0.70***	–0.60***	0.39*	0.71***
SM								–0.50**	0.26	0.50**
SS									–0.22	–0.51**
ST										0.49**

[a]Numbers correlated were the animal means (mean of two or three locations per muscle).
[b]LD = longissimus thoracis et lumborum; AD = adductor; BF = biceps femoris; GM = gluteus medius; IS = infraspinatus; PM = psoas major; RF = rectus femoris; SM = semimembranosus; SS = supraspinatus; ST = semitendinosus; and TB = triceps brachii.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

Table 9. Simple correlation coefficients among muscles for desmin proteolysis[a,b]

Muscle[c]	AD	BF	GM	IS	PM	RF	SM	SS	ST	TB
LD	0.29	0.76***	0.26	0.41*	0.25	0.45*	0.70***	0.39*	0.50**	0.57***
AD		0.42*	0.07	0.39*	0.20	0.67***	0.58***	0.48**	0.38*	0.31
BF			0.34	0.51**	0.41*	0.59***	0.79***	0.39*	0.39*	0.56***
GM				0.34	0.60***	0.41*	0.31	0.40*	0.39*	0.28
IS					0.56**	0.46*	0.54**	0.60***	0.33	0.66***
PM						0.46**	0.44*	0.54**	0.36*	0.50**
RF							0.65***	0.45*	0.47**	0.30
SM								0.55**	0.37*	0.60***
SS									0.37*	0.60***
ST										0.51**

[a]Percentage of at-death desmin that was degraded.
[b]Numbers correlated were the animal means (mean of two or three locations per muscle).
[c]LD = longissimus thoracis et lumborum; AD = adductor; BF = biceps femoris; GM = gluteus medius; IS = infraspinatus; PM = psoas major; RF = rectus femoris; SM = semimembranosus; SS = supraspinatus; ST = semitendinosus; and TB = triceps brachii.
*$P < 0.05$.
**$P < 0.01$.
***$P < 0.001$.

Table 10. Simple correlation coefficients among muscles for percentage of cooking loss[a]

Muscle[b]	AD	BF	GM	IS	PM	RF	SM	SS	ST	TB
LD	0.05	0.54**	0.53**	–0.02	0.44*	0.43*	0.51**	0.56***	0.26	0.50**
AD		0.10	0.11	0.02	0.01	0.34	0.21	0.09	0.11	0.15
BF			0.43*	0.03	0.39*	0.48**	0.29	0.48**	0.44*	0.32
GM				–0.04	0.45*	0.47*	0.51**	0.49**	0.13	0.24
IS					–0.11	–0.11	0.12	0.15	0.21	0.24
PM						0.27	0.37*	0.26	0.05	0.22
RF							0.36*	0.39*	0.31	0.08
SM								0.48**	0.30	0.34
SS									0.34	0.44*
ST										0.31

[a]Numbers correlated were the animal means (mean of two or three locations per muscle for Warner-Bratzler shear force and one location for sensory evaluation).

[b]LD = longissimus thoracis et lumborum; AD = adductor; BF = biceps femoris; GM = gluteus medius; IS = infraspinatus; PM = psoas major; RF = rectus femoris; SM = semimembranosus; SS = supraspinatus; ST = semitendinosus; and TB = triceps brachii.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

expected given the large among-muscle variation in calpastatin activity (Koohmaraie et al., 1995).

Correlations among muscles for percentage cooking loss were low to moderate (Table 10). The LD, BF, GM, and SS were correlated with six or seven other muscles for cooking loss. The PM, RF, and SM were correlated with four or five other muscles, whereas the AD and IS had no correlation with other muscles for cooking loss. The ST was correlated only with the BF, and the TB was correlated with the LD and SS for cooking loss.

It would be very useful if a single muscle could be used to represent carcass tenderness and tenderness-related biochemical traits or if a less-valuable muscle could be used to represent the LD. However, the relationships between muscles for tenderness and other traits do not appear to be strong enough for these kinds of predictions to be successful. Thus, direct evaluation appears to be needed for each muscle for which information is desired.

