Marker Assisted Selection-Tenderness and Marbling

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Introduction:

Marker assisted selection (MAS) is a process that enables the accurate selection of specific segments of DNA that are associated with a measurable difference or effect on a complex trait, like weaning weight or marbling score. MAS can be an effective way to increase or decrease the frequency of specific DNA sequences in a population. It is important to note that many genes control complex traits, like marbling or tenderness; they are polygenic in nature. Markers for specific variations in DNA sequences are available for only a few genes that contribute to marbling or tenderness. There are many other 'unmarked' and unknown genes, as well as the production environment, that affect the observed phenotypes for these traits. Therefore, MAS selection will only account for a portion of the genetic variation. Measures of net genetic merit for a trait, such as Expected Progeny Differences (EPD) should be considered when making selection decisions even when marker information is available. EPD provide an estimate of the overall (net) merit of the genes an animal has for a trait including the 'marked' and 'unmarked' genes. MAS should be seen as an additional method of selection, but not a replacement of proven selection tools like EPD.

Several of the following sections provide background information on DNA and DNA markers. If you are already familiar with these concepts you may skip ahead to the section labeled 'Benefits of Marker Assisted Selection.'

What is a DNA marker?

All living organisms are made up of cells. Within most cells, there is a nucleus that contains several large molecules called **deoxyribonucleic acid (DNA).** DNA is the material that carries genetic instructions, is transmitted from one generation to the next, and determines the differences in many of the physical characteristics of individuals and species. Each large DNA molecule, which is sometimes packaged in a tightly wound coil, is called a **chromosome**. Chromosomes come in pairs, one inherited from each parent. Cattle have 30 pairs of chromosomes. Collectively, all the pairs of chromosomes are called the **genome**. Every cell nucleus contains a copy of all the chromosomes. Therefore, each nucleated cell contains the complete genome of the animal.

DNA is a large double helix molecule that looks like a twisted ladder (see figure below). Each rung of this ladder is composed of a pair of **nucleotides**. The pairs are 'A' with 'C', and 'G' with 'T'. These pairs are strung together in a long sequence that codes for specific **amino acids**. Amino acids are linked together to form larger molecules called **proteins**. A sequence of DNA that codes for all the amino acids that makes up a single

protein is called a **gene**. There are thousands of proteins in the body, which are coded for by thousands of genes. It is the interaction and structure of these proteins that determines the appearance or **phenotype** of individual. The term **genotype** refers to the genetic sequence of an individual for a particular marker or gene.

