Heritabilities and Phenotypic and Genetic Correlations for Bovine Postrigor Calpastatin Activity, Intramuscular Fat Content, Warner-Bratzler Shear Force, Retail Product Yield, and Growth Rate[1]

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ABSTRACT: To estimate the heritability (h^2) of postrigor calpastatin activity (CA), 555 steers were reared and processed conventionally. Breed-types included purebreds (Angus [A], Braunvieh [B], Charolais [C], Gelbvieh [G], Hereford [H], Limousin [L], Pinzgauer [P], Red Poll [RP], and Simmental [S]), composite populations (MARC I [1/4 C, 1/4 B, 1/4 L, 1/8 H, 1/8 A], MARC II [1/4 S, 1/4 G, 1/4 H, 1/4 A], and MARC III [1/4 RP, 1/4 H, 1/4 P, 1/4 A]), and F_1 crosses (H, A, C, G, P, Shorthorn, Galloway, Longhorn, Nellore, Piedmontese, or Salers × H or A). Steers were serially slaughtered on an age-constant (across breed groups) basis. Heritability estimates for CA, i.m. fat content (IMF), Warner-Bratzler shear (WBS) force, retail product yield (RPY), and ADG were .65 ± .19, .93 ± .02, .53 ± .15, .45 ± .18, and .32 ± .26, respectively. The genetic correlations (r_g) of CA with WBS, RPY, and ADG were .50 ± .22, .44 ± .25, and −.52 ± .37, respectively. The r_g of IMF with WBS, RPY, and ADG were −.57 ± .16, −.63 ± .15, and −.04 ± .11, respectively. These h^2 and r_g estimates indicate that it should be possible to select for improvements in CA, IMF, and WBS. However, selection against CA may be a more suitable approach for improving meat tenderness than selection for increased IMF because the level of genetic antagonism between CA and RPY was not as great as that between IMF and RPY.

Key Words: Beef, Genetic Correlation, Heritability, Calpastatin, Tenderness

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Introduction

The National Beef Tenderness Survey indicated that a high proportion of beef retail cuts were unacceptable in tenderness (Morgan et al., 1991). Numerous studies have indicated differences in tenderness among breed-groups. Meat from *Bos indicus* cattle has been reported to be less tender than that from *Bos taurus* cattle (Koch et al., 1982b; Crouse et al., 1989).

Final tenderness of meat is determined by the rate and extent of postmortem proteolysis. It is now generally accepted that proteolysis of key myofibrillar proteins is responsible for the improvement in meat tenderness. Results of numerous experiments have indicated that the calpain proteolytic system has a major role and perhaps is responsible for the meat tenderization during postmortem storage. The calpain proteolytic system (for review see Croall and DeMartino, 1991) consists of 1) μ-calpain (requires micromolar Ca^{2+} for activity); 2) m-calpain (requires millimolar Ca^{2+} for activity); and 3) calpastatin (the endogenous inhibitor of the calpains). Numerous experiments have indicated that calpastatin is the major regulator of the calpain proteolytic system in postmortem muscle (for review see Koohmaraie 1988, 1992a,b,c).

The decreased tenderness associated with *Bos indicus* breeding seems to be highly related to increased calpastatin activity (**CA**) at 24 h postmortem (Whipple et al., 1990a; Shackelford et al., 1991b). However, it is not known whether CA varies between and within *Bos taurus* breeds. Moreover, it seems that

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Table 1. Number of sires per breed and number of progeny per sire[a]

