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Evaluation of the Ovine *Callipyge* Locus: III. Genotypic Effects on Meat Quality Traits^{1,2}

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ABSTRACT: A resource flock of 362 F₂ lambs provided phenotypic and genotypic data to estimate effects of *callipyge* (*CLPG*) genotypes (NN, NC, CN, and CC) on meat quality traits. The mutant allele is represented as C, the normal allele(s) as N, and the paternal allele of a genotype is given first. Lambs of each genotype born in 1994 and 1995 were serially slaughtered in six groups at 3-wk intervals starting at 23 wk of age. Warner-Bratzler shear force and subjective evaluation of marbling were collected during both years from longissimus. Calpastatin activity was measured on longissimus from the 1994 group, and ELISA quantification of calpastatin protein was obtained from the 1995 group. Significant additive and paternal polar overdominance effects on meat quality traits were detected. This is in contrast to previous research that detected only polar overdominance effects on slaughter and carcass traits in this population. The magnitude of genotypic effects on shear force differed significantly between years; however, additive ($P < .01$), paternal polar overdominance ($P < .001$), and maternal dominance ($P < .01$) effects adjusted for variation in carcass weight were detected within each year. Shear force data adjusted to the mean slaughter

age or carcass weight indicated that the means and variances of CN and CC genotypes were greater than values of NC and NN. Shear force values were greatest for CN and were intermediate for CC. The difference in shear force (adjusted for variation in slaughter age) between homozygous genotypes (additive effect) was supported by calpastatin activity data with 2-df F-tests of 3.66 ($P < .05$) and 11.84 ($P < .001$) at d 0 and 7 postmortem, respectively. Corresponding values for the paternal polar overdominance effects on calpastatin activity were 53.80 ($P < .001$) and 87.43 ($P < .001$). Calpastatin ELISA data (d 0, adjusted for slaughter age) exhibited a paternal polar overdominance effect exclusively with a 2-df F-test of 57.63 ($P < .001$). Additive and paternal polar overdominance effects on marbling adjusted for slaughter age had F-tests of 6.41 ($P < .01$) and 93.29 ($P < .001$), respectively. Consequences of increased longissimus shear force must be addressed if the advantages of CN lambs for dressing percentage and carcass composition are to be realized. Further research is needed to establish whether selection targeted at changing the background genome can mitigate the negative effects of the C allele on meat tenderness.

Key Words: *Callipyge*, Sheep, Meat Quality, Genotypes

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Introduction

Knowledge of *callipyge* (*CLPG*) phenomena has increased rapidly since the initial reports of Jackson and Green (1993) and Jackson et al. (1993a,b). The *CLPG* locus was reported to be near the terminal

region of chromosome 18 and a unique form of parental imprinting, polar overdominance, was documented (Cockett et al., 1994, 1996; Freking et al., 1998a). Lambs expressing the *callipyge* phenotype were characterized by more rapid muscle accretion, less rapid fat accretion, greater dressing percentage,

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and compact, lean carcasses relative to lambs representing normal phenotypes (Snowder et al., 1994; Jackson et al., 1997; Freking et al., 1998b). However, the *callipyge* phenotype was also associated with adverse effects on meat quality traits, particularly tenderness of the longissimus (Koochmaraie et al., 1995; Field et al., 1996; Shackelford et al., 1997).

Callipyge phenotypic effects on meat quality traits were estimated in these previous studies from data collected on heterozygous (mutant *CLPG* allele inherited from the sire) and noncarrier lambs. Each lamb represented one of two *CLPG* genotypes and was subjectively classified as expressing either the *callipyge* or the normal phenotype. Statistical inferences of previously reported phenotypic effects applied to restricted ranges of slaughter end points, and relationships of meat quality traits with slaughter age or carcass weight within phenotype were not estimated. Evaluation of all four *CLPG* genotypes over wide ranges of biological and economical slaughter end points is needed to provide complete information to sheep industries in the United States and abroad. Therefore, objectives were to test models of gene action and to estimate effects involving all four *CLPG* genotypes, inferred from flanking DNA-based markers, on meat quality traits recorded throughout an experiment of serial slaughter design.

