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Relationship of molecular breeding value for beef tenderness with heifer traits through weaning of their first calf[☆]

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ABSTRACT

Polymorphisms in μ-calpain (*CAPN1*) that beneficially associate with beef tenderness are reported to antagonistically associate with calving day in beef heifers and post-partum interval to estrus in beef cows. We, therefore, hypothesized that a molecular breeding value for slice shear force, calculated based on *CAPN1* and calpastatin (*CAST*) genotypes, would demonstrate an antagonistic relationship between genomically predicted slice shear force and ordinal calving date in replacement beef heifers. A secondary objective of this study was to evaluate the association of a polymorphism in diacylglycerol O-acyl-transferase (*DGAT1*) with reproductive traits in beef heifers. One hundred eighty-seven MARC III heifers (¼ Angus, ¼ Hereford, ¼ Red Poll, and ¼ Pinzgauer) that had been selectively bred to increase the frequency of these polymorphisms were submitted for monthly ultrasound exams beginning at 333 d of age and continuing until the start of breeding to determine pubertal status. At the last exam before breeding, all antral follicles were counted, and the length and height of each ovary was measured to determine if genomic selection for slice shear force associated with ovarian follicle number. Calving date, calf gender, and calf birth weight were recorded at parturition. Regression analysis of the molecular breeding value for slice shear force of the heifers on ordinal calving date indicated no association between genomic prediction of tenderness and calving date (P = 0.16); however, there was a tendency for age at puberty to be delayed in heifers as genetic merit for tenderness improved (P = 0.09). The results of the present study indicate that within experimental precision, selecting for tenderness using genomic predictions had minimal or no antagonistic association with reproductive performance in heifers. Further analysis of reproductive performance as cows is needed within this population but applying these genetic markers to select for tenderness in steers does not antagonize reproductive traits influencing conception or first calf birth date and birth weight in replacement beef heifers.

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1. Introduction

Selection for meat tenderness in beef cattle may have off-target impacts on female reproduction. Genetic correlation estimates for carcass traits and female reproduction, based on measurements and pedigree, have been near zero [1]. Currently, genetic evaluations for many carcass traits depend increasingly on genetic markers in addition to carcass measurements. Because some of the genes used as markers for carcass traits also have been reported to have roles in uterine function and pregnancy [2], the relationships of marker-based genetic evaluations of carcass traits with reproductive traits may be different than those based solely on carcass measurements.

Polymorphisms in μ-calpain (*CAPN1*) were associated with slice shear force in steers from cattle populations at the U.S. Meat Animal Research Center [3,4]. In other studies, alleles of *CAPN1* that associated with tenderness also associated with increased post-partum interval to estrus in beef cows [5], indicating that using the marker to increase tenderness might delay re-breeding in the cow herd. Similarly, our laboratory reported a potential antagonistic relationship between two specific *CAPN1* haplotypes associated with slice shear force in Angus steers and ordinal calving date of the first calf in their half-sisters [6]. We, therefore, believed the common *CAPN1* haplotypes required further investigation to validate this potential antagonistic association between tenderness markers and calving day in beef heifers.

Polymorphisms in calpastatin (*CAST*) [3,7] were also associated with slice shear force in populations of steers at the U.S. Meat Animal Research Center. Additionally, polymorphisms in *CAST* were associated with fertility and reproductive longevity in Holstein cows [8,9]; however, a polymorphism in *CAST* was not associated with fertility traits in Angus heifers at the U.S. Meat Animal Research Center [6]. The current experiment was designed to test the hypothesis that a molecular breeding value for slice shear force, calculated based on *CAPN1* and *CAST* genotypes, would demonstrate an antagonistic relationship directly between genomically predicted slice shear force and ordinal calving date in heifers. We further applied these data to survey the association of a polymorphism in diacylglycerol O-acyltransferase (*DGAT1*) on reproductive traits in beef heifers, because a polymorphism in this gene also has been reported to associate with days open in Holstein cows [9], and the selection process for the heifers in the present study increased the frequency of a DGAT1 minor allele.