Breed group	No. of sires with n progeny													Total
	1	2	3	4	5	6	7	8	9	10	11	12	13	
GPU														
Angus	6	2	1	1	0	2	0	0	0	0	0	0	0	12
Braunvieh	3	6	0	1	1	1	1	0	0	0	0	0	0	13
Charolais	5	3	2	1	0	0	0	1	0	0	0	0	0	12
Gelbvieh	4	5	2	1	0	0	1	1	0	0	0	0	0	14
Hereford	5	3	0	0	1	2	0	0	0	0	0	1	0	12
Limousin	3	3	2	0	1	0	1	0	0	0	0	0	1	11
Pinzgauer	5	7	1	0	1	0	0	0	0	0	0	0	0	14
Red Poll	5	1	0	2	0	0	0	0	0	1	0	0	0	9
Simmental	2	4	0	1	1	1	1	0	0	0	0	0	0	10
MARC I	7	2	3	2	0	1	0	0	0	0	0	0	0	15
MARC II	9	5	1	1	0	2	0	0	0	0	0	0	0	18
MARC III	7	2	0	2	0	0	1	1	0	0	0	0	0	13
Total	61	43	12	12	5	9	5	3	0	1	0	1	1	153
GPE[b]														
Angus	7	4	1	0	0	0	0	0	0	0	0	0	0	12
Charolais	7	0	0	0	1	0	0	0	0	0	0	0	0	8
Galloway	4	2	0	0	0	0	0	0	0	0	0	0	0	6
Gelbvieh	0	1	1	1	0	0	0	0	0	0	0	0	0	3
Hereford	8	4	1	0	0	0	0	0	0	0	0	0	0	13
Longhorn	2	2	2	0	0	0	0	0	0	0	0	0	0	6
Nellore	1	4	1	0	0	0	0	0	0	0	0	0	0	6
Piedmontese	3	3	1	0	0	0	0	0	0	0	0	0	0	7
Pinzgauer	1	0	0	2	0	0	0	0	0	0	0	0	0	3
Salers	3	2	0	0	0	0	0	0	0	0	0	0	0	5
Shorthorn	10	2	1	0	0	0	0	0	0	0	0	0	0	13
Total	46	24	8	3	1	0	0	0	0	0	0	0	0	82

[a]The total number of progeny per breed are reported in Tables 4 and 5 for the Germplasm Utilization project (GPU) and the Germplasm Evaluation project (GPE), respectively.
[b]Sire breed.

CA is more highly related to aged meat tenderness than is i.m. fat (**IMF**) content (Whipple et al., 1990a; Shackelford et al., 1991b). Therefore, the present study was conducted 1) to estimate the heritability of CA and its genetic relationship to tenderness and other economically important traits and 2) to develop a procedure for the quantification of calpastatin activity on a large number of samples.

Materials and Methods

Animals. Steers (n = 555) sampled were from two different animal breeding projects at the U.S. Meat Animal Research Center (**MARC**). The Germplasm Utilization (**GPU**; n = 404) project consisted of purebred Angus (**A**), Braunvieh (**B**), Charolais (**C**), Gelbvieh (**G**), Hereford (**H**), Limousin (**L**), Pinzgauer (**P**), Red Poll (**RP**), and Simmental (**S**) and three composite populations, MARC I (1/4 C, 1/4 B, 1/4 L, 1/8 H, 1/8 A), MARC II (1/4 S, 1/4 G, 1/4 H, 1/4 A), and MARC III (1/4 RP, 1/4 H, 1/4 P, 1/4 A). The Germplasm Evaluation (**GPE**; n = 151) project consisted of F_1 crossbreds out of H and A dams and sired by H, A, C, G, P, Galloway, Longhorn, Nellore, Piedmontese, Salers, and Shorthorn bulls. The number of sires per breed and the number of progeny per sire are indicated in Table 1. The total number of progeny per breed are shown as part of results in Tables 4 and 5 for GPU and GPE, respectively.

From weaning until the steers weighed approximately 320 kg, steers were fed a growing diet containing approximately 2.7 Mcal of ME/kg of dry matter and 12.9% CP. For the remainder of the finishing period, GPE steers were fed a finishing diet containing about 3.0 Mcal of ME/kg of dry matter and 11.5% CP until they were slaughtered at 385 to 450 d of age. The GPU steers were randomly assigned to one of two diets that differed in energy density (2.85 vs 3.15 Mcal of ME/kg of dry matter). Rate of gain (**ADG**) was determined during the growing-finishing phase. Steers were slaughtered serially, in four kill groups (balanced across breed groups) spanning 63 d, at a commercial beef processing facility located approximately 90 km from MARC.

Immediately after slaughter and dressing, carcass sides were electrically stimulated (68 V, 3 s on, 3 s off; 70 V, 2 s on, 3 s off; 70 V, 2 s on, 3 s off; 70 V, 2 s on, 3 s off) and chilled (24 h at 0°C) according to standard operating procedures for that beef processing facility. A spray chilling system was employed that involved spraying carcasses with a fine mist of 2°C water for 30 s every 5 min. Spray chilling was terminated at approximately 12 h postmortem.