Materials and Methods

Animal Population and Phenotypic Data

The resource population, genotypic data, statistical approaches, and effects of *CLPG* genotypes on growth, slaughter, and carcass traits were described by Freking et al. (1998a,b). Briefly, nine Dorset rams exhibiting the *callipyge* phenotype were mated to Romanov ewes, and selected F₁ rams and ewes were *inter se*-mated during two breeding seasons. The resulting F₂ progeny, born in 1994 and 1995, exhibited segregation at the *CLPG* locus. A total of 362 F₂ ewe and wether lambs were serially slaughtered at 23, 26, 29, 32, 35, and 38 wk of age (n = 30 per age group per year) at the Roman L. Hruska U.S. Meat Animal Research Center. Each F₂ lamb was subjectively evaluated for expression of the *callipyge* or normal phenotype at 20 wk of age to ensure representation of phenotypes within each sex and slaughter group combination.

Following a 24-h chill, the right side of each split carcass was separated between the 12th and 13th ribs, and the 12th rib cross-section of the longissimus was subjectively scored for marbling (0 = Devoid, 200 = Traces, 400 = Small, 600 = Moderate). The right side was subsequently used to estimate genotypic effects on carcass composition (Freking et al., 1998b). Loin chops were collected from the left side of each carcass to evaluate meat quality traits. Chops (2.54 cm thick)

were vacuum-packaged, aged for 14 d at 4°C, and then frozen at -20°C until shear force could be measured (range 2 wk to 5 mo). Frozen chops were thawed to 5°C, broiled to an internal temperature of 40°C, turned, and then broiled to an internal temperature of 75°C using an open-hearth electric broiler (Farberware, Bronx, NY). Chops were cooled (4°C) for 24 h before a total of six cores (1.27 cm diameter) from three chops were obtained parallel to the muscle fibers. Each core was sheared once with a Warner-Bratzler shear attachment using an Instron Universal Testing Machine (Model 1132, Instron; Canton, MA) with a 50-kg load cell and cross head speed of 50 mm/min. The mean shear force of the six cores was analyzed. Equipment malfunction led to invalid measurement of shear force for the 35-wk slaughter group born in 1995 (n = 30). These data were deleted from all subsequent analyses of shear force.

Longissimus calpastatin activity was quantified by different methods in the 2 yr. Calpastatin is an endogenous inhibitor of the calpain proteolytic system that is primarily responsible for postmortem proteolysis, which results in meat tenderization (see review by Koochmaraie, 1992). Longissimus homogenates from carcasses of 1994-born lambs were evaluated using a heated (crude) calpastatin activity assay described by Shackelford et al. (1994) with the modifications as indicated by Koochmaraie et al. (1995). Longissimus from carcasses of 1995-born lambs were analyzed for levels of calpastatin protein using an indirect antibody enzyme-linked immunosorbent assay (ELISA) described by Doumit et al. (1996). This ELISA method required less resources to obtain calpastatin data. The coefficient of determination between calpastatin ELISA and conventional enzymatic assay of calpain inhibitory activity was .89 when measured on prerigor lamb skeletal muscle (Doumit et al., 1996). The current experiment included calpastatin activity measured at d 0 and d 7 postmortem (1994) and quantity of ELISA calpastatin protein recorded d 0 postmortem (1995).

Genotypic Probabilities

Description of genotypic data and calculation of *CLPG* genotypic probabilities were presented previously (Freking et al., 1998a). Briefly, genotypic data were collected for 25 marker loci that spanned 87.2 cM of ovine chromosome 18. Probabilities of CC, CN, NC, and NN genotypes were calculated for each F₂ lamb as a function of the recombination rate between the two informative marker loci flanking position 86 cM. The mutant allele is represented as C, the normal allele(s) represented as N, and the paternal allele of a genotype given first. Probabilities of each genotype ranged continuously between zero and one. Genotypic probabilities summed to one within animal, creating a dependency. For example, an individual F₂ lamb had probabilities of .0003, .9995, .0000, and .0002 for CC, CN, NC, and NN genotypes, respectively.