2. Materials and methods

2.1. Heifer population

All animal procedures were approved by the U.S. Meat Animal Research Center (USMARC) Institutional Animal Care and Use Committee. A composite population of MARC III heifers (¼ Angus, ¼ Hereford, ¼ Red Poll, and ¼ Pinzgauer) was used in this experiment as described by Tait et al. [3]. Starting with mating in 2005, the population was selected to change frequencies of a haplotype in *CAPN1* based on two single nucleotide polymorphisms (SNP), a SNP in its inhibitor *CAST*, and a SNP pair dinucleotide variant in *DGAT1*. The haplotype for CAPN1 is defined by the combinations of SNP 316 alleles C and G [rs17872000]; [10] and SNP 4751 alleles C and T [rs17872050]; [11] forming the common (higher frequency) haplotypes CAPN1hCC, CAPN1hGC, and CAPN1hGT. Haplotype CT occurs at very low frequency. The *CAST* minor allele C [CASTaC; rs109221039]; [12] was considerably less frequent than CASTaT. The dinucleotide substitution in *DGAT1* [rs109234250 and rs109326954]; [13] results in a lysine AA allele (DGAT1aK) with lower frequency or an alanine AA allele (DGAT1aA). Samples of

blood were collected in 10 mL syringes with 4 % EDTA and frozen until DNA was extracted using a Qiagen QIAmp DNA mini blood kit (Qiagen, Valencia, CA). Genotypes were obtained using a MassArray system (Sequenom, Inc., San Diego, CA) as described by Stone et al. [14]. Selection goals were to equalize frequencies of the three common *CAPN1* haplotypes at 0.33 and to increase minor allele frequencies for *CAST* and *DGAT1* to improve statistical power of estimating genetic marker and breeding value associations [3].

An evaluation phase was conducted with calves born in 2010, 2011, and 2012. Steers and heifers were measured for pre-weaning traits while only steers were measured for growth in the feedlot, carcass, and meat traits. Estimates of marker effects for pre-weaning, steer growth, carcass, and meat traits were reported by Tait et al. [3]. Sires were chosen for heterozygosity for as many of the three genes as possible during the evaluation phase. These sires could potentially produce calves with any possible genotype combination except homozygotes of the *CAPN1* haplotype not in the sire's heterozygous *CAPN1* genotype. Statistical power was increased by comparing many genetic combinations within sire. About 63% of heifers born could be retained for evaluation and breeding each year. Retention was based on birth as a single, survival past weaning when blood was sampled for genotyping and successful genotyping of SNP. Heifers with over-represented genotypes were reduced by random culling within sire. Retained heifers (n = 187) were progeny of 24 sires and 151 dams. Table 1 shows the distribution of genotypes of retained heifers. Retained heifers were contemporary herd mates and half-sibs of the evaluation phase steers that were used to calculate the molecular breeding value for slice shear force described below (section 2.4).

2.2. Heifer development

After weaning, heifers were moved to the USMARC feedlot. Half were assigned to a standard heifer replacement diet and the other half to a stair-step development diet [15—17]. Heifers in the standard diet were fed for constant gain between weaning and breeding to attain approximately 65% of mature weight by breeding. Heifers assigned to the standard and stair-step diets were balanced across genotypes and sires. Data from this and three other populations were combined to evaluate diet effects [18].

Table 1
Frequencies of CAPN1, CAST, and DGAT1 genotypes of heifers (n = 187) evaluated for reproductive traits.

