

The effects of Piedmontese inheritance and myostatin genotype on the palatability of longissimus thoracis, gluteus medius, semimembranosus, and biceps femoris¹

T. L. Wheeler², S. D. Shackelford, E. Casas, L. V. Cundiff, and M. Koohmaraie³

Roman L. Hruska U.S. Meat Animal Research Center, ARS, USDA, Clay Center, NE 68933-0166

ABSTRACT: The objective of this study was to determine the relative contributions of Piedmontese inheritance (0, 25, 50, or 75%) and myostatin genotype (+/+, mh/+, and mh/mh) to tenderness of four major muscles. Matings were made to produce animals with 0 (+/+), 1 (mh/+), or 2 (mh/mh) inactive myostatin alleles that were known to result in normal muscling, heavy muscling, and extremely heavy muscling, respectively. Over a 4-yr period, 395 steers and heifers (14 to 17 mo of age) were humanely slaughtered and the carcasses were chilled 48 h at 0°C. An eight-member trained descriptive attribute panel evaluated tenderness, ease of fragmentation, connective tissue amount, juiciness, and beef flavor intensity of longissimus thoracis (LD), gluteus medius (GM), semimembranosus (SM), and biceps femoris (BF) steaks at 14 d postmortem. Data were analyzed for the main effects of group (eight combinations of myostatin genotype and percentage Piedmontese; [+/+]/0%, [+/+]/25%, [+/+]/50%, [mh/+]/25%, [mh/+]/50%, [mh/+]/75%, [mh/mh]/50%, [mh/mh]/75%) and muscle. Muscle × group interactions were not significant ($P > 0.05$). Within myostatin genotypes, contrasts

to test the effect of percentage Piedmontese were not significant ($P > 0.05$). Data were reanalyzed for the main effects of myostatin genotype and muscle. Tenderness, ease of fragmentation, and amount of connective tissue ratings were higher ($P < 0.05$) for the mh/+ and mh/mh genotypes relative to +/+ in all muscles. In biceps femoris, mh/mh had higher ($P < 0.05$) tenderness, ease of fragmentation, and amount of connective tissue ratings than the mh/+ genotype. Juiciness ratings were lower ($P < 0.05$) for mh/mh than for mh/+ in all muscles and were lower for mh/mh than for +/+ in all muscles except gluteus medius. Beef flavor intensity ratings were lower ($P < 0.05$) for mh/mh than for +/+ in all muscles. Muscle ranks for tenderness within myostatin genotype were LD > GM > SM > BF, LD > GM > SM > BF, LD > GM > BF > SM, for +/+, mh/+, and mh/mh genotypes, respectively. The effects of Piedmontese inheritance on meat tenderness were all due to myostatin genotype. Piedmontese mh/mh bulls could be used as terminal sires to produce mh/+ progeny with improved carcass value due to improved tenderness in the four muscles studied.

Key Words: Beef, Double Muscling, Genes, Muscles, Piedmont, Tenderness

©2001 American Society of Animal Science. All rights reserved.

J. Anim. Sci. 2001. 79:3069–3074

Introduction

It was recently shown that an inactivated myostatin gene is responsible for the double-muscling phenotype in cattle (Kambadur et al., 1997; Smith et al., 1997), but the inactivating mutation is not the same in all breeds (Grobet et al., 1997, 1998; McPherron and Lee, 1997). In Piedmontese, the inactivating mutation is due

to a single base transition (Kambadur et al., 1997; Grobet et al., 1998). It has been reported that breed source (Piedmontese or Belgian Blue) of the double-muscling allele was not significant for birth weight or carcass composition traits (Casas et al., 1998). This implies that the myostatin allele is responsible for all of the effects of double muscling. However, Hanset (1982) concluded that selection resulted in an additional increase in muscling of Belgian Blue cattle homozygous for double muscling after the myostatin gene was fixed, indicating other genes were contributing to muscling independent of the inactive myostatin.

Most studies of double-muscling in cattle indicate that meat tenderness is improved relative to meat from homozygous normal cattle, although many studies have involved only the longissimus (for review see Arthur, 1995). In addition, there is some question whether het-

¹Names 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.

²Correspondence: P. O. Box 166 (phone: 402-762-4229; fax: 402-762-4149; E-mail: wheeler@email.marc.usda.gov).

³The authors express their gratitude to P. Beska, K. Mihm, and P. Tammen for technical assistance and to M. Bierman for secretarial assistance.

Received February 20, 2001.

Accepted July 23, 2001.