Statistical Analyses

Meat quality traits were defined on an individual lamb basis. The statistical model for shear force and marbling score included fixed effects of year, sex, and sire to partially account for environmental and polygenic effects. Regressions on CC, CN, NC, and NN probabilities (NN effect was set to zero to remove dependency) and genotype-specific linear regressions on slaughter age or carcass weight also were estimated. Calpastatin traits were analyzed with a similar model with the exception of year effects.

A single contrast involving *CLPG* genotypic effects provided sums of squares (6 df) to measure variation due to the *CLPG* locus. These sums of squares were expressed as a percentage of corrected sums of squares (percentage variation, Table 1), a conservative approach. Three orthogonal contrasts, each with 2 df, were derived to partition variation due to *CLPG* genotypic effects. Based on previous results (Freking et al., 1998a,b), orthogonal contrasts of CC, CN, NC, and NN effects were evaluated to test additive (1, 0, 0, -1), maternal dominance (-1, 0, 2, -1), and paternal polar overdominance (-1, 3, -1, -1) models of gene action, respectively. Nominal, rather than genome-wide, levels of significance were used due to prior positioning of the *CLPG* locus (Freking et al., 1998a).

Inspection of the relationship between predicted and residual values from analysis of shear force revealed that dispersion of residuals increased with greater values of shear force suggesting a non-normal distribution. A similar phenomenon was observed with shear force data from a bovine *Bos indicus* × *Bos taurus* resource population (Keele et al., 1999). Furthermore, analysis of shear force on the observed scale caused a spurious shift in the most likely position of *CLPG* (data not tabulated). Following logarithmic transformation, residual values seemed to be normally distributed, and *CLPG* was positioned consistent with other traits. Thus, shear force was transformed by natural logarithm prior to analyses to account for the proportional relationship between standard deviations and means of *CLPG* genotypes.

A significant interaction of year and *CLPG* genotypic effects (full model) was detected for shear force. An F-test with 6 numerator and 308 denominator degrees of freedom was derived from the difference in residual sums of squares between full and reduced models ($F = 5.29$; $P < .01$). This significant interaction was due exclusively to differences in the means of the CN genotype; the means of the remaining three *CLPG* genotypes were consistent between years. Therefore, final analysis of shear force (log transformed) was conducted separately for each year.

Relationships of meat quality traits with slaughter age or carcass weight for each *CLPG* genotype were estimated by linear regression equations. Covariate values were coded as deviations from the mean of the covariate. Thus, intercept values represent means of

CLPG genotypes at the mean of the covariate. Regression equations for slaughter age have inference from 161 to 266 d and are in the context of a Dorset and Romanov genetic background. Predicted values of carcass weight at intended ages of 161 and 266 d represent the range of inference for carcass weight. Predicted carcass weight ranged from 20.2 to 29.4 kg for normal (CC, NC, and NN) and from 22.4 to 31.4 kg for *callipyge* (CN) phenotypes (genotypes).

Results and Discussion

Genotype × Year Interaction

Similar ranking of genotypes between years provided consistent results concerning gene action (Table 1). However, a significant difference between years in the CN mean was observed for Warner-Bratzler shear force, but means of the remaining three genotypes were consistent between years (Tables 2 and 3). Inspection of the genotypic means from the three sires used both years indicated this phenomenon was consistent within sires. In this case, the joint effects of genotype and year (environment) were not predictable from their separate average effects (Dickerson, 1962). Lambs and carcasses were treated similarly each year to the extent possible. Shear force means of slaughter groups were similar within year, indicating that the environmental effect was not associated with a specific slaughter group. In contrast, under less controlled commercial slaughter conditions, Keele et al. (1999) reported significant genotype × slaughter group interactions for shear force in a bovine resource population. The interaction from the current experiment was the result of an undetermined environmental effect(s) that specifically impacted shear force of the CN genotype. We can offer no explanation for the nature of this effect. Such an interaction was not detected for any trait previously analyzed in this population. Measures of calpastatin activity were confounded with year and could not be tested for this interaction. Due to the interaction, genotypic effects on shear force are presented separately for each year.