Carcasses subsequently were transported to MARC for fabrication into totally trimmed (0 cm of fat remaining) boneless cuts and removal of longissimus steaks for assessment of WBS and IMF. Details of the fabrication procedure were reported by Koch et al. (1976). Retail product yield (**RPY**) was calculated as a proportion of hot carcass weight. For determination of CA, samples were obtained at 18 to 24 h postmortem from the longissimus muscle (13th rib), refrigerated (2°C), and transported to MARC for analysis.

Quantification of Calpastatin Activity. To facilitate the quantification of CA on a large number of samples, a procedure was developed that did not require chromatography or dialysis. Unless stated otherwise, all samples and buffers were held at 2 to 4°C. Samples (5 g) were extracted at 24 to 31 h postmortem in 25 mL of 100 m*M* Tris, 5 m*M* EDTA, 10 m*M* β-mercaptoethanol (pH 8.3) by homogenizing for 3 × 30 s with a polytron with a 30-s rest between each burst. The homogenate was centrifuged for at least 30 min at 35,000 × *g* and the supernatant was filtered through cheesecloth and glass wool. The supernatant was transferred to 13- × 100-mm borosilicate test tubes and heated in a water bath (preheated to 95°C) for 15 min to denature calpains. Calpastatin retains its activity under these conditions. Following heating, samples were chilled in an ice water bath for 15 min and the coagulated protein was scrambled with a small glass rod to facilitate separation of the supernatant and pellet during centrifugation. Final centrifugation was accomplished in a two-step process to minimize sample loss. First, the samples were centrifuged for 10 min at 1,500 × *g* in the 13- × 100-mm borosilicate test tubes and then the supernate was transferred to 50-mL centrifuge tubes and centrifuged at 35,000 × *g* for 30 min. Following centrifugation, the volume of the supernatant was determined and recorded for subsequent calculation of CA. Calpastatin activity was determined according to Koohmaraie (1990) with slight modifications (for details see Shackelford [1992]).

The heated procedure was verified by comparison against the procedure of Koohmaraie (1990), which includes dialysis and ion-exchange chromatography. Verification was conducted on 26 of the samples in the present study (24-h postmortem beef longissimus muscle) and 15 samples obtained from 0-h postmortem beef longissimus muscle. In both cases, 50-g muscle samples were extracted and assayed according to Koohmaraie (1990), whereas 5-g muscle samples were extracted and assayed as described above. The samples ranged from 1.3 to 5.9 units of CA/g of muscle. The correlation between results of the two procedures was .88 (Figure 1). Our procedure overestimated CA, as determined by Koohmaraie (1990), by 1.2 units/g of muscle ($P < .05$). However, the slope of a regression line (.97) between the results of the two assays did not differ from 1 ($P > .05$). Thus, the heated assay was capable of accurately detecting relative differences in CA.

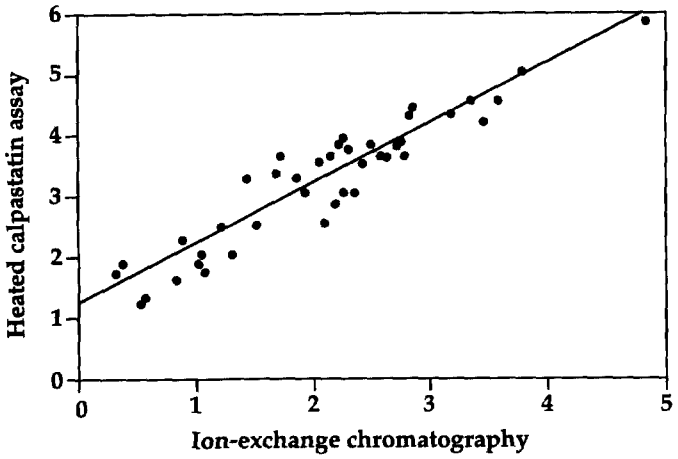

Figure 1. Accuracy (r^2 = .88, n = 41) of heated calpastatin assay as compared to the ion-exchange chromatography procedure of Koohmaraie (1990).

Warner-Bratzler Shear Force. Warner-Bratzler shear (**WBS**) force was determined at 9 d postmortem for the steers in the GPU project, and shear force was determined at 7 d postmortem for steers in the GPE project. Longissimus steaks were vacuum-packaged and aged at 2°C until the appropriate day postmortem and then frozen at −30°C. Steaks were cooked and sheared as described by Whipple et al. (1990b).