Table 1. Number of animals

Piedmontese inheritance, %	Myostatin genotype ^a			Total
	+/+	mh/+	mh/mh	
0	90	—	—	90
25	60	58	—	118
50	23	60	15	98
75	—	64	25	89
Total	173	182	40	395

^a+/+ = 0 inactive myostatin alleles; mh/+ = 1 inactive myostatin allele; mh/mh = 2 inactive myostatin alleles.

erozygotes for the double-muscling mutation have been correctly identified in some of the existing literature (Arthur, 1995). Thus, the magnitude of the effect on tenderness of one and two copies of inactivated myostatin is not clear. The discovery of the gene responsible for double-muscling (Kambadur et al., 1997; Smith et al., 1997) has made its genotyping much more accurate (Braun et al., 1997; Fahrenkrug, et al., 1999). The objective of this study was to determine the relative contributions of percentage Piedmontese inheritance and myostatin genotype to palatability of longissimus thoracis, gluteus medius, semimembranosus, and biceps femoris.

Materials and Methods

Animals. The Roman L. Hruska U.S. Meat Animal Research Center (MARC) Animal Care and Use Committee approved the use of animals in this study. Over a 4-yr period, 25 to 37 F₁ Piedmontese × Hereford (or 31 to 56 Piedmontese × Angus) females (depending on year) from Cycle IV of the Germ Plasm Evaluation project (Wheeler et al., 1996) were mated to Piedmontese, F₁ Piedmontese × Hereford (or Piedmontese × Angus), or Hereford (or Angus) bulls to produce 305 Piedmontese crossbred steers (n = 190) and heifers (n = 115). These progeny had 25:75, 50:50, or 75:25 ratios of Piedmontese:Hereford (or Piedmontese:Angus) inheritance and had 0 (+/+), 1 (mh/+), or 2 (mh/mh) copies of inactive myostatin alleles (Table 1). In addition, 45 Hereford and 45 Angus steers were produced from the same Hereford and Angus germ plasm for comparison as 0% Piedmontese. All Piedmontese-cross animals were genotyped to determine the number of inactive myostatin alleles. For samples from the first 2 yr, the myostatin gene was sequenced at exon 3 using an ABI377 automated sequencer (Perkin-Elmer, Foster City, CA). For samples from the 3rd yr, a PCR-based allele-specific test was used (Fahrenkrug et al., 1999). For samples from the 4th yr, genotyping was accomplished with a mass spectrometry assay that detected the transition mutation specific to Piedmontese (Braun et al., 1997).

Steers and heifers were weaned at approximately 200 d of age and fed a corn and corn silage diet for 215 to 278 d and humanely slaughtered, and the carcasses were chilled 48 h at 0°C in the MARC abattoir. Car-

casses were not electrically stimulated. At 48 h post-mortem, right carcass sides were ribbed (USDA, 1997) between the 12th and 13th ribs and experienced MARC personnel measured USDA quality and yield grade factors (USDA, 1997). The longissimus thoracis (ribeye), gluteus medius (top sirloin), semimembranosus (top round), and biceps femoris (bottom round) from the right sides were removed, vacuum-packaged, stored at 2°C, and frozen at -30°C at 14 d postmortem (AMSA, 1995). These muscles were selected because they vary in palatability and they are large, economically important muscles.

The frozen muscles were cut (from the posterior end of the longissimus thoracis and from the center of the other muscles) into 2.54-cm-thick steaks using a band saw. Two steaks from the longissimus (steaks two and three) and one steak each from the gluteus medius, semimembranosus, and biceps femoris were evaluated by a trained descriptive attribute sensory panel.

Cooking. Steaks were thawed and cooked as described by Wheeler et al. (1998) with the following modifications. The preheat platen on the belt grill was set at 149°C, rather than disconnected. That change necessitated reducing the cooking time from 5.7 to 5.5 min. Cooking losses are the sum of thaw losses and cooking losses.

Trained Sensory Panel Analysis. Cooked steaks were evaluated by an eight-member trained descriptive attribute panel as described by Wheeler et al. (1998).