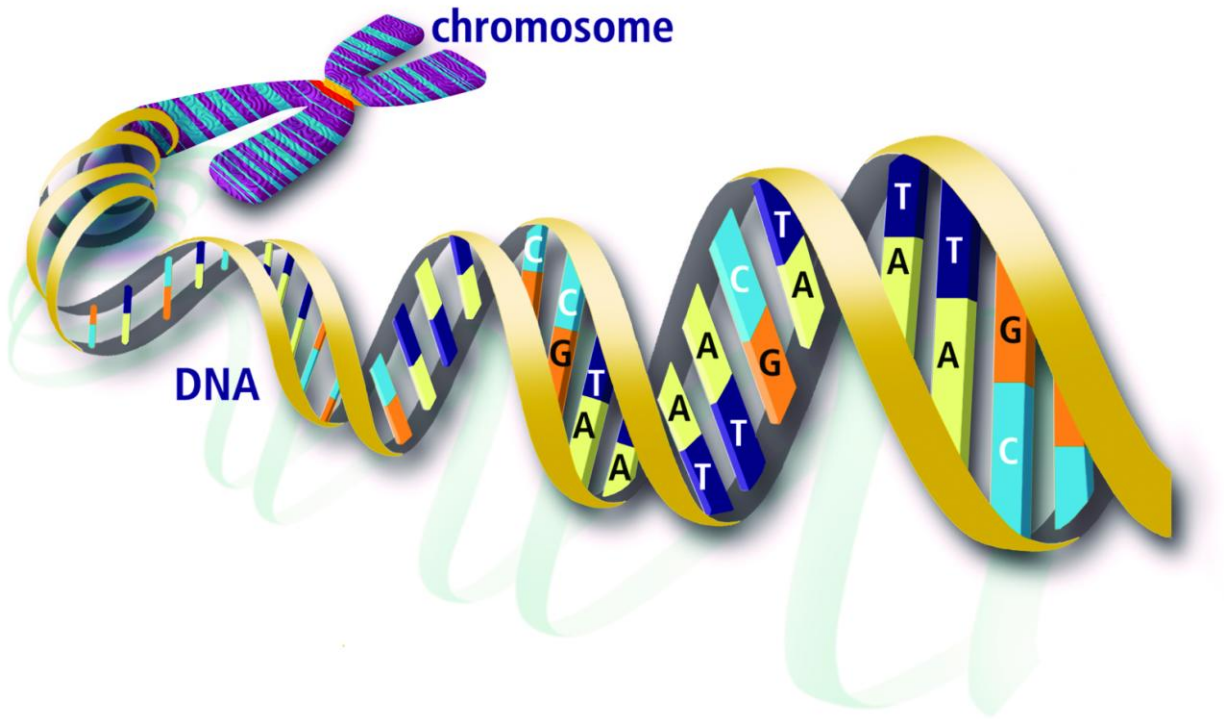

Image Credit: U.S. Department of Energy Human Genome Program, http://www.ornl.gov/hgmis.

The sequence of DNA can vary from one individual to another. In fact, the sequence of DNA for a gene on one chromosome can be different than the sequence for the gene on the other chromosome in the pair. These genetic variants of a gene are called **alleles**. The variation in their sequence may change the amino acid sequence for which they code and can result in a change in the structure of the protein they encode. Alternately, the variation may result in production of different quantities of the protein (**expression**). Differences in either the protein structure or the level of expression can have an effect on phenotype.

Each individual receives one-half of its genetic make up from their father (sire) and one-half from their mother (dam). So, one-half of the chromosomes in a cell are from the sire and one-half from the dam. If the DNA sequence for a specific gene is the same on each chromosome in the pair, then the individual is said to be **homozygous**. If the DNA sequences are different for the gene, that is, there is a variation, then the individual is said to be **heterozygous**.