Genotypes	No.	%
CAPN1[a]		
CAPN1hCC:CAPN1hCC	19	10.2
CAPN1hCC:CAPN1hGC	43	23.0
CAPN1hCC:CAPN1hGT	33	17.7
CAPN1hGC:CAPN1hGC	20	10.7
CAPN1hGC:CAPN1hGT	46	24.6
CAPN1hGT:CAPN1hGT	26	13.6
CAST[b]		
CASTaC:CASTaC	32	17.1
CASTaC:CASTaT	97	51.9
CASTaT:CASTaT	58	31.0
DGAT1[c]		
DGAT1aA:DGAT1aA	70	37.4
DGAT1aA:DGAT1aK	87	46.5
DGAT1aK:DGAT1aK	30	16.0

[a] Diplotypes composed of the 3 most common haplotypes of 2 ordered SNP in *CAPN1* (316C or G; 4751 C or T), e.g., CAPN1hCC:CAPN1hGT is the genotype formed by haplotypes CC and GT.
[b] Genotypes composed of the 2 SNP alleles in *CAST* (CASTaC and CASTaT).
[c] Genotypes composed of the Alanine (A) and Lysine (K) coding alleles in *DGAT1*.

2.3. Reproductive management of heifers

Pubertal status of the heifers was determined by a series of three transrectal ultrasonographic examinations of the ovaries [6,19]. At an average of about 11-months of age, all heifers were weighed and submitted for ultrasonographic examination. The number and location of corpora lutea were recorded to determine pubertal status. Those that did not have a CL at 11-months of age were examined again at an average of about 12-months of age. Following weighing at 13-months of age, all heifers were submitted for ultrasonographic evaluation of the ovaries during which visible antral follicles were counted, the location of CL was recorded, and a cross-sectional image of each ovary was measured for length and height [19,20]. Average palpation ages were 322, 364, and 405 d for heifers born in 2010; 331, 373, and 394 d for 2011; and 346, 372, and 403 d for 2012. The puberty status value analyzed was based on when puberty was first detected: 1, 2, or 3 for the first, second, or third palpation or 4 if puberty was not detected at any of the palpations.

Breeding of heifers began at an average age of 13.7 mo and was 13—20 d after the last ultrasonographic reproductive tract evaluation. Heifers born in 2010 were bred to 15 bulls by AI for 21 d and then divided in two breeding pastures with a single bull in each pasture for 42 d. Personnel assigning heifers to AI bulls and pastures did not have access to genotypes. Heifers born in 2011 and 2012 were bred by natural service for 63 d in a single pasture with four bulls and three bulls, respectively. Approximately 50 d after removal of the bulls, heifers were evaluated for pregnancy by transrectal ultrasonography. Hip height, body weight and body condition score (9-point scale; 1 = emaciated, 9 = obese) were collected at pregnancy evaluation (18 months, Table 2) and before first calving season (23 months, Table 2). Calving date, calf sex, and calf birth weight were recorded in the USMARC database at the time of tagging. At weaning, the weaning weight of the calf was added to the USMARC database.

2.4. Molecular breeding value calculation and regression analysis

A regression analysis was performed to estimate the effects of selection to reduce slice shear force (SSF) or increase number of *DGAT1* K alleles on heifer traits. A molecular breeding value for SSF (MBVSSF) was calculated using SSF estimates for *CAST* and *CAPN1* from steer herd mates [3] and each heifer's genotypes for *CAST* and *CAPN1*. Values for MBVSSF averaged 2.81 kg (0.0—4.11 kg) with lower values associated with tender meat (Fig. 1) and number of K alleles for *DGAT1* (0, 1, or 2).

Key dependent variables are presented in Table 2. Dependent variables for the heifers were pubertal status, antral follicle count, ovarian length (the average of the two ovaries within a heifer), ovarian height (the average of the two ovaries within a heifer), body weights at key management points, and hip heights at those same management times. Dependent variables for the first calf included calving date, calf birth weight, and calf weaning weight. Statistical models were fitted using the GLIMMIX procedure in SAS (Cary, NC). The basic statistical model for traits included fixed effects of three birth years, four ages of dams of the heifers (2, 3, 4, or 5 years and older), two heifer development diets, and a regression coefficient for age at measurement when appropriate. Age of dam of the heifer was included in the model because in previous studies age of the dam has influenced reproductive performance of heifers [21,22]. Sire of the heifer was included as a random effect. Fixed regression coefficients for MBVSSF and DGAT1aK were both added to the model. Analyses for continuous traits were considered normally distributed. Percentage traits were considered to have a binary distribution and analyzed with logit link. The four categories of puberty determination were considered an ordered multinomial distribution and analyzed with a cumulative probit link.