Statistical Analysis. Overall means and standard deviations were determined using SAS (1985). Data were analyzed by use of an animal model using the REML program of Meyer (1990). The model was (P = project (GPU or GPE); B = breed-group; A = animal; K = kill group; D = diet) as follows: $Y_{ijkl} = \mu + P_i + B_j(P_i) + A(B_j) + K_k + D_l(P_i) + e_{ijkl}$. The random effects were $A(B_j)$ and e_{ijkl}. Variances were

$$\text{Var}\begin{bmatrix} a \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & 0 \\ 0 & I\sigma_e^2 \end{bmatrix}$$

All other effects were considered fixed effects. $E(Y_{ijkl}) = \mu + P_i + B_j(P_i) + K_k + D_l(P_i)$.

Results and Discussion

Maeda et al. (1991) reported moderate to high heritability estimates ($\hat{h}^2_{Sire} = .58 \pm .35$, $\hat{h}^2_{Dam} = .35 \pm .28$, $\hat{h}^2_{Sire + Dam} = .46 \pm .25$) for calpain activity in Japanese quail. However, their results should be interpreted with caution because they assayed a crude muscle homogenate that contained all components of the calpain system (μ- and m-calpain and calpastatin). Moreover, the calcium concentration in their assay was 6 m*M* and, thus, was high enough to activate m-calpain, which requires 200 to 300 μ*M* Ca^{2+}

Table 2. Simple statistics for dependent variables

Variable	Mean	Standard deviation	Minimum value	Maximum value
Calpastatin activity[a]	2.8	.7	1.2	5.4
Intramuscular fat content, %	3.9	1.2	1.6	8.8
Shear force, kg[b]	5.2	1.4	2.3	10.7
Retail product yield, %	65.5	4.4	53.1	77.0
Average daily gain, kg/d	1.3	.1	.9	1.8

[a]Units of calpastatin activity per gram of muscle.
[b]Data were pooled for the Germplasm Utilization project (9 d postmortem) and the Germplasm Evaluation project (7 d postmortem).

for activation (Dayton, 1982). Because the Ca^{2+} requirement for m-calpain far exceeds the Ca^{2+} levels in muscle (Goll et al., 1983), it has been concluded that m-calpain is not activated in vivo or during normal postmortem storage of meat (Koohmaraie et al., 1987). Although m-calpain activity may have been highly heritable, it is difficult to conceive a biological significance for this finding.

In the present study, we chose to measure the activity of calpastatin, the endogenous inhibitor of calpains, rather than calpain activity because CA at 24 h postmortem has been reported to be highly related to beef tenderness (Whipple et al., 1990a; Shackelford et al., 1991b).

The design of this study (31 breed-groups of cattle fed to four slaughter end points) provided a great amount of variation in CA, IMF, WBS, RPY, and ADG (Table 2). The CV for WBS force was 26.9%. This coefficient may have been inflated by the use of WBS values at 7 d postmortem for GPE cattle and 9 d postmortem for GPU cattle. However, the CV in WBS was similar and large for the two populations of cattle (GPE = 22.8; GPU = 24.0).

Calpastatin activity was highly heritable ($\hat{h}^2$ = .65 ± .19) and accounted for a significant portion of the genetic variation in WBS force (r_g = .50 ± .22; Table 3). The phenotypic correlation coefficient between CA and WBS force was lower than those reported previously (r_p = .27 vs .66 and .39; Whipple et al., 1990a and Shackelford et al., 1991b, respectively). Numerous factors may have contributed to the low r_p between CA and WBS force in the present study. The logistics of this study (up to 168 steers per kill group, steers slaughtered in a commercial packing plant, etc.) resulted in samples being extracted from 24 to 31 h postmortem.

In the present experiment, IMF was as strongly related genetically with WBS as was CA, and the r_g of IMF with WBS was of slightly greater magnitude than was the r_g of CA with WBS. Genetic antagonisms existed between RPY and CA, IMF, and WBS. The magnitude of the genetic antagonism between RPY and IMF was greater than that between RPY and CA. Thus, selection against postrigor CA may provide a more suitable approach to simultaneously select for tenderness and cutability than would selection for increased IMF. Moreover, CA was negatively associated with ADG (r_g = −.52 ± .37; r_p = −.15 ± .04). Thus, selection against postrigor CA may result in improved growth rate. Others have associated higher CA with an increased rate of muscle deposition in β-adrenergic agonist-treated vs control wethers (Koohmaraie et al., 1991) and steers (Wheeler and Koohmaraie, 1992) and in bulls vs steers (Morgan et al.,

Table 3. Heritabilities and genetic and phenotypic correlations[a]