Gene Action of the *Callipyge* Locus for Meat Quality Traits

Previous analyses indicated that additive and maternal dominance genetic effects of the *CLPG* locus did not contribute significantly to variation of growth, slaughter, and carcass traits (Freking et al., 1998a,b). These contrasts are orthogonal to the paternal polar overdominance contrast. To evaluate the hypothesis that meat quality traits displayed similar gene action, *CLPG* genotypic effects on shear force, marbling score, and calpastatin traits were tested using these same three orthogonal contrasts.

Table 1. Number of observations, F-tests for additive, maternal dominance, and paternal polar overdominance gene action, and variation accounted for by genotypes^a

Dependent variable	Number of observations	Covariate	F-test			Percentage variation ^b
			Additive	Maternal dominance	Paternal polar overdominance	
Warner-Bratzler shear force						
Year 1994	189	Slaughter age	17.40***	2.50	43.68***	44.64
		Carcass weight	18.11***	3.43*	38.47***	42.82
Year 1995	143	Slaughter age	6.60**	2.45	76.91***	50.18
		Carcass weight	6.97**	6.19**	73.21***	53.19
Calpastatin activity (1994)	189					
Day 0		Slaughter age	3.66*	3.85*	53.80***	41.87
		Carcass weight	3.32*	1.81	58.00***	44.13
Day 7		Slaughter age	11.84***	2.54	87.43***	56.11
		Carcass weight	10.94***	2.34	84.01***	55.15
ELISA calpastatin (1995)						
Day 0	170	Slaughter age	1.36	1.12	57.63***	39.51
		Carcass weight	1.77	.49	58.55***	40.69
Marbling score	362	Slaughter age	6.41**	.23	93.29***	35.84
		Carcass weight	6.76**	.10	111.85***	41.71

^aF-tests (2 df) associated with additive, maternal dominance, and paternal polar overdominance contrasts of regressions on genotypic probabilities and genotype-specific covariates (slaughter age or carcass weight).

^bVariation due to CLPG locus as a percentage of corrected sum of squares.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

Numbers of observations for each trait, tests of models of gene action, and the percentage of variation accounted for by genotypic effects are presented in Table 1. Results are presented from analyses fitting either slaughter age or carcass weight as covariates. The 6 df associated with genotypic effects were

partitioned into the three orthogonal models of gene action (2 df each) described above.

All traits exhibited effects of paternal polar overdominance, ranging from an F value of 38.47 for 1994 shear force data adjusted for carcass weight ($P < .001$) to an F value of 111.85 for marbling score

Table 2. Genotype-specific regression coefficients on slaughter age^a

Item	Warner-Bratzler shear force, kg log _e		Calpastatin activity (1994), U/g muscle		ELISA calpastatin (1995), O.D. (450 nm) ^b	Marbling score ^c
	1994	1995	Day 0	Day 7	Day 0	
NN genotype						
Intercept	1.19116	1.21119	3.22850	2.19145	.66001	406.31
Linear	-.00029	-.00263*	-.00672	.00155	-.00112	1.38***
NC genotype						
Intercept	1.24107	1.19412	4.00175	3.20126	.77855	371.13
Linear	-.00014	-.00550***	-.01904***	-.00307	-.00244**	1.34***
CC genotype						
Intercept	1.55334	1.54300	3.76647	3.23987	.75115	352.52
Linear	-.00217	-.00566	-.01269*	-.00488	-.00290	1.39***
CN genotype						
Intercept	1.74211	2.14657	5.29691	4.96084	1.21765	243.80
Linear	-.00037	-.00245	-.00886*	-.00396	-.00397***	.38
RSD	.26312	.29329	.93778	.93624	.21258	77.92

^aCovariate values are deviations from the mean value of 214.9 d. Thus, intercept values are means of genotypes at the mean slaughter age.

^bO.D. = optical density.