Table 2
Means, unadjusted SD, and ranges for traits and ages.

Item	No.	Mean	SD	Min	Max
Birth date, ordinal	187	104.0	19.0	66.0	157.0
12-mo ave. BW[a], kg	187	325.0	42.0	211.0	417.0
18-mo BW, kg	187	389.0	35.0	294.0	501.0
18-mo height, cm	187	123.2	3.5	112.0	132.0
18-mo condition score	187	5.5	0.6	4.0	7.0
23-mo BW, kg	166	430.0	40.0	305.0	528.0
23-mo height, cm	166	126.8	3.9	116.0	137.0
23-mo condition score	166	5.5	0.6	4.0	7.0
Age 1st palpation[b], d	187	333.0	21.0	273.0	371.0
Total follicles, no.	187	21.7	8.4	7.0	46.0
Ovarian length, mm[c]	187	26.8	4.0	13.0	36.0
Ovarian height, mm[c]	187	13.9	2.2	5.0	19.0
Calf birth date, ordinal	162	89.0	16.0	59.0	134.0
Calf birth BW, kg	162	33.4	4.4	17.0	46.0
Calf weaning age, d	152	174.0	17.0	127.0	207.0
Calf weaning BW, kg	152	183.0	26.0	121.0	248.0

[a] Average of 4 wt (average ages of 337, 359, 380, and 400 d) spanning the 3 palpation dates for puberty.

[b] Heifers were palpated to determine puberty on 3 dates each year. All were palpated on the 1st and 3rd dates. Those not pubertal on the first date were also palpated on the 2nd date.

[c] Average length and average height of the two ovaries within a heifer.

3. Results

Descriptive statistics for the traits evaluated are presented in Table 2. Contrary to the hypothesis, regression of the MBVSSF on heifer performance traits did not identify a relationship between genetic merit for tenderness and heifer ordinal calving date (Table 3). There was a tendency for age at puberty to be delayed as genetic merit for tenderness improved (P = 0.09; Table 3 and Fig. 2). There was no association of MBVSSF with antral follicle count or average size of the ovaries (Table 3).

As number of K alleles for *DGAT1* increased, first calf birth weight increased (P = 0.04; Table 3) and calving day tended (P = 0.08) to increase. There was no association of number of *DGAT1* K alleles with antral follicle count (Table 3); however, there was a small but significant genetic association of the number of K alleles for *DGAT1* with height of the ovary (P = 0.01) measured on the ultrasound screen, such that height of the ovary increased as the number of K alleles increased. Hip height at 23 months of age also increased as the number of K alleles for *DGAT1* increased (P = 0.04).
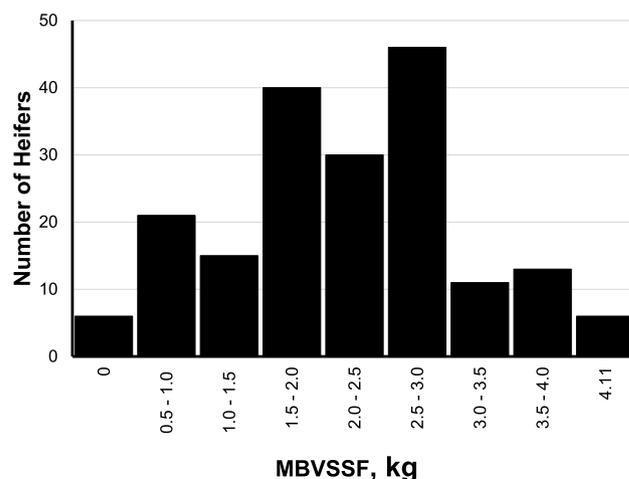

Fig. 1. Distribution of heifers within MBVSSF based on *CAPN1* and *CAST* genotypes.