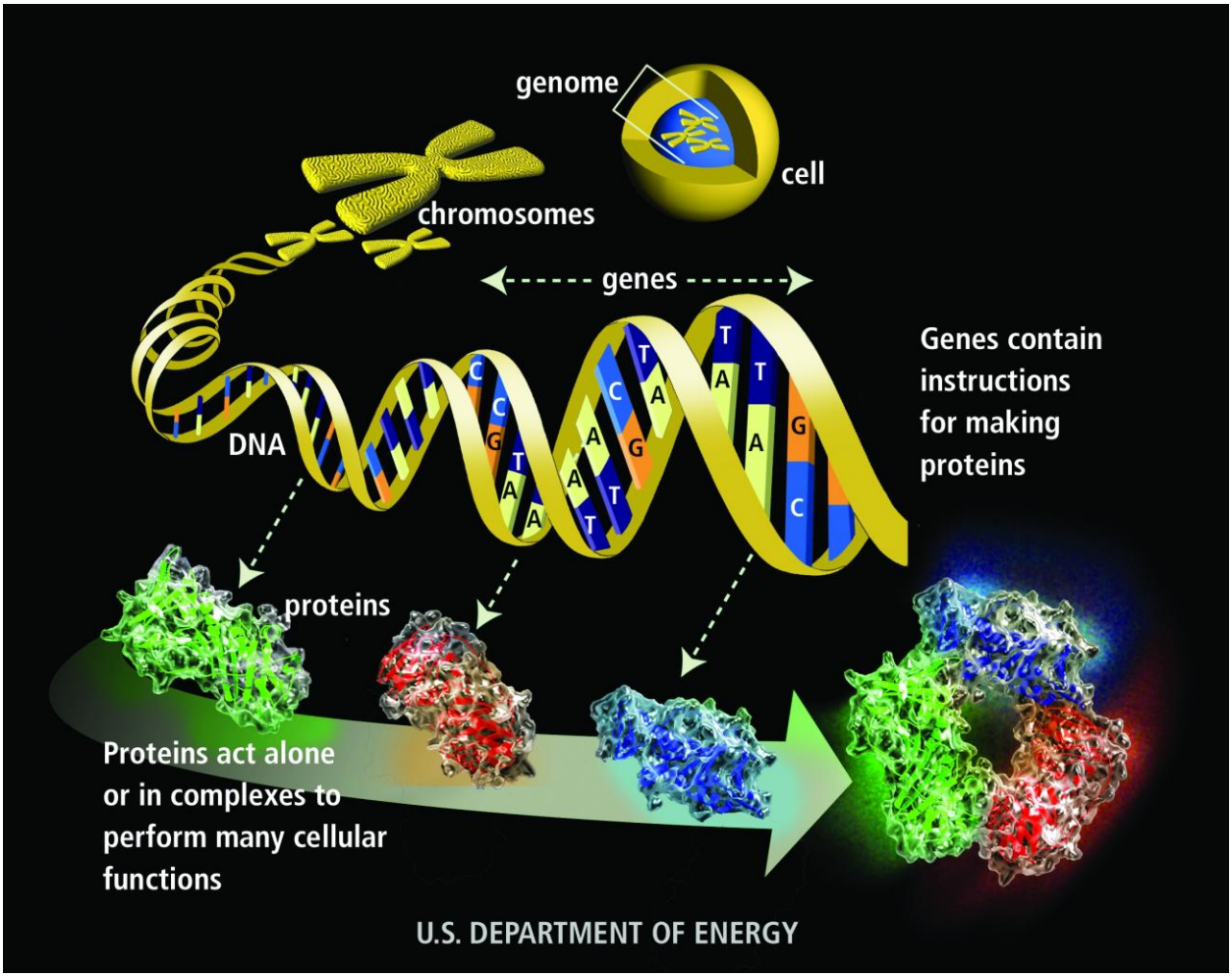

Image Credit: U.S. Department of Energy Human Genome Program, http://www.ornl.gov/hgmis.

Not all DNA is made up of genes. There are large pieces of DNA whose purpose is unknown. Some DNA helps regulate the expression of other genes. A genes coding sequence may be broken into several sections. The term **locus** can be used to describe a specific sequence of DNA within or outside of gene coding sequence.

Marker Basics:

A DNA marker is simply a sequence of nucleotides that uniquely identifies a location of in the genome. This location can be in a gene or nearby a gene and used to identify a specific allele. Mutations, or changes in the coding sequence of a gene, can be used as DNA markers. These mutations may or may not cause a change in the protein product. Variation nearby a gene can also be used as a DNA marker.

The two main classes of markers used to identify different alleles in beef cattle are **microsatellite markers** and **single nucleotide polymorphisms** (SNPs, pronounced *snips*). Microsatellite markers are di-nucleotide repeats where the count of the number of pairs of nucleotides varies. Microsatellites are in the non-coding sequences of DNA and are used to identify alleles of a **quantitative trait loci (QTL)** via association

between the markers and phenotype. A QTL is simply an area of the genome that is likely to harbor a gene that influences a quantitative trait and for which a set of markers can be used to track inheritance of the various alleles of the gene. SNPs are single base pair variations in the DNA coding sequence. SNPs used as DNA markers may be the causative mutation that results in an alternate form of the protein, it may be in the coding sequence but not cause a change in amino acid sequence, or may be nearby a gene in the non-coding sequence of DNA. Microsattelites or SNP marker panels may be used to identify or validate parentage of individuals.

DNA markers can be used to track the inheritance of simple traits controlled by a single gene or complex traits controlled by many genes. Examples of simple traits include coat color, horn status, and some genetic diseases; complex traits include traits like weaning weight, tenderness and marbling which are controlled by many genes. DNA markers simply identify a sequence of DNA just as ear tags identify individual calves.