Correlations Within Muscles

Sensory tenderness rating was significantly correlated ($P < 0.05$) with all other traits when all muscles were combined (Table 11). Connective tissue rating had the strongest correlation with tenderness rating, and tenderness rating was highly correlated ($r > 0.60$) with shear force, sarcomere length, and collagen concentration. Juiciness rating, desmin proteolysis, and cooking loss were weakly, but significantly ($P < 0.05$), correlated with tenderness rating. The lower correlation between tenderness rating and desmin proteolysis was partially due to the high tenderness ratings and relatively small percentage of desmin degradation for the PM and IS, and the opposite results for the BF. The correlation between shear force and desmin proteolysis was not significant ($P > 0.05$) when all muscles were combined. Collagen concentration was highly correlated with the detectable amount of connective tissue. Juiciness rating was moderately correlated with shear force and cooking loss. Beef flavor intensity was highly correlated with off-flavor intensity and was weakly correlated with all other traits except shear force and collagen concentration. Sarcomere length was weakly to moderately correlated with all traits except cooking loss. However, other correlations among sensory ratings were generally low, indicating an apparent low level of autocorrelation, and, thus, these correlations were not artificially high. In agreement with Wheeler and Koohmaraie (1999), within individual muscles, sarcomere length was never correlated with desmin proteolysis. Those authors demonstrated that, irrespective of shortening, muscle went through similar proteolysis and tenderization; thus, within a muscle, desmin proteolysis was independent of sarcomere length.

Within a muscle, fewer correlations among traits were significant than when all muscles were combined (Table 11). In all muscles, there were relatively high correlations between tenderness rating and both shear force and connective tissue rating, and between beef flavor intensity and off-flavor ratings. Correlations between shear force and tenderness rating within individual muscles were greater than 0.45 in all muscles and were higher than those reported by Shackelford et al. (1995) for all muscles except the LD. Correlations among all traits were generally fewest and lowest in the AD, whereas the LD had the most correlations among all traits (Table 11). Among the biochemical traits expected to be related to tenderness, desmin proteolysis was more highly correlated with tenderness rating in the LD and TB; collagen was more highly correlated with tenderness rating in the SM, RF, IS, and BF; sarcomere length and collagen concentration were both highly correlated with tenderness rating in the PM; and sarcomere length and desmin proteolysis were both highly correlated with

Table 11. Simple correlation coefficients for various traits within and among muscles

Trait[a]	ACT	JUI	BFI	OFF	WBS[b]	SL[b]	COL[b]	DES[b]	CKL[c]
All muscles									
TEND[d]	0.90***	0.33***	–0.14*	–0.16**	–0.73***	0.68***	–0.61***	–0.13*	–0.27***
ACT[e]		0.19***	–0.11*	–0.05	–0.58***	0.58***	–0.66***	–0.18**	–0.17**
JUI[f]			0.13*	–0.01	–0.43***	0.14**	–0.09	0.16**	–0.53***
BFI[g]				0.71***	0.04	–0.31***	0.07	0.34***	–0.20***
OFF[h]					0.14*	–0.32***	0.01	0.31***	–0.13*
WBS						–0.56***	0.32***	–0.10	0.46***
SL							–0.31***	–0.42***	–0.04
COL								0.13**	0.13
DES									–0.34***
Adductor									
TEND[d]	0.67***	0.44*	–0.07	–0.12	–0.45*	0.06	–0.31	0.19	0.09
ACT[e]		0.22	–0.04	0.03	–0.12	0.44*	–0.25	0.17	–0.24
JUI[f]			0.25	–0.25	–0.35	0.26	0.03	0.17	–0.23
BFI[g]				0.58***	–0.22	0.03	0.25	0.33	–0.12
OFF[h]					0.06	0.10	0.01	0.27	–0.37
WBS						–0.04	0.22	–0.32	0.27
SL							0.08	–0.17	–0.47**
COL								–0.03	0.16
DES									–0.32
Biceps femoris									
TEND[d]	0.81***	0.10	–0.12	–0.35	–0.65***	0.31	–0.51**	0.27	–0.36*
ACT[e]		0.04	–0.03	–0.24	–0.50**	0.26	–0.54**	0.11	–0.31
JUI[f]			–0.19	–0.03	–0.07	0.06	0.10	–0.03	–0.49**
BFI[g]				0.67***	0.10	–0.07	–0.15	–0.09	0.14
OFF[h]					0.41*	–0.27	0.19	–0.00	0.31
WBS						–0.45*	0.60***	–0.30	0.34
SL							–0.07	0.17	–0.11
COL								–0.24	0.08
DES									–0.04
Gluteus medius									
TEND[d]	0.79***	0.20	–0.01	–0.03	–0.71***	0.34	–0.22	0.15	–0.20
ACT[e]		0.02	–0.08	–0.05	–0.58***	0.32	–0.34	–0.01	–0.17
JUI[f]			0.14	0.00	–0.34	0.13	–0.03	0.21	–0.36*
BFI[g]				0.67***	–0.07	–0.31	–0.12	0.16	–0.11
OFF[h]					0.18	–0.28	–0.22	0.09	0.05
WBS						–0.44*	0.11	–0.36*	0.05
SL							–0.06	–0.09	–0.13
COL								0.21	0.50**
DES									0.15
Infraspinatus									
TEND[d]	0.82***	0.45*	–0.07	0.11	–0.85***	0.19	–0.36*	0.15	–0.14
ACT[e]		0.20	0.03	0.23	–0.69***	0.17	–0.53**	–0.16	0.24
JUI[f]			–0.02	–0.09	–0.33	–0.14	–0.04	0.27	–0.21
BFI[g]				0.67***	0.08	0.11	–0.38*	0.03	0.06
OFF[h]					–0.23	0.15	–0.56**	–0.09	–0.06
WBS						–0.30	–0.27	–0.16	0.12
SL							0.03	0.02	–0.11
COL								0.21	–0.09
DES									–0.32
Longissimus									
TEND[d]	0.80***	0.42*	0.16	–0.18	–0.74***	0.26	–0.30	0.56***	–0.39*
ACT[e]		0.39*	0.10	–0.02	–0.65***	0.02	–0.45*	0.58***	–0.55**
JUI[f]			0.44*	0.28	–0.15	–0.17	–0.16	0.07	–0.38*
BFI[g]				0.67***	–0.04	0.13	–0.09	–0.14	–0.21
OFF[h]					0.20	–0.13	–0.17	–0.30	–0.30
WBS						–0.41*	0.09	–0.62***	0.32
SL							–0.05	0.08	–0.01
COL								–0.18	0.68***
DES									–0.31