4. Discussion

The novel aspect of the current study is using molecular breeding value for slice shear force instead of component genotypes to test the hypothesis that genomic selection for beef tenderness would increase ordinal calving date in beef heifers. Combining CAPN1 and CAST into a single breeding value is a more holistic approach to evaluating antagonisms with application of genomic selection for beef tenderness. Because these were replacement heifers not destined for the abattoir, this provided a method to further validate the potential antagonism observed in our previous study for two haplotypes of CAPN1 (Tait) in a different population of heifers. Based on our previous study, we believed that ordinal calving date in heifers might be delayed as genetic merit for tenderness improved [6]; however, the results of the current study did not support this hypothesis. Because previous studies have demonstrated a beneficial relationship between the number of antral follicles detectable by ultrasonography at a pre-breeding exam and calving day in heifers [19,23], we investigated the relationship between MBVSSF and antral follicle count. There was no change in antral follicle count across the range of the MBVSSF. Differences in the association of *CAPN1* on ordinal calving date between this study in MARC III composites and our previous study in Angus [6] could be due to population differences or the use of combined breeding value *vs.* CAPN1 haplotypes and CAST genotypes.

Age at puberty tended to be delayed in heifers that were predicted to have greater tenderness using the MBVSSF. While only a tendency, this is supportive of the previously observed delay in calving day in USMARC Angus heifers having the *CAPN1* allele that associated with tenderness [6] and the increased post-partum interval in cows having the *CAPN1* allele that associated with
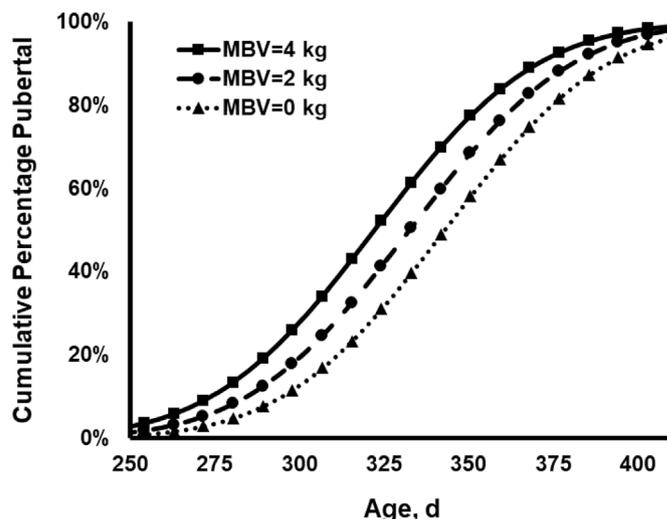

Fig. 2. Predicted percentage of pubertal heifers between 250 and 400 d of age based on molecular breeding value for slice shear force. There was a tendency (P = 0.09) for puberty to be delayed as genetic merit for slice shear force improved.

tenderness [5]. Breed differences across the three studies may explain differences in intensity and form of the phenotype observed. It is, however, unlikely that the degree of these antagonisms is enough to seriously impede reproductive efficiency in the heifer or the cow.

A recent study reported no association of the *DGAT1* polymorphism with reproductive traits in Japanese Black (Wagyu) cows [24]. Overall, the results of the present study would agree with that conclusion, although there was a tendency for calving day to be delayed by an increase in the number of K alleles for *DGAT1*. An interesting result of the present study was an association of number of *DGAT1* K alleles with height of the ovary measured on the ultrasound screen at the pre-breeding exam. To our knowledge, there are no published roles of *DGAT1* in ovarian development or function. This could be a false positive because a difference of 0.5 mm is almost definitely beyond the sensitivity of the calipers. Furthermore, there is no reason to think that a difference in ovarian height, if real, influences reproductive performance in beef heifers in any way. Additional verification and investigation of the biological implications of this association are warranted before any conclusions can be drawn from these results.

The identification of the association of the number of K alleles for *DGAT1* with hip height at 23 months of age is also novel to the current study and will require further validation. While *DGAT1* is well-known for its role in triglyceride synthesis, it also has been demonstrated to have a role in bone development and bone health [25]. Thus, the increasing hip height as cows approach maturity suggests the possibility that *DGAT1* may affect closure of the bone growth plates, although it is intriguing that this difference in long bone growth was not observed earlier in life. This may be because at a younger age, the influence of *DGAT1* on bone development is reduced compared to genes with a greater role in bone development. Bone health is important for structural soundness and longevity. Selection for this marker could, therefore, help improve longevity in the cow herd and decrease replacement costs.