^c0 = Devoid, 200 = Traces, 300 = Slight; 400 = Small; 500 = Modest.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

Table 3. Genotype-specific regression coefficients on carcass weight^a

Item	Warner-Bratzler shear force, kg log _e		Calpastatin activity (1994), U/g muscle		ELISA calpastatin (1995), O.D. (450 nm) ^b	Marbling score ^c
	1994	1995	Day 0	Day 7	Day 0	
NN genotype						
Intercept	1.19934	1.23687	3.15653	2.15944	.67187	406.35
Linear	.00497	-.02103**	-.07145*	-.01481	-.01054	11.02***
NC genotype						
Intercept	1.25939	1.18431	3.63417	3.14626	.77761	383.75
Linear	.01283	-.05020***	-.15382**	-.02406	-.01520*	12.90***
CC genotype						
Intercept	1.55693	1.62368	3.57915	3.20832	.79076	354.21
Linear	-.00781	.00456	-.13177*	-.03320	-.02555	12.68***
CN genotype						
Intercept	1.74035	2.17479	5.27341	4.95250	1.26322	239.24
Linear	.01414	-.00971	.00071	-.01280	-.02149***	1.73
RSD	.26170	.29818	.96658	.94094	.21772	77.23

^aCovariate values are deviations from the mean value of 25.63 kg. Thus, intercept values are means of genotypes at the mean carcass weight.

^bO.D. = optical density.

^c0 = Devoid; 200 = Traces; 300 = Slight; 400 = Small; 500 = Modest.

* $P < .05$.

** $P < .01$.

*** $P < .001$.

adjusted for carcass weight ($P < .001$). With the exception of ELISA calpastatin, all traits exhibited significant additive effects ($P < .05$). Maternal dominance effects also were detected for shear force (carcass weight as covariate; $P < .05$, 1994; $P < .01$, 1995) and calpastatin activity on d 0 (slaughter age as covariate; $P < .05$, 1994).

Results established that paternal polar overdominance accounted for *CLPG* genotypic effects on ELISA calpastatin, but failed to uniquely describe genotypic effects on shear force, calpastatin enzymatic activity, and marbling. These latter traits were more complexly regulated at the *CLPG* locus because three genotypic distributions were necessary to describe variation (see Figure 1 as an example). Furthermore, gene action was not consistent among meat quality traits as described below. These conclusions are in contrast with the paternal polar overdominance model of *CLPG* genotypic effects used to describe inheritance of the *callipyge* phenotype and measures of carcass shape or composition (Cockett et al., 1996; Freking et al., 1998a,b). Investigating the novel interaction of genotypes and phenotypes associated with this locus may offer opportunities to improve understanding of the complex relationships involving muscle growth and meat quality traits. Future research should consider use of orthogonal contrasts of genotypic effects to evaluate these unique forms of gene action.

Warner-Bratzler Shear Force Distribution

Distributions generated from the probability density function assuming a log normal model of shear force values were transformed back to the observed

scale and are presented for each genotype by year (Figure 1). The mean and SD were largest for CN followed by CC, which was intermediate relative to NC and NN. Means in kilograms on the log normal scale for each genotype at the average slaughter age or carcass weight are presented as intercept values in Tables 2 and 3, respectively. Adjusted to an age-constant basis, the SD values in 1994 on the observed scale were .91, .96, 1.31, and 1.58 kg for NN, NC, CC, and CN, respectively. Corresponding SD in 1995 were

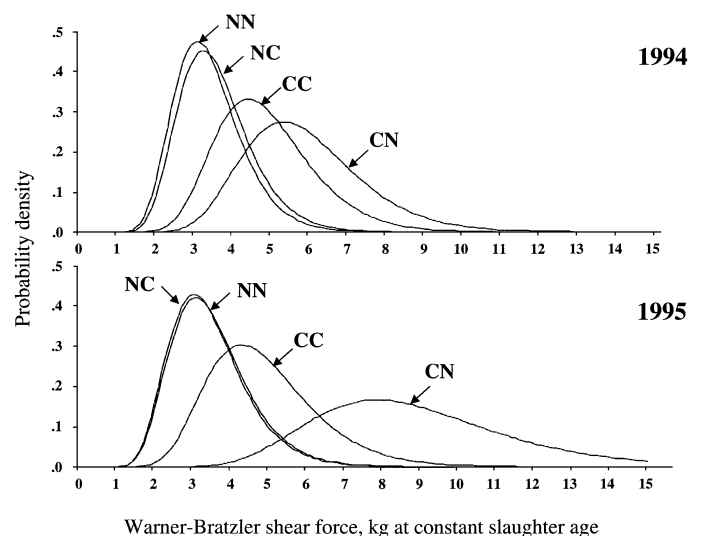


Figure 1. Derived genotype-specific distributions for Warner-Bratzler shear force of longissimus at 14 d postmortem in 1994 and 1995.