Continued

Table 11 (*continued*). Simple correlation coefficients for various traits within and among muscles

Trait[a]	ACT	JUI	BFI	OFF	WBS[b]	SL[b]	COL[b]	DES[b]	CKL[c]
Psoas major									
TEND[d]	0.66***	–0.07	–0.22	–0.44*	–0.53**	0.39*	–0.40*	0.09	–0.32
ACT[e]		–0.09	–0.24	–0.32	–0.55**	0.23	–0.15	–0.14	0.05
JUI[f]			0.10	0.01	–0.05	–0.28	0.24	0.17	–0.01
BFI[g]				0.57***	0.07	–0.33	–0.02	–0.09	0.11
OFF[h]					–0.42*	–0.36*	0.10	–0.14	0.28
WBS						–0.40*	0.18	0.14	0.18
SL							–0.34	–0.01	–0.14
COL								0.28	0.58***
DES									0.03
Rectus femoris									
TEND[d]	0.79***	0.37*	0.12	0.08	–0.71***	0.20	–0.40*	0.23	0.12
ACT[e]		0.26	0.13	0.12	–0.56**	–0.01	–0.41*	0.19	0.03
JUI[f]			0.23	–0.07	–0.39*	0.46**	0.01	0.04	–0.33
BFI[g]				0.73***	–0.11	–0.09	0.32	0.03	0.03
OFF[h]					0.01	–0.07	0.09	0.08	0.15
WBS						–0.43*	0.56**	–0.21	0.02
SL							–0.37*	–0.30	–0.29
COL								0.26	0.03
DES									0.05
Semimembranosus									
TEND[d]	0.80***	0.27	0.25	0.14	–0.65***	0.21	–0.51**	0.29	–0.10
ACT[e]		0.17	0.21	0.20	–0.66***	0.08	–0.37*	0.40*	–0.26
JUI[f]			0.16	0.23	–0.42*	0.08	–0.32	0.15	–0.43*
BFI[g]				0.60***	–0.10	–0.23	–0.05	0.11	–0.11
OFF[h]					–0.19	0.09	–0.02	0.11	–0.15
WBS						–0.23	0.55**	–0.58***	0.43*
SL							–0.20	–0.02	–0.07
COL								–0.18	0.42*
DES									–0.46**
Supraspinatus									
TEND[d]	0.88***	0.29	0.34	0.40*	–0.79***	0.44*	–0.15	0.37*	0.24
ACT[e]		0.16	0.27	0.37*	–0.69***	0.35	–0.04	0.23	0.27
JUI[f]			0.12	0.23	–0.17	0.08	0.13	–0.03	–0.42*
BFI[g]				0.66***	–0.29	–0.05	0.05	0.18	0.26
OFF[h]					–0.28	–0.12	0.23	0.13	0.13
WBS						–0.49**	0.05	–0.42*	–0.24
SL							0.11	0.01	0.38*
COL								0.14	0.15
DES									0.25
Semitendinosus									
TEND[d]	0.84***	0.26	0.19	0.01	–0.66***	0.44*	–0.20	0.48**	–0.34
ACT[e]		0.14	0.17	–0.11	–0.43*	0.29	–0.06	0.41*	–0.33
JUI[f]			0.12	–0.10	–0.15	0.03	–0.10	0.07	–0.33
BFI[g]				0.51**	–0.10	–0.13	–0.27	0.10	0.04
OFF[h]					–0.11	–0.08	–0.49**	0.12	0.11
WBS						–0.47**	0.14	–0.53**	0.50**
SL							–0.16	0.25	–0.27
COL								0.12	0.13
DES									–0.44*

Continued

tenderness rating in the SS and ST, compared to other biochemical traits. Collectively, the traits related to tenderness rating and shear force were highly variable in individual muscles, and numerous factors were associated with meat tenderness.