Statistical Analysis. Data were analyzed by analysis of variance using the GLM procedures of SAS (SAS Inst. Inc., Cary, NC) for a completely randomized design for the main effects of muscle (longissimus thoracis, gluteus medius, semimembranosus, and biceps femoris) and group (all eight combinations of percentage Piedmontese and myostatin genotype). Mean separation for significant ($P < 0.05$) muscle and group effects was accomplished by the PDIF option (a pairwise t -test) of the least squares means procedures of SAS. Specific 1-df contrasts were used to test the effects of percentage Piedmontese within myostatin genotype. Because percentage Piedmontese was not significant ($P > 0.05$) for any trait, the data were reanalyzed by analysis of variance for a completely randomized design for the main effects of muscle (longissimus thoracis, gluteus medius, semimembranosus, and biceps femoris) and myostatin

Table 2. Interaction and main effect least squares means \pm SEM for percentage Piedmontese/genotype group and muscle for trained sensory panel tenderness rating^a

Group ^b Myostatin genotype/%Piedmontese	Muscle				Group mean
	Longissimus	Gluteus medius	Semimembranosus	Biceps femoris	
[+/+]/00%	6.2 \pm 0.09	5.9 \pm 0.09	5.4 \pm 0.09	5.0 \pm 0.09	5.6 \pm 0.04 ^g
[+/+]/25%	6.5 \pm 0.11	6.1 \pm 0.14	5.6 \pm 0.14	5.4 \pm 0.11	5.9 \pm 0.06 ^f
[+/+]/50%	6.2 \pm 0.17	5.9 \pm 0.22	5.6 \pm 0.22	5.1 \pm 0.17	5.7 \pm 0.10 ^{fg}
[mh+]/25%	6.9 \pm 0.11	6.5 \pm 0.13	6.0 \pm 0.13	5.8 \pm 0.11	6.3 \pm 0.06 ^d
[mh+]/50%	7.0 \pm 0.11	6.5 \pm 0.12	5.8 \pm 0.12	5.6 \pm 0.11	6.2 \pm 0.06 ^{de}
[mh+]/75%	7.0 \pm 0.10	6.3 \pm 0.12	5.6 \pm 0.12	5.6 \pm 0.10	6.1 \pm 0.06 ^e
[mh/mh]/50%	6.9 \pm 0.22	6.7 \pm 0.24	6.2 \pm 0.24	6.3 \pm 0.22	6.5 \pm 0.11 ^c
[mh/mh]/75%	7.2 \pm 0.17	6.6 \pm 0.20	5.9 \pm 0.20	6.3 \pm 0.17	6.5 \pm 0.09 ^c
Muscle mean	6.7 \pm 0.05 ^c	6.3 \pm 0.06 ^d	5.8 \pm 0.06 ^e	5.6 \pm 0.05 ^e	—

^a1 = extremely tough, 8 = extremely tender. Muscle \times group interaction was not significant ($P > 0.05$).

^bGroup = eight combinations of myostatin genotype and percentage Piedmontese: [+/+]/0%, [+/+]/25%, [+/+]/50%, [mh+]/25%, [mh+]/50%, [mh+]/75%, [mh/mh]/50%, and [mh/mh]/75%. +/+ = 0 inactive myostatin alleles; mh/+ = 1 inactive myostatin allele; mh/mh = 2 inactive myostatin alleles.

^{c,d,e,f,g}Within a main effect, means without a common superscript letter differ ($P < 0.05$).

genotype (+/+, mh/+, and mh/mh) with animal(genotype) in the model to use as the error term for testing genotype effects. Mean separation for significant ($P < 0.05$) muscle and myostatin effects was accomplished by the PDIFF option (a pairwise t -test) of the least squares means procedures of SAS, again using animal (genotype) as the error term for genotype effects.

Results and Discussion

Group and muscle effects were significant ($P < 0.05$) for all sensory traits, but the means are shown for tenderness rating only (Table 2). When pooled across groups, tenderness ratings were different ($P < 0.05$) with longissimus > gluteus medius > semimembranosus = biceps femoris (Table 2). Differences in tenderness rating among the eight groups followed differences in myostatin genotype with mh/mh > mh/+ > +/+. Within myostatin genotype, there was no effect of percentage Piedmontese (vs Hereford or Angus) inheritance on any sensory trait. Thus, percentage Piedmontese was pooled across myostatin genotypes and the data were reanalyzed for the interaction of myostatin genotype and muscle (Table 3). To our knowledge, no other study has addressed the question of what proportion of the effects on meat tenderness of the Piedmontese breed was due to myostatin genotype and what proportion was due to other genes that had diverged in frequency due to selection, drift, or mutation over time in this breed. Our data indicate that myostatin genotype accounts for all of the effects on tenderness of Piedmontese. However, Hanset (1982) has concluded that continued selection using polygenic variation in muscling led to additional improvement in muscularity in Belgian Blue cattle after the major gene myostatin was fixed in this breed. However, there is no information on whether this also has occurred for meat tenderness.