Trait	Calpastatin activity	Intramuscular fat content	Shear force	Retail product yield	Average daily gain
Calpastatin activity	.65	−.19	.27	.21	−.15
	(.19)	(.03)	(.04)	(.04)	(.04)
Intramuscular fat content	−.34	.93	−.27	−.46	.12
	(.11)	(.02)	(.03)	(.02)	(.01)
Shear force	.50	−.57	.53	.15	−.06
	(.22)	(.16)	(.15)	(.04)	(.04)
Retail product yield	.44	−.63	.70	.45	−.18
	(.25)	(.15)	(.30)	(.18)	(.04)
Average daily gain	−.52	−.04	−.40	−.62	.32
	(.37)	(.11)	(.31)	(.60)	(.26)

[a]Heritability estimates are shown along the diagonal. Genetic correlations are in the lower triangle and phenotypic correlations are in the upper triangle. Parenthetical values are standard errors of the estimates.

1993). Although it might seem that the negative association between CA and ADG in the present experiment conflicts with the findings of those experiments, it must be recognized that those experiments involved measurement of CA at 0 h postmortem, whereas the present experiment involved measurement of CA at 24 to 31 h postmortem.

The high genetic correlation between postrigor CA and WBS suggests that it may be possible to improve meat tenderness via selection against CA. However, because the specific time point at which CA has been reported to be correlated to tenderness was 24 h postmortem and, more importantly, because CA at 0 h postmortem was not correlated to tenderness (Whipple et al., 1990a; Shackelford et al., 1991b), a full understanding of the mechanism controlling the rate of postmortem decline in CA must be achieved. The parameter estimates reported in the present study encompass all the factors that affect residual CA. Thus, the parameter estimates are a reflection of the factor(s) controlling the rate of inactivation of calpastatin.

The heritability of WBS force detected was higher (.53 vs .31) than that reported by Koch et al. (1982a). There are several differences between these studies that could have contributed to this discrepancy. The present study consisted of both purebred, composite, and F_1 breed-groups, whereas the cattle of Koch et al. (1982a) were F_1 crosses. Moreover, steaks in the present study were cooked to a more advanced degree of doneness (70 vs 65°C).

Least squares means for the dependent variables stratified by breed are listed in Tables 4 and 5 for the GPU and GPE cattle, respectively. Purebred P, C, and G had significantly higher CA than A, L, H, MARC I, MARC II, and MARC III. For each of the composite populations, CA was lower than the mean of the weighted-average of the contributing breeds. The mean CA of the breeds contributing to MARC II and to MARC III composites was approximately 2.9, whereas the mean for the composite populations was approximately 2.5. In the GPU population, the ranking of breeds for CA was not related to the ranking of breeds for WBS. In fact, the ranking of breeds with respect to IMF more accurately reflected breed differences in WBS. However, in the GPE project, breed differences in CA accounted for a greater proportion (41 vs 7%) of breed differences in WBS than did IMF. As expected based on previous research with *Bos indicus* breeds of cattle (Wheeler et al., 1990; Whipple et al., 1990b; Shackelford et al., 1991a), the Nellore-sired steers were tough and had high CA at 24 h postmortem. However, Gelbvieh crosses had numerically ($P > .05$) higher CA and WBS than did Nellore crosses. Piedmontese crosses had the lowest WBS despite having the second-lowest amount of IMF. Additionally, Piedmontese crosses had the fourth most calpastatin activity. Thus, these data suggest that the extreme tenderness of muscle-hypertrophied cattle cannot be explained by variation in CA or marbling. Further studies to elucidate the mechanism responsible for the extreme tenderness of muscle-hypertrophied cattle must be conducted.

Table 4. Least squares means of calpastatin activity, intramuscular fat content, shear force, retail product yield, and average daily gain for breed-groups in the Germplasm Utilization project[a]