Benefits of Marker Assisted Selection:

Marker assisted selection can be used to increase the frequency of desirable forms of a gene within a population by selection of parent stock that carry the gene. Selection of parents that are homozygotes for the desired allele ensures that all gametes (sperm or egg cells) produced by that parent have the desired allele. Of course, to use MAS, markers must be available for the trait and alleles of interest. The potential benefits of MAS are greatest for traits that (Van Eenennaam, 2005; Dekkers, 2003):

1. have low heritability (traits with observed or measured values that are poor indicators of breeding value),
2. are difficult and/or expensive to measure (disease resistance),
3. cannot be measured until later in life potentially after the animal has reproduced (carcass or maternal traits),
4. are not routinely measured or selected for currently (tenderness), and
5. are genetically correlated with another trait you do not want to change. (e.g. At the polygenic level the traits may be positively correlated, but selection for a marker of a gene for marbling that is not associated with increases carcass fatness might be desirable. This would entail selection for marbling genes without pleitropic effects on fatness.)

The expected benefits of changing allele frequencies and the resulting changes in phenotype vary depending on the type of trait. The following categories are ordered from greatest to least expected benefit from MAS (Van Eenennaam, 2005):

1. simply inherited traits (coat color, horn status, genetic defects),
2. carcass quality and palatability attributes,
3. fertility and reproductive efficiency,
4. carcass quantity and yield,
5. milk production and maternal ability, and
6. growth trait performance.

The ranking above follows from a number of considerations including the relative difficulty of measuring and recording performance data, the amount of genetic and phenotypic variation in trait and their proportion (heritability), the age at which performance records are collected on the animal, and how much performance data is currently available.

The traits of carcass marbling and tenderness are likely to benefit from MAS due to a number of reasons. Although both traits have moderate levels of heritability, data collection of both measures is relatively difficult to obtain. In fact, collection of Warner-Bratzler Shear force data is especially challenging due to the costs of obtaining large numbers of steak samples from sire identified animals and then obtaining shear force values from qualified labs. Obviously, the animals from which these observations are obtained are not able to reproduce, thus, selection focuses on the sires of animals with desirable characteristics. Bulls with carcass trait and tenderness evaluations are typically 4-5 years of age and have sired a number of progeny. The ability to select young sires with desirable genetics would minimize progeny test costs and focus data collection efforts on bulls with desirable genotypes.

Limitations/Challenges of Marker Assisted Selection for Marbling and Tenderness:

Selection based on marker information for a single gene with the exclusion of other sources of genetic information such as EPD will yield poor results for overall improvement in a trait. Ignoring information about the net merit of an animal's genotype via phenotypicly derived genetic predictors such as EPD is discouraged. Both marbling and tenderness are complex traits controlled by many genes, with only a few genes that have useful markers associated with them. More response to selection will be obtained if both MAS and EPD are used. EPD should, however, be the primary driver in selection decisions, with marker data playing a secondary role for selection of specific known alleles.

To date, markers for only a few genes affecting marbling and tenderness are available. These markers account for a relative small amount of the genetic variation and a smaller portion of phenotypic variation for the traits. It remains to be seen if the realized gain in performance due to MAS for marbling and tenderness is of sufficient economic value to justify its use. The cost:benefit ratio may be a challenge for the use of MAS today. Many of the tests are relatively expensive ($30-50). Testing large numbers of animals may not be feasible.

Researchers continue to investigate the bovine genome and find DNA markers associated with a wide variety of traits. Interpretation of genotyping results is already fairly complicated with just a few genes on the market. Introduction of a large number of DNA marker tests will quickly generate an overwhelming amount of data. The challenge will be to make these genotypes into useful information. One way this may happen is with the inclusion of the genotype data into the computation of EPD. The augmentation of EPD with DNA marker data will reduce data overload and continue to

focus selection decisions on measures of net merit. The markers will allow for improved accuracy of prediction of the EPD at an earlier age.

Marbling Markers:

As of January 1, 2006 only one commercially available marker panel for marbling score has been validated by the National Beef Cattle Evaluation Consortium (NBCEC). This test is marketed by Bovigen Solutions LLC (http://www.bovigensolutoins.com) and is name GeneSTAR® Quality. The panel is comprised of two markers (TG5 and M2) that have been reported to be associated with increased quality grade in company trials. The increase in marbling score due to the favorable forms of TG5 and M2 was found to be insignificant in the Charolais x Angus reference population used by the NBCEC for validation (NBCEC, 2005). However, it was estimated that the addition of a favorable TG5 allele or 'star' was associated with a significant increase (p=0.06) of 8.6% in the number of animals grading USDA Choice or Prime, and the addition of a M2 favorable allele or 'star' was associated with 2.9% increase in the number of animals grading USDA Choice or Prime (NBCEC, 2005). Complete results from the NBCEC website are given below.