The main effect of muscle was significant ($P < 0.05$) for all traits, the main effect of myostatin was signifi-

cant for all traits except cooking losses, and their interaction was significant ($P < 0.05$) for all traits except beef flavor intensity, cooked temperature, and cooking losses (Table 3). All muscles were more tender ($P < 0.05$) in mh/+ than in +/+ (Table 4). Only biceps femoris was further increased ($P < 0.05$) in tenderness with mh/mh relative to mh/+. In agreement with our findings, the general conclusion from most studies of myostatin (double muscling) in cattle is that mh/mh have more tender meat than +/+ (for review see Arthur, 1995). Bailey et al. (1982) reported that longissimus from homozygous double-muscling Charolais bulls was more tender than longissimus from normal Charolais bulls. Also consistent with our data, although for a different muscle, Bouton et al. (1982) found no difference in Warner-Bratzler shear force of semitendinosus between mh/+ and mh/mh animals using steers and heifers (from Murray Grey bulls and Angus \times Jersey cows). Furthermore, Bouton et al. (1978) reported that mh/+ Angus \times Jersey steers (mates to the cows from the above experiment) had more tender semitendinosus than +/+ steers. However, Tatum et al. (1990) reported that F₁ Piedmontese steers from mating Piedmontese bulls (presumably mh/mh) to British cross and Continental cross cows did not have more tender longissimus than did F₁ Red Angus steers. Wheeler et al. (1996) found that mh/+ F₁ Piedmontese steers had longissimus tenderness ratings and Warner-Bratzler shear forces similar to those of Hereford \times Angus reciprocal cross steers. Wheeler et al. (2001) reported that mh/+ F₁ Piedmontese steers were not different in longissimus tenderness rating or shear force from mh/+ F₁ Belgian Blue steers or Hereford \times Angus cross steers. However, the mh/+ Belgian Blue steers had higher shear force and lower tenderness rating in longissimus than did the Hereford \times Angus cross steers. Liboriussen (1982) found that longissimus from F₁ Piedmontese was more tender than longissimus from F₁ Belgian Blue or Angus. They also reported that F₁ Piedmontese and Belgian Blue were

Table 3. Analysis of variance

Effect	df	Mean squares						
		Tenderness	Ease of fragmentation	Amount of connective tissue	Juiciness	Beef flavor intensity	Cooked temperature, °C	Cooking losses, %
Myostatin genotype ^a	2	45.16***	44.21***	23.62***	2.50*	1.77**	22.11**	30.54
Animal (myostatin)	392	1.49***	1.51***	0.54***	0.65***	0.37***	3.24***	17.10**
Muscle	3	59.74***	31.71***	152.28***	1.62***	0.67***	180.12***	702.44***
Myostatin × muscle	6	2.48***	1.90***	2.21***	0.46***	0.13	2.89	9.64
Error	992	0.40	0.37	0.22	0.08	0.07	2.33	13.47

^a+/+ = 0 inactive myostatin alleles; mh/+ = 1 inactive myostatin allele; mh/mh = 2 inactive myostatin alleles. The error term for testing myostatin genotype was animal (myostatin).

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

similar in semitendinosus tenderness but both had more tender semitendinosus than did Angus. Short et al. (2001) reported no differences in Warner-Bratzler shear force of the longissimus among Piedmontese (including +/+, mh/+, and mh/mh), Hereford, or Limousin F₂ cross progeny. Uytterhaegen et al. (1994) reported that normal conformation Belgian Blue White bulls had longissimus with lower shear force than did Belgian Blue White bulls with double-muscling conformation. Some of the contradiction in relative tenderness due to inactive myostatin may be due to the uncertainty of genotypes in various experiments and/or differences in slaughter and chilling conditions. Contradiction in tenderness effects also could be due to epistatic interactions with other loci (Casas et al., 1998).