1.05, 1.03, 1.46, and 2.68 kg. The variance of shear force for CN was 2.9 times larger in 1995 than in 1994. Genotypic means and SD for shear force adjusted to a mean carcass weight were virtually identical to the age-constant values.

In the current study, a larger portion of the CN distribution was overlapping with distributions of NN and NC in 1994 than in 1995, where the overlap was slight. The CC distribution is intermediate and overlaps with all other distributions. The CN variability reveals a problem with product uniformity, but also allows for potential improvement through selection if part of this variation is genetic in nature. Important environmental effects, as yet unknown, would need to be addressed by antemortem treatment of lambs and by postmortem treatment of carcasses.

Genotypic Effects and Relationships with Slaughter Age and Carcass Weight

Coefficients for linear regression equations on days of age at slaughter and carcass weight are presented in Tables 2 and 3, respectively. Due to the complexity of gene action, all four genotype-specific relationships are given for each meat quality trait. Shear force decreased slightly as slaughter age increased for each genotype. Effects of carcass weight on shear force also were small but less consistent in sign. Linear regression coefficients on age and carcass weight for NN and NC genotypes in 1995 were the only significant relationships with shear force. Some research prior to *callipyge* experiments also had indicated a general trend of decreased shear force in lamb as age or carcass weight increased within the typical marketing range (Kemp et al., 1976; 1980).

Large differences existed between genotypes in the force necessary to shear core samples from broiled longissimus chops aged 14 d. The CN genotype exhibited the greatest mean for shear force in both years. Transformed back to the observed scale, the age-adjusted CN mean exceeded the NN mean by 2.4 kg in 1994. In 1995, the magnitude of the difference was greater (5.2 kg). These results are in general agreement with Koohmaraie et al. (1995), who reported large unfavorable effects (4.9 kg higher) of CN compared to NN on longissimus shear force through 21 d of postmortem storage. This increased shear force is apparently primarily associated with the strength of the myofibrillar fraction of muscle rather than changes in connective tissue. Field et al. (1996) reported that collagen percentage and degree of maturation of the collagen crosslinks were lower in *callipyge* than normal phenotype lambs, thus failing to explain the increased shear force in *callipyge* lambs.

Carpenter et al. (1996) identified a shift toward larger fast-twitch glycolytic fibers of muscles that displayed hypertrophy in *callipyge* lambs. Koohmaraie et al. (1995) reported a shift toward the same (alpha-

white) fibers that increased the overall average fiber area in affected muscles from *callipyge* lambs. Experimental data from rats indicated that muscles that had a larger functional area composed of fast-twitch fibers had lower protein turnover (Garlick et al., 1989). Research conducted by Lorenzen et al. (1997) indicated a decrease in fractional rates of protein synthesis and protein degradation in hypertrophied skeletal muscles of *callipyge* lambs at 8 wk of age. Bovine muscles, with larger average fiber size, tended to have greater calpastatin activity and shear force (Koohmaraie et al., 1988). This information might suggest that increased average fiber area associated with a shift in fiber type distribution is correlated with lower protein turnover and higher levels of calpastatin activity antemortem and postmortem, resulting in a detrimental effect on shear force. No information has been reported on the fiber type distribution of muscles from CC and NC lambs, which do not express the hypertrophy phenotype. As indicated by the significant additive effect, CC also had greater values (1.43 kg in 1994 and 1.32 kg in 1995) of shear force relative to NN, but was intermediate compared to CN. Significant maternal dominance effects indicated that NC was different from the mean of the two homozygotes when carcass weight was fitted as a covariate. In this case, NC was similar to NN for shear force.