Results

A. Significance of gene effects under an additive model (regression on number of alleles)

Reference Population	Trait	Number Head	Contrast				
			Effect (s)	Coefficient (= 1 star)	DF	F	p
Charolais x Angus	Marbling Score	387	GSQ** (TG5 & M2)	5.7	3	1.80	0.18
			TG5*	9.7	1	2.65	0.10
			M2*	0.1	1	0.00	0.99

Reference Population	Trait	Number Head	Contrast				
			Effect (s)	Coefficient (= 1 star)	DF	F	p
Charolais x Angus	% Choice and Prime	387	GSQ** (TG5 & M2)	6.2	3	3.7	0.06
			TG5*	8.6	1	3.6	0.06
			M2*	2.9	1	0.3	0.58

** GSQ = GeneSTAR® Quality combined marker panel = total number of favorable TG5 and M2 alleles; value of an average star.
*effect of TG5 and M2 estimated separately; TG5 has a larger effect than M2.
The frequency of one of the alleles was too low in the Hereford population to detect marker effects and so this group was not included in the analysis.

Source: NBCEC GeneSTAR® Quality Grade Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/GeneSTARQualityGrade/geneSTAR_quality_grade_test_results.htm

B1. Combined Two-marker Genotype Effects (contrasted to TG5 "0 stars", M2 "0 stars"), Standard Errors and Frequencies in Reference Samples

Reference Population	Trait	No. Head	Allele		Sample Frequency	Estimated Effect	Standard Error
			TG5	M2			
Charolais x Angus	Marbling Score	387	2	2	0.01	19.5	33.2
				1	0.02	19.4	26.3
				0	0.02	19.3	19.3
			1	2	0.01	9.9	23.6
				1	0.12	9.8	16.6
				0	0.21	9.7	9.7
			0	2	0.03	0.2	13.9
				1	0.20	0.1	7.0
				0	0.38	0.0	0.0

Reference Population	Trait	No. Head	Allele		Sample Frequency	Estimated Effect	Standard Error
			TG5	M2			
Charolais x Angus	% Choice and Prime	387	2	2	0.01	22.9	19.6
				1	0.02	20.0	14.3
				0	0.02	17.1	9.1
			1	2	0.01	14.4	15.0
				1	0.12	11.5	9.8
				0	0.21	8.6	4.5
			0	2	0.03	5.8	10.5
				1	0.20	2.9	5.2
				0	0.38	0	0.0

The frequency of one of the alleles was too low in the Hereford population to detect marker effects and so this group was not included in the analysis.

Source: NBCEC GeneSTAR® Quality Grade Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/GeneSTARQualityGrade/geneSTAR_quality_grade_test_results.htm

B2. Effect of One Star on the Target Trait

Reference Population	Trait	No. Head	No.of Stars	Estimate	SE	N	%
Charolais x Angus	Marbling Score	387	4	**22.7**	16.9	4	1.0
			3	**17.0**	12.7	10	2.6
			2	**11.4**	8.5	67	17.3
			1	**5.7**	4.2	159	41.1
			0	**0**		147	38.0

Reference Population	Trait	No. Head	No.of Stars	Estimate	SE	N	%
Charolais x Angus	% Choice and Prime	387	4	**24.7**	12.9	4	1.0
			3	**18.6**	9.7	10	2.6
			2	**12.4**	6.5	67	17.3
			1	**6.2**	3.2	159	41.1
			0	**0**		147	38.0

Source: NBCEC GeneSTAR® Quality Grade Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/GeneSTARQualityGrade/geneSTAR_quality_grade_test_results.htm

Tenderness Markers:

As of January 1, 2006, two commercially available marker panels have been validated by the NBCEC. Tenderness of beef carcasses has been identified as area of improvement for the beef industry. Improvement in beef tenderness improves the value of beef products, which in turn should improve consumer demand of beef products. Research has suggested that a 10% improvement in beef tenderness would result in a 1% improvement in industry revenues (Moser et al, 204). The NBCEC validation results of the two commercially available marker panels are listed below.