In carcasses from normal (+/+) animals only, all muscles were different ($P < 0.05$) from one another in tenderness rating with longissimus > gluteus medius > semimembranosus > biceps femoris. However, gluteus medius from mh/+ or mh/mh were higher ($P < 0.05$) in tenderness rating than was longissimus from +/+ (Table 4). Biceps femoris from mh/mh were not different ($P > 0.05$) in tenderness rating from longissimus from +/+. Thus, lower-quality muscles were improved in tenderness by just one copy of inactive myostatin. Shackelford et al. (1995, 1997) concluded that it was not appropriate to use Warner-Bratzler shear force to compare differences in tenderness among muscles and that trained sensory panel evaluation should be used for muscle comparisons. However, there are several studies in the literature that include a comparison of the same four muscles as in the present study using trained sensory panels. Similar to our data, Shackelford et al. (1995) found the longissimus lumborum was the most tender, followed by gluteus medius, and semimembranosus and biceps femoris were similar to one another. Morgan et al. (1991) reported that longissimus was most tender, then gluteus medius, followed by biceps femoris, and semimembranosus was least tender. However, in that study the longissimus and gluteus medius were broiled and biceps femoris and semimembranosus were braised. McKeith et al. (1985) reported the longissimus

was the most tender and the other three muscles were not different from one another. The inability to detect differences in tenderness (either among genotypes or muscles) could be due to inconsistency in cooking and/or the inability of the sensory panel to discriminate adequately.

Both ease of fragmentation (a measure of myofibrillar tenderness) and amount of connective tissue ratings were higher ($P < 0.05$) in all muscles from mh/+ than in muscles from +/+ (Table 4). Amount of connective tissue ratings were further increased ($P < 0.05$) in mh/mh compared to mh/+ in gluteus medius and biceps femoris, but ease of fragmentation ratings were further increased ($P < 0.05$) for mh/mh compared to mh/+ only in the biceps femoris. In all muscles except biceps femoris, juiciness ratings were lower ($P < 0.05$) for mh/+ compared to the +/+ genotype. In all muscles, juiciness ratings were lower ($P < 0.05$) for mh/mh compared to the +/+ or mh/+ genotypes. For the main effect of muscle, longissimus received higher ($P < 0.05$) beef flavor intensity ratings than did the other three muscles. For the main effect of myostatin genotype, beef flavor intensity ratings were lower ($P < 0.05$) for mh/mh than for the +/+ genotype. In contrast to our results, it has been reported that mh/+ (Tatum et al., 1990) or mh/mh (Bailey et al., 1982) were not different in longissimus juiciness or flavor compared to +/+ genotypes. However, Wheeler et al. (1996) found that mh/+ F₁ Piedmontese had lower beef flavor intensity rating in longissimus than did Hereford × Angus but were not different in juiciness rating. Wheeler et al. (2001) reported that mh/+ F₁ Belgian Blue and mh/+ F₁ Piedmontese had lower longissimus juiciness ratings than did Hereford × Angus but were not different in beef flavor intensity ratings.

The interaction of muscle and myostatin genotype was not significant ($P > 0.05$) for final cooked temperature or cooking losses (Table 4). The main effect of muscle was significant for both cooking traits. Final cooked temperature was highest ($P < 0.05$) for longissimus, followed by gluteus medius, then semimembranosus, and was lowest ($P < 0.05$) for biceps femoris. Cooking

Table 4. Effect of myostatin genotype and muscle on least squares means ± SEM for trained sensory panel and cooking traits