In conclusion, some muscles vary greatly in proteolysis, rigor shortening, and/or connective tissue, potentially contributing to their tenderness variation. Thus, these results on the relative contribution of various factors to variation in the tenderness of individual muscles provide the basis for cut-specific strategies for improving tenderness. Lower valued cuts (top round, bottom round, and mock tender) with muscles (SM, BF, AD, and SS) that are reduced in tenderness due to rigor shortening could be improved in tenderness by applying methods to stretch these muscles, such as

Table 11 (*continued*). Simple correlation coefficients for various traits within and among muscles

Trait[a]	ACT	JUI	BFI	OFF	WBS[b]	SL[b]	COL[b]	DES[b]	CKL[c]
	Triceps brachii								
TEND[d]	0.66***	0.53**	–0.10	–0.28	–0.59***	–0.05	–0.26	0.41*	–0.05
ACT[e]		0.38*	–0.03	0.03	–0.19	–0.09	–0.09	0.19	0.20
JUI[f]			–0.20	–0.10	–0.36*	0.02	0.10	0.33	–0.08
BFI[g]				0.60***	0.09	0.20	–0.11	–0.09	–0.25
OFF[h]					0.32	0.25	–0.01	–0.26	–0.02
WBS						0.22	0.25	–0.42*	0.20
SL							0.25	–0.25	0.41*
COL								–0.02	0.19
DES									–0.13

[a]TEND = overall tenderness; ACT = amount of connective tissue; JUI = juiciness; BFI = beef flavor intensity; WBS = Warner-Bratzler shear force; SL = sarcomere length; COL = collagen concentration; DES = percentage of desmin degraded; CKL = cooking loss.

[b]Numbers correlated were the animal means (mean of two or three locations per muscle).

[c]Numbers correlated were the animal means (mean of two or three locations per muscle for Warner-Bratzler shear force and one location for sensory evaluation).

[d]1 = extremely tough, 2 = very tough, 3 = moderately tough, 4 = slightly tough, 5 = slightly tender, 6 = moderately tender, 7 = very tender, and 8 = extremely tender.

[e]1 = abundant, 2 = moderately abundant, 3 = slightly abundant, 4 = moderate, 5 = slight, 6 = traces, 7 = practically none, and 8 = none.

[f]1 = extremely dry, 2 = very dry, 3 = moderately dry, 4 = slightly dry, 5 = slightly juicy, 6 = moderately juicy, 7 = very juicy, and 8 = extremely juicy.

[g]1 = extremely bland, 2 = very bland, 3 = moderately bland, 4 = slightly bland, 5 = slightly intense, 6 = moderately intense, 7 = very intense, and 8 = extremely intense.

[h]1 = intense, 2 = moderate, 3 = slight, and 4 = none.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

aitchbone suspension (Tenderstretch) or Tendercut. Lower valued cuts (mock tender, sirloin tip, top round, shoulder clod, and eye of round) with muscles (SS, RF, AD, TB, and ST) that are reduced in tenderness due to limited postmortem proteolysis could be improved in tenderness by treating with a marinade that 1) activates the calpains to enhance normal postmortem proteolysis or activates some other endogenous proteolytic system (not normally active in postmortem muscle), 2) includes an exogenous enzyme (such as the plant enzymes papain or ficin) that can degrade myofibrillar proteins, or 3) includes ingredients that solubilize myofibrillar proteins (i.e., salt and phosphate). Lower valued cuts (mock tender, eye of round, bottom round, top round, shoulder clod, and sirloin tip) with muscles (SS, ST, BF, SM, TB, RF, AD) that are reduced in tenderness due to excess collagen could be improved in tenderness by a variety of methods (the use of genetics with inactivated myostatin [Wheeler et al., 2001], precooking with slow heat, and acid or collagenase marinades that act on collagen). Some cuts may need a combination of treatments to overcome their tenderness deficiencies. In addition, location effects within muscles for meat tenderness indicate that muscles such as the ST and SM could be fabricated so as to utilize the more tender portions for steaks and the remainder as roasts or further processed to improve tenderness as described above.

Implications

Results indicate that tenderness and tenderness-related traits are highly variable within and among many major beef muscles. The basis for this variation in tenderness is the complex interaction of various biochemical traits that changes from muscle to muscle. This information will facilitate the development of cut-specific strategies for improving tenderness by targeting specific muscle characteristics that have been shown to decrease tenderness. Providing consumers with more consistently tender beef products will increase consumer satisfaction and should improve the value of the enhanced beef cuts and, thus, carcasses back through the production chain.

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