The greater longissimus shear force of CN and CC relative to NN is supported by data collected on quantity and activity of calpastatin. Calpain-mediated postmortem tenderization of longissimus fibers via proteolysis would be inhibited by increased calpastatin activity. Previous research had shown no detrimental effect of the *callipyge* phenotype on either m- or μ -calpain enzyme activity at death (Koohmaraie et al., 1995). Levels of calpastatin activity at d 0 and 7 postmortem were greatest for CN at all ages (Table 2). The difference between CN and NN for calpastatin activity at d 7 postmortem (2.8 U/g muscle) is slightly larger than the difference (1.9 U/g muscle) reported by Koohmaraie et al. (1995). Measurements of calpastatin activity of NC and CC were lower than CN, but higher than NN. Similar to shear force, calpastatin showed a slight general trend of decreased activity as slaughter age increased from 161 d to 266 d and as carcass weight increased (Tables 2 and 3). In contrast to shear force data, however, calpastatin activity of NC was similar to CC, rather than NN. Genotypic effects on shear force are not entirely consistent with the magnitude of the effects on calpastatin activity (Figure 2).

The relationship between shear force and calpastatin was characterized by a different measurement in yr 2 of the experiment. Levels of a 130 kDa skeletal muscle calpastatin protein were quantified in the 1995-born lambs with an indirect antibody ELISA

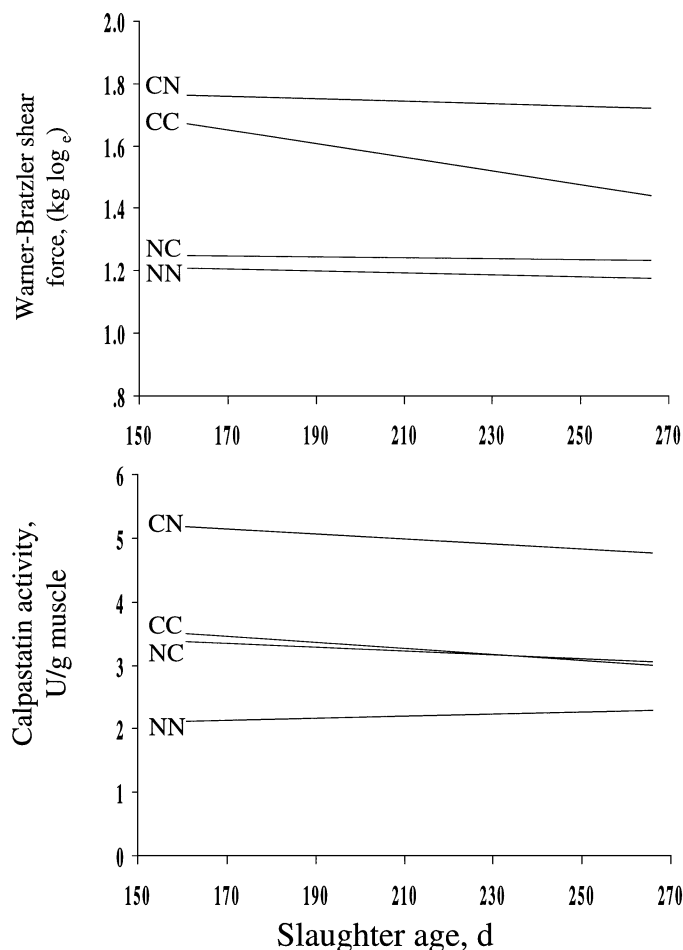


Figure 2. Genotype-specific relationships with slaughter age for Warner-Bratzler shear force (14 d postmortem) and calpastatin activity (7 d postmortem) of longissimus.

(Doumit et al., 1996). Calpastatin protein levels of longissimus were substantially higher in CN at d 0 postmortem (Tables 2 and 3). Small, but consistently negative trends were observed for ELISA calpastatin as slaughter age and carcass weight increased. Levels of calpastatin protein measured by ELISA for CC and NC were numerically intermediate to CN and NN, but not statistically different from NN. As with 1994 data, genotypic effects on ELISA calpastatin are not consistent with effects on shear force.