Trait ^a and muscle	Myostatin genotype ^e			Muscle mean
	+/+	mh/+	mh/mh	
Tenderness^b				
Longissimus	6.3 ± 0.06 ⁱ	7.0 ± 0.06 ^f	7.1 ± 0.13 ^f	6.8 ± 0.04
Gluteus medius	6.0 ± 0.07 ^j	6.5 ± 0.07 ^{gh}	6.7 ± 0.15 ^g	6.4 ± 0.05
Semimembranosus	5.6 ± 0.07 ^k	5.8 ± 0.07 ^j	6.0 ± 0.15 ^j	5.8 ± 0.05
Biceps femoris	5.2 ± 0.06 ^l	5.6 ± 0.06 ^k	6.3 ± 0.13 ^{hi}	5.7 ± 0.04
Genotype mean	5.8 ± 0.05	6.2 ± 0.05	6.5 ± 0.11	—
Ease of fragmentation^b				
Longissimus	6.3 ± 0.06 ^h	7.0 ± 0.06 ^f	7.1 ± 0.13 ^f	6.8 ± 0.04
Gluteus medius	6.0 ± 0.07 ^{ij}	6.5 ± 0.07 ^{gh}	6.7 ± 0.15 ^g	6.4 ± 0.05
Semimembranosus	5.8 ± 0.07 ^k	6.0 ± 0.07 ^{ij}	6.2 ± 0.15 ^{hi}	6.0 ± 0.05
Biceps femoris	5.5 ± 0.06 ^l	6.0 ± 0.06 ^j	6.5 ± 0.13 ^g	6.0 ± 0.04
Genotype mean	5.9 ± 0.05	6.4 ± 0.05	6.6 ± 0.11	—
Amount of connective tissue^b				
Longissimus	7.3 ± 0.04 ^g	7.6 ± 0.04 ^f	7.7 ± 0.09 ^f	7.5 ± 0.03
Gluteus medius	6.8 ± 0.05 ⁱ	7.1 ± 0.05 ^h	7.3 ± 0.10 ^g	7.0 ± 0.04
Semimembranosus	6.0 ± 0.05 ^l	6.2 ± 0.05 ^k	6.3 ± 0.10 ^k	6.1 ± 0.04
Biceps femoris	5.2 ± 0.04 ⁿ	5.6 ± 0.04 ^m	6.4 ± 0.09 ^j	5.7 ± 0.03
Genotype mean	6.3 ± 0.03	6.6 ± 0.03	6.9 ± 0.07	—
Juiciness^b				
Longissimus	5.6 ± 0.04 ^g	5.7 ± 0.04 ^f	5.4 ± 0.07 ^h	5.6 ± 0.02
Gluteus medius	5.6 ± 0.04 ^g	5.7 ± 0.04 ^f	5.5 ± 0.09 ^{gh}	5.6 ± 0.02
Semimembranosus	5.6 ± 0.04 ^g	5.5 ± 0.04 ^h	5.2 ± 0.09 ^j	5.4 ± 0.02
Biceps femoris	5.7 ± 0.04 ^f	5.7 ± 0.04 ^f	5.5 ± 0.07 ^h	5.6 ± 0.02
Genotype mean	5.6 ± 0.03	5.6 ± 0.03	5.4 ± 0.07	—
Beef flavor intensity^c				
Longissimus	4.9 ± 0.03	4.8 ± 0.03	4.6 ± 0.06	4.8 ± 0.02 ^f
Gluteus medius	4.8 ± 0.03	4.7 ± 0.03	4.6 ± 0.07	4.7 ± 0.02 ^g
Semimembranosus	4.8 ± 0.03	4.7 ± 0.03	4.7 ± 0.07	4.7 ± 0.02 ^g
Biceps femoris	4.7 ± 0.03	4.6 ± 0.03	4.6 ± 0.06	4.7 ± 0.02 ^h
Genotype mean	4.7 ± 0.03 ^f	4.7 ± 0.03 ^{fg}	4.6 ± 0.06 ^g	—
Cooked temperature, °C^c				
Longissimus	70.3 ± 0.12	70.6 ± 0.12	70.6 ± 0.25	70.5 ± 0.10 ^f
Gluteus medius	69.2 ± 0.14	69.4 ± 0.14	69.9 ± 0.29	69.5 ± 0.12 ^g
Semimembranosus	68.9 ± 0.14	68.8 ± 0.14	69.8 ± 0.29	69.2 ± 0.12 ^h
Biceps femoris	68.2 ± 0.12	68.4 ± 0.12	68.8 ± 0.25	68.5 ± 0.10 ⁱ
Genotype mean	69.1 ± 0.08 ^g	69.3 ± 0.08 ^g	69.8 ± 0.16 ^f	—
Cooking losses, %^d				
Longissimus	20.7 ± 0.29	21.1 ± 0.28	21.3 ± 0.60	21.0 ± 0.23 ^g
Gluteus medius	24.7 ± 0.32	24.7 ± 0.34	23.3 ± 0.68	24.2 ± 0.28 ^f
Semimembranosus	24.9 ± 0.32	25.0 ± 0.33	24.3 ± 0.68	24.7 ± 0.28 ^f
Biceps femoris	21.4 ± 0.29	21.3 ± 0.28	21.3 ± 0.60	21.3 ± 0.23 ^g
Genotype mean	22.9 ± 0.17	23.0 ± 0.18	22.6 ± 0.37	—

^a1 = extremely tough, extremely difficult, abundant, extremely dry, and extremely bland; 8 = extremely tender, extremely easy, none, extremely juicy, and extremely intense.

^bInteraction ($P < 0.05$).

^cInteraction ($P > 0.05$). Genotype and muscle ($P < 0.05$).

^dInteraction ($P > 0.05$). Genotype ($P > 0.05$). Muscle ($P < 0.05$).

^e+/+ = 0 inactive myostatin alleles; mh/+ = 1 inactive myostatin allele; mh/mh = 2 inactive myostatin alleles. The error term for testing myostatin genotype was animal (myostatin).