Igenity *Tender*GENE™ (http://www.igenity.com) is a DNA marker panel test that consists of three markers (UofGCAST1, Calpain 4751, and Calpain 316). UofGCAST1 tests for a single nucleotide substitution in Calpastatin. Calpastatin inhibits the post-mortem tenderizing activity of the enzyme, Calpain. Calpain 4751 and 316 are nucleotide substitutions in the gene µ-calpain, which codes for an enzyme involved, in post-mortem tenderization of beef. The markers Calpain 4751 and 316 are nearby each other and are consider jointly or as a haplotype. A haplotype is a set of alleles inherited together. The NBCEC has validated an association between these markers and tenderness measured as Warner-Bratzler shear force and observed in commercial cattle. Each substituition with a “C” allele in calpastatin was associated with a 0.42 lb. decrease in Warner-Bratzler Shear force. Additionally, replacement of the Calpain 4751

"T"-316 "G" with the Calpain 4751 "C"- 316 "C" was related to a 0.72 lb decrease in Warner-Bratzler Shear force (NBCEC, 2005). Complete results from the NBCEC website are given below.

Results

A. Significance of gene effects under an additive model (regression on number of alleles and/or haplotypes)

Reference Population	Trait	Number Head	Contrast			
			Gene(s)	DF	F	p
Combined	Warner-Bratzler Shear Force (lb)	**1209**	**ITG** (UofG-Cast1 & CAPN1)**	**4**	**10.6**	**1.9E-08**
			UofG-Cast1*	**1**	**14.1**	**1.8E-04**
			CAPN1 (4751 & 316 haplotype)*	**3**	**9.3**	**4.7E-06**
Brangus		181	ITG** (UofG-Cast1 & CAPN1)	4	1.7	0.16
			UofG-Cast1*	1	0.04	0.84
			CAPN1 (4751 & 316 haplotype)*	3	2.2	0.09
Charolais x Angus		400	ITG** (UofG-Cast1 & CAPN1)	4	8.0	3.1E-06
			UofG-Cast1*	1	8.2	4.4E-03
			CAPN1 (4751 & 316 haplotype)*	3	8.2	2.8E-05
Red Angus		310	ITG** (UofG-Cast1 & CAPN1)	4	2.9	0.02
			UofG-Cast1*	1	1.2	0.27
			CAPN1 (4751 & 316 haplotype)*	3	3.1	0.03
Brahman		318	ITG** (UofG-Cast1 & CAPN1)	3	4.3	0.01
			UofG-Cast1*	1	5.8	0.02
			CAPN1 (4751 & 316 haplotype)*	2	3.7	0.03

** ITG = Igenity *Tender*GENE™ combined marker panel = total number of favorable UofG-Cast1 alleles & CAPN1 haplotypes.

*effect of UofG-Cast1 and CAPN1 haplotype estimated separately; CAPN1 haplotype has a larger effect than UofG-Cast1.

* Genotype effects constructed from effects estimated in the haplotype analysis (Table B2)

Source: NBCEC Igenity *Tender*GENE™ Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/IGENITYTenderGene/IGENITY_tenderGENE_test_results.htm

B1. Combined Three-marker Genotype Effects (contrasted to UoG-Cast1 "GG", Capn4751 "TT", Capn316 "GG"), Standard Errors and Frequencies* in Reference Samples