The significant difference between *CLPG* homozygous genotypes for shear force warrants further investigation into the biological basis of why shear force differences were detected without associated differences in muscle hypertrophy. It would be informative to examine the variability between the four *CLPG* genotypes in prerigor tenderness (Wheeler and Koohmaraie, 1994) to determine whether effects on shear force can be explained to some extent before the delayed postmortem proteolysis. This research indicates the potential complexity of traits that may

contribute to genetic and nongenetic differences in meat tenderness.

Amount of intramuscular fat evaluated by subjective assignment of marbling score was lowest in CN. Typical increases at later ages for this fat depot were not apparent for CN lambs because the difference between genotypic groups became greater over time. This trend is clearly represented by the differences among genotypes in linear regression coefficients on slaughter age (Table 2). The mean value for marbling score in CN lambs did not exceed the "Slight" category (300 = Slight 00) at any age. In comparison, the other genotypes increased from the "Slight" category at the initial slaughter groups to the "Small" category (400 = Small 00) at the last slaughter group. Deposition of intramuscular fat in CN was substantially delayed, consistent with reported decreased deposition of carcass fat. Previous studies also reported significant reductions in marbling of longissimus of *callipyge* phenotype lambs (Koohmaraie et al., 1995; Jackson et al., 1997). Intramuscular fat has been shown to have a small, positive effect on shear force, flavor, and juiciness of beef longissimus (Wheeler et al., 1994), and it could have a small effect on tenderness, flavor, and juiciness of lamb chops.

Improving Tenderness of *Callipyge* Lamb

Several postmortem treatment technologies have been evaluated to reduce the detrimental effect of CN on longissimus tenderness (Solomon et al., 1995; Duckett et al., 1998; Koohmaraie et al., 1998). These treatments can reduce the antagonism with tenderness, but are costly, and not readily implemented with a traditional fresh-lamb market system. An alternative approach, which has not been investigated, would involve long-term selection for tenderness within terminal sire populations fixed for the C allele. Progeny testing a large number of CC sires may identify individuals that consistently produce CN offspring with values on the lower portion of the shear force distribution. The current study is not designed to estimate genetic (co)variances. However, indication of genetic variance for shear force within *CLPG* genotypes would be of value. The effect of sires (of the F₂ generation) was treated as a fixed effect in the current analysis; it was a significant source of shear force variation in 1995, but it was not significant in 1994 (slaughter age as a covariate). After accounting for effects of year, sex, sires, *CLPG* genotypes, and slaughter age, the residual phenotypic correlation of lean accretion rate (fat-free lean adjusted to a constant age) with shear force was .18 ($P < .001$). The genetic (co)variances of this antagonistic phenotypic correlation need to be estimated to evaluate the potential impact of selection for improved tenderness.

Differences between Dorset and Romanov breed-specific alleles at independently segregating loci can be investigated in this population. Discovery of such

loci would allow selection efforts to reduce the antagonism with shear force. Genetic maps to draw direct comparisons between the bovine and ovine genomes have evolved dramatically in recent years (Kappes et al., 1997; de Gortari et al., 1998). Genomic regions affecting tenderness are being identified in bovine populations (Keele et al., 1999). Investigation of allelic variation at the homologous regions of the ovine genome would seem to be logical targets for study. It is reasonable that a genome scan within this experimental population could identify regions of the genome that modify the impact of *CLPG* on tenderness. The heritability of shear force has been estimated as .3 to .5 in beef cattle (Koch et al., 1982; Shackelford et al., 1994). This moderate heritability and identification of putative loci from genome scans targeting meat tenderness would suggest that there are several loci potentially contributing to the genetic regulation of meat tenderness in bovinds that may be exploited by selection.

Implications

Increased shear force values from longissimus must be addressed if the advantages of *callipyge* lambs for lean growth rate, muscle shape, and carcass composition are to be realized. Unique forms of gene action were detected for various meat quality traits; these findings contrast previous research that described the association of genotypes with the *callipyge* phenotypes. Greater means and variances for shear force were associated with CC and CN genotypes. This large variation may provide an opportunity for long-term selection schemes to improve tenderness. Identification of the genetic and biochemical pathways by which the *CLPG* locus is influencing accretion of muscle protein and chemical fat, as well as altering longissimus shear force, would provide valuable knowledge to improve understanding of muscle biology and meat tenderness irrespective of species.

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