^{f,g,h,i,j,k,l,m,n}Means within a sensory trait and main effect lacking a common superscript letter differ ($P < 0.05$).

losses were higher ($P < 0.05$) in gluteus medius and semimembranosus than in biceps femoris and longissimus. For the main effect of myostatin genotype, cooked temperature increased as inactive myostatin alleles increased (+/+, mh/+, mh/mh), indicating the meat cooked slightly faster. Consistent with our data, Bouton et al. (1978, 1982) found no differences in cooking losses be-

tween +/+ and mh/+ or between mh/+ and mh/mh genotypes. However, Uytterhaegen et al. (1994) reported that double muscling in Belgian Blue bulls increased cooking losses in the longissimus.

The present experiment indicates that in Piedmontese, mh/+ or mh/mh improves the tenderness of all four muscles evaluated relative to the +/+ genotype. Further-

more, round and sirloin muscles from mh/mh seem to be at least as tender as longissimus from +/+, and gluteus medius from mh/+ was as tender as longissimus from +/+ cattle. The values of round cuts, chuck cuts, and lean trimmings have decreased 20 and 23, and 31%, respectively, relative to total carcass value, whereas the values of rib and loin cuts have increased (Cattle Fax, 1998). The beef industry has made it a priority to improve the value of these three lower-quality carcass components, which make up 66% of the carcass. Our data imply that producing mh/+ cattle not only improves the tenderness of the valuable longissimus but also could be one method of improving the quality of lower-valued cuts. At current prices, improving the value of top sirloin to that of ribeye and strip loin improves carcass value by about \$50. It seems likely that many lower-quality muscles would be improved significantly in mh/+ cattle, resulting in substantial improvement in total carcass value.

Implications

These results indicate that mh/mh Piedmontese bulls could be used as terminal sires to produce mh/+ progeny with improved tenderness in at least four muscles, resulting in a substantial increase in carcass value in addition to the previously demonstrated advantage in yield of saleable product.