Breed group	n	Calpastatin activity[b]	Intramuscular fat content, %	Shear force, kg[c]	Retail product yield, %	Average daily gain, kg
Red Poll	25	3.15^{ef}	4.07^{fgh}	4.60^{ghi}	64.1^{i}	1.17^{k}
Braunvieh	37	3.11^{ef}	3.67^{hij}	4.35^{hi}	67.2^{h}	1.28^{hi}
Hereford	40	2.80^{fg}	4.09^{fg}	4.99^{fgh}	62.9^{j}	1.20^{jk}
Angus	29	2.71^{fg}	4.49^{ef}	4.65^{ghi}	62.6^{j}	1.25^{ij}
Simmental	32	3.07^{ef}	3.34^{jk}	5.27^{ef}	68.6^{fg}	1.35^{ef}
Limousin	40	2.81^{f}	2.66^{l}	5.47^{ef}	70.9^{e}	1.19^{jk}
Charolais	29	3.18^{e}	3.12^{jkl}	5.13^{efg}	68.2^{gh}	1.39^{e}
Gelbvieh	39	3.17^{e}	2.88^{kl}	5.50^{e}	69.9^{ef}	1.34^{fg}
Pinzgauer	27	3.21^{e}	4.01^{ghi}	4.00^{i}	67.8^{gh}	1.29^{ghi}
MARC I	34	2.94^{f}	3.53^{ij}	4.61^{ghi}	67.0^{h}	1.32^{fgh}
MARC II	38	2.53^{g}	4.34^{efg}	4.48^{hi}	65.0^{i}	1.34^{fg}
MARC III	34	2.49^{g}	4.85^{e}	4.88^{fghi}	62.5^{j}	1.30^{ghi}
RMSE[d]	—	.61	.78	1.11	2.5	.11

[a]For more precise estimates of least squares breed group means for all traits except calpastatin activity, see Gregory et al. (1994), who report results for these traits on approximately four times as many animals for each breed group from the same experiment.

[b]Units of calpastatin activity per gram of muscle.

[c]Shear force was determined at 9 d postmortem.

[d]RMSE = root mean square error. The standard error of a least squares mean can be determined by dividing the RMSE by the square root of the number of steers per sire line.

[e,f,g,h,i,j,k,l]Means within a column with a common superscript letter do not differ ($P > .05$).

Table 5. Least squares means of calpastatin activity, intramuscular fat content, shear force, retail product yield, and average daily gain for sire breeds in the Germplasm Evaluation project[a]

Sire breed	n	Calpastatin activity[b]	Intramuscular fat content, %	Shear force, kg[c]	Retail product yield, %	Average daily gain, kg
Hereford	19	2.61^{f}	4.75^{e}	5.87^{gh}	60.2^{i}	1.30^{fgh}
Angus	18	2.55^{f}	4.79^{e}	6.35^{fg}	61.0^{hi}	1.27^{gh}
Charolais	12	2.84^{ef}	4.40^{ef}	6.24^{fg}	65.2^{fg}	1.39^{ef}
Gelbvieh	9	3.30^{e}	3.44^{g}	7.29^{e}	65.5^{fg}	1.40^{e}
Pinzgauer	9	2.76^{ef}	4.80^{e}	5.81^{gh}	64.7^{fg}	1.34^{fgh}
Shorthorn	17	2.77^{ef}	4.61^{ef}	6.85^{ef}	59.9^{i}	1.36^{ef}
Galloway	8	2.84^{ef}	4.92^{e}	6.47^{efg}	63.2^{gh}	1.23^{hi}
Longhorn	12	2.97^{ef}	4.26^{ef}	6.84^{ef}	63.5^{fg}	1.16^{i}
Nellore	12	3.25^{e}	4.25^{ef}	7.14^{ef}	64.3^{fg}	1.17^{i}
Piedmontese Nellore	12	2.90^{ef}	3.79^{fg}	5.45^{h}	68.5^{e}	1.30^{fgh}
Salers	7	2.80^{ef}	4.26^{ef}	6.11^{fgh}	66.1^{ef}	1.35^{efg}
RMSE[d]	—	.61	.78	1.11	2.5	.11

[a]For more precise estimates of least squares breed group means for all traits except calpastatin activity, see Cundiff et al. (1993), who report results for these traits on approximately five times as many animals for each breed group from the same experiment.
[b]Units of calpastatin activity per gram of muscle.
[c]Shear force was determined at 7 d postmortem.
[d]RMSE = root mean square error. The standard error of a least squares mean can be determined by dividing the RMSE by the square root of the number of steers per sire line.
[e,f,g,h,i]Means within a column with a common superscript letter do not differ ($P > .05$).

Implications

Rapid genetic response to selection against calpastatin activity may be possible because postrigor calpastatin activity is highly heritable. Selection against calpastatin might result in improved beef tenderness without compromising growth rate. Research must be conducted to determine those factors controlling the rate of postmortem inactivation of calpastatin so that selection of breeding animals can be improved for tenderness.

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