Finally, there was an association between maternal *DGAT1* genotype and first calf birth weight. Given the role of *DGAT1* in metabolic processes, the most likely mechanism would be a change in nutrient partitioning that allows for greater nutrient supply to the developing fetus, but this, also, is a previously unrecognized effect of *DGAT1* that will require further investigation before we can

Table 3
Estimated regression coefficients for molecular breeding value for slice shear force (MBVSSF) and number of K alleles for DGAT1.

Trait	MBVSSF			No. of K Alleles of *DGAT1*		
	Estimate	SE	P	Estimate	SE	P-value
12-mo ave. weight[a], kg	1.0	2.0	0.63	3.6	2.7	0.18
18-mo weight, kg	1.9	2.3	0.42	3.9	3.1	0.22
18-mo height, cm	−0.03	0.25	0.63	0.5	0.3	0.16
18-mo condition score	0.02	0.04	0.63	0.1	0.1	0.37
23-mo weight, kg	3.8	2.6	0.15	4.4	3.4	0.19
23-mo height, cm	0.1	0.3	0.65	0.8	0.4	0.04
23-mo condition score	0.0	0.1	0.87	−0.0	0.1	0.92
Puberty age, d	−3.7	2.2	0.09	−3.5	2.9	0.23
Puberty detection value[b]	−0.1	0.1	0.13	−0.1	0.1	0.21
Total follicles	0.7	0.7	0.25	1.3	0.9	0.13
Ovarian length[c], mm	0.5	0.3	0.07	0.4	0.4	0.28
Ovarian height[c], mm	−0.0	0.2	0.88	0.5	0.2	0.01
Calving day[d], ordinal	−1.9	1.3	0.16	3.1	1.8	0.08
Calf birth weight[d], kg	−0.3	0.4	0.34	1.0	0.5	0.04
Calf weaning weight[d], kg	−0.2	1.6	0.90	0.1	1.9	0.94
Pregnant at 18-mo[e], %	3.2	2.4	0.20	2.4	3.3	0.47
Pregnant at calving[e], %	4.3	2.6	0.11	3.0	3.6	0.39
Weaned a calf[e], %	4.8	3.0	0.12	4.0	4.1	0.33

[a] Average of 4 wt (average ages of 337, 359, 380, and 400 d) spanning the 3 palpation dates for puberty.
[b] Values were based on which of 3 palpation dates puberty was first detected. Estimates and SE are from analysis using an identity link and P-values are from analysis using cumulative probit link. Negative values indicate numerically earlier puberty detection associated with increased MBVSSF and number of K alleles for *DGAT1*.
[c] Average length and average height of the two ovaries within a heifer.
[d] Regression calf's birth date, birth weight, and weaning weight on heifer dam's MBVSSF and number of K alleles for *DGAT1*.
[e] Percentage of heifers at breeding. Estimates and SE are from analysis using an identity link and P values are from analysis using a logit link.

be sure that we can use this marker to select for calf birth weight in beef cows.

5. Conclusion

The results of the present study indicate that within experimental precision, selecting for more tender MBVSSF had minimal or no antagonistic influence on reproductive performance in heifers. Cow-calf producers should be able to use these genetic markers to improve tenderness within their herd without negatively impacting reproductive function of replacement heifers.

Author credit statement

Experimental Design: Cushman, Bennett, Smith, Casas, Heifer Management and Ultrasound Data Collection: Cushman, McNeel, Freetly, Genotyping and genetic selection: Bennett, Smith, Casas, Data analysis: Bennett, Tait, Manuscript preparation: Cushman, Bennett, Tait, McNeel, Smith, Casas, Freetly.

Declaration of competing interest

The authors have no conflicts of interest to report.

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