Literature Cited

- AMSA. 1995. Research guidelines for cookery, sensory evaluation, and instrumental tenderness measurements of fresh meat. American Meat Science Association, Chicago, IL.
- Arthur, P. F. 1995. Double muscling in cattle: A review. *Aust. J. Agric. Res.* 46:1493–1515.
- Bailey, A. J., M. B. Enser, E. Dransfield, D. J. Restall, and N. C. Avery. 1982. Muscle and adipose tissue from normal and double muscled cattle: Collagen types, muscle fibre diameter, fat cell size and fatty acid composition and organoleptic properties. In: J. W. B. King and F. Menissier (ed.) *Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production: Current Topics in Veterinary Medicine and Animal Science*. vol 16. pp 178–202. Martinus Nijhoff, The Hague.
- Bouton, P. E., P. V. Harris, W. R. Shorthose, and R. W. Ellis. 1978. Comparison of some properties of meat from normal steers and steers heterozygous for muscular hypertrophy. *Meat Sci.* 2:161–167.
- Bouton, P. E., P. V. Harris, W. R. Shorthose, R. W. Ellis, and D. Phillips. 1982. Comparison of some properties of beef from animals homozygous or heterozygous for muscular hypertrophy. *Meat Sci.* 6:309–318.
- Braun, A., D. P. Little, and H. Koster. 1997. Detecting CFTR gene mutations by using primer oligo base extension and mass spectrometry. *Clin. Chem.* 43:1151–1158.
- Casas, E., J. W. Keele, S. D. Shackelford, M. Koohmaraie, T. S. Sonstegard, T. P. L. Smith, S. M. Kappes, and R. T. Stone. 1998. Association of the muscle hypertrophy locus with carcass traits in beef cattle. *J. Anim. Sci.* 76:468–473.
- Cattle Fax. 1998. Operating Plan for Fulfilling the Long-Range Plan and Achieving Greater Focus. National Cattlemen's Beef Association, Denver, CO.
- Fahrenkrug, S. C., E. Casas, J. W. Keele, and T. P. L. Smith. 1999. Technical note: Direct genotyping of the double-muscling locus (*mh*) in Piedmontese and Belgian Blue cattle by fluorescent PCR. *J. Anim. Sci.* 77:2028–2030.
- Grobet, L., L. J. R. Martin, D. Poncelet, D. Pirottin, B. Brouwers, J. Riquet, A. Schoeberlein, S. Dunner, F. Menissier, J. Massabanda, R. Fries, R. Hanset, and M. Georges. 1997. A deletion in the bovine myostatin gene causes the double-muscled phenotype in cattle. *Nat. Genet.* 17:71–74.
- Grobet, L., D. Poncelet, L. J. Royo, B. Brouwers, D. Pirottin, C. Michaux, F. Menissier, M. Zanotti, S. Dunner, and M. Georges. 1998. Molecular definition of an allelic series of mutations disrupting the myostatin function and causing double-muscling in cattle. *Mamm. Genome* 9:210–213.
- Hanset, R. 1982. Muscular hypertrophy as a racial characteristic: The case of the Belgian Blue breed. In J. W. B. King and F. Menissier (ed.) *Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production: Current Topics in Veterinary Medicine and Animal Science*. vol 16. pp 437–449. Martinus Nijhoff, The Hague.
- Kambadur, R., M. Sharma, T. P. L. Smith, and J. J. Bass. 1997. Mutations in myostatin (*GDF8*) in double-muscled Belgian Blue and Piedmontese Cattle. *Genome Res.* 7:910–915.
- Liboriussen, T. 1982. Comparison of sire breeds represented by double muscled and normal sires. In: J. W. B. King and F. Menissier (ed.) *Muscle Hypertrophy of Genetic Origin and Its Use to Improve Beef Production: Current Topics in Veterinary Medicine and Animal Science*. vol. 16. pp 637–643. Martinus Nijhoff, The Hague.
- McKeith, F. K., D. L. DeVol, R. S. Miles, P. J. Bechtel, and T. R. Carr. 1985. Chemical and sensory properties of thirteen major beef muscles. *J. Food. Sci.* 50:869–872.
- McPherron, A. C., and S. J. Lee. 1997. Double muscling in cattle due to mutations in the myostatin gene. *Proc. Natl. Acad. Sci. USA* 94:12457–12461.
- Morgan, J. B., J. W. Savell, D. S. Hale, R. K. Miller, D. B. Griffin, H. R. Cross, and S. D. Shackelford. 1991. National beef tenderness survey. *J. Anim. Sci.* 69:3274–3283.
- Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 1995. Relationship between shear force and trained sensory panel tenderness ratings of 10 major muscles from *Bos indicus* and *Bos taurus* cattle. *J. Anim. Sci.* 73:3333–3340.
- Shackelford, S. D., T. L. Wheeler, and M. Koohmaraie. 1997. Repeatability of tenderness measurements in beef round muscles. *J. Anim. Sci.* 75:2411–2416.
- Short, R. E., M. D. MacNeil, M. D. Grosz, D. E. Gerrard, and E. E. Grings. 2001. Pleiotropic effects in Hereford, Limousin, and Piedmontese F₂ crossbred calves of genes controlling muscularity including the Piedmontese myostatin allele. *J. Anim. Sci.* (In press).
- Smith, T. P. L., N. L. Lopez-Corrales, S. M. Kappes, and T. S. Sonstegard. 1997. Myostatin maps to the interval containing the bovine *mh* locus. *Mamm. Genome* 8:742–744.
- Tatum, J. D., K. W. Gronewald, S. C. Seideman, and W. D. Lamm. 1990. Composition and quality of beef from steers sired by Piedmontese, Gelbvieh and Red Angus bulls. *J. Anim. Sci.* 68:1049–1060.
- USDA. 1997. Official United States standards for grades of carcass beef. Agric. Marketing Serv., USDA, Washington, DC.
- Uytterhaegen, L., E. Claeys, D. Demeyer, M. Lippens, L. O. Fiems, C. Y. Boucque, G. Van de Voorde, and A. Bastiaens. 1994. Effects of double-muscling on carcass quality, beef tenderness and myofibrillar protein degradation in Belgian Blue White bulls. *Meat Sci.* 38:255–267.
- Wheeler, T. L., L. V. Cundiff, R. M. Koch, and J. D. Crouse. 1996. Characterization of biological types of cattle (Cycle IV): Carcass traits and longissimus palatability. *J. Anim. Sci.* 74:1023–1035.
- Wheeler, T. L., L. V. Cundiff, S. D. Shackelford, and M. Koohmaraie. 2001. Characterization of biological types of cattle (Cycle V): Carcass traits and longissimus palatability. *J. Anim. Sci.* 79:1209–1222.
- Wheeler, T. L., S. D. Shackelford, and M. Koohmaraie. 1998. Cooking and palatability traits of beef longissimus steaks cooked with a belt grill or an open hearth electric broiler. *J. Anim. Sci.* 76:2805–2810.