GENOTYPE			Estimate (lbs.)	Standard Error	Number Obs.	%
UoG-Cast1	Capain 4751	Capain 316				
CC	CC	CC	-2.3	0.4	18	1.5
		CG	-1.9	0.3	60	5.0
		GG	-1.6	0.3	33	2.7
	CT	CC	-1.1	0.6	8	0.7
		CG	-1.5	1.0	123	10.2
		GG	-1.2	0.5	181	15.0
	TT	CC	0.1	1.0	0	0.0
		CG	-0.4	0.5	9	0.7
		GG	-0.8	0.2	212	17.5
CG	CC	CC	-1.9	0.3	9	0.7
		CG	-1.5	0.2	42	3.5
		GG	-1.2	0.3	23	1.9
	CT	CC	-0.7	0.5	1	0.1
		CG	-1.1	0.2	74	6.1
		GG	-0.8	0.2	91	7.5
	TT	CC	0.5	1.0	0	0.0
		CG	0.1	0.5	4	0.3
		GG	-0.4	0.1	204	16.9
GG	CC	CC	-1.4	0.3	2	0.2
		CG	-1.1	0.2	7	0.6
		GG	-1.1	0.2	5	0.4
	CT	CC	-0.2	0.5	1	0.1
		CG	-0.7	0.1	9	0.7
		GG	-0.4	0.1	30	2.5
	TT	CC	1.0	1.0	0	0.0
		CG	0.5	0.5	0	0.0
		GG	0	.	63	5.2

The yellow shaded genotypes involve the rare "T-C" haplotype. The low number of animals with this genotype in the data set made it difficult to accurately estimate the size of its effect.

Source: NBCEC Igenity *Tender*GENE™ Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/IGENITYTenderGene/IGENITY_tenderGENE_test_results.htm

B2. Effect of One Copy of a UoGCAST1 Allele or CAPN1 Haplotype on the Target Trait

Population	Trait	No. Head	Gene	Allele/ Haplotype	Sample Frequency	Estimated Effect	Standard Error
Combined	Warner-Bratzler Shear Force (Tenderness)	1209	UoGCAST	C	0.72	-0.42	0.11
				T	0.28	0.00	0.00
			CAPN1 4751 & 316	C-C	0.16	-0.72	0.15
				C-G	0.22	-0.40	0.13
				T-C	0.01	0.48	0.50
				T-G	0.61	0	0.00
Brangus	Warner-Bratzler Shear Force (Tenderness)	181	UoGCAST	C	0.79	-0.05	0.26
				T	0.21	0.00	0.00
			CAPN1 4751 & 316	C-C	0.17	-0.72	0.28
				C-G	0.37	-0.12	0.23
				T-C	0.00	-0.23	1.78
				T-G	0.45	0	0.00
Charolais x Angus	Warner-Bratzler Shear Force (Tenderness)	400	UoGCAST	C	0.79	-0.40	0.14
				T	0.21	0.00	0.00
			CAPN1 4751 & 316	C-C	0.20	-0.76	0.16
				C-G	0.26	-0.37	0.16
				T-C	0.03	0.55	0.41
				T-G	0.51	0	0.00
Red Angus	Warner-Bratzler Shear Force (Tenderness)	310	UoGCAST	C	0.74	-0.19	0.17
				T	0.26	0.00	0.00
			CAPN1 4751 & 316	C-C	0.23	-0.55	0.19
				C-G	0.25	-0.24	0.20
				T-C	0.01	0.86	0.85
				T-G	0.51	0	0.00
Brahman	Warner-Bratzler Shear Force (Tenderness)	318	UoGCAST	C	0.43	-0.73	0.30
				T	0.57	0.00	0.00
			CAPN1 4751 & 316	C-C	0.02	-1.27	1.19
				C-G	0.07	-1.36	0.56
				T-C	0		
				T-G	0.92	0	0.00

The yellow shaded genotypes involve the rare "T-C" haplotype. The low number of animals with this genotype in the data set made it difficult to accurately estimate the size of its effect.

Source: NBCEC Igenity *Tender*GENE™ Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/IGENITYTenderGene/IGENITY_tenderGENE_test_results.htm

GeneSTAR® Tenderness (www.bovigensolutions.com) is a marker panel test consisting of the markers CAST-T1 and Calpain 316-T2. Increased beef tenderness is associated with substitution of the “C” allele at CAST-T1 (calpastatin) and the “C” allele at Calpain 316-T2 (μ-calpain). Favorable alleles of these genes are designated as ‘star’ in company reporting and have been related to enhanced tenderness in corporate

research. These results were successfully validated by the NBCEC. The favorable "C" form of calpastatin was associated with a 0.3 lb. decrease in Warner-Bratzler Shear force while the favorable form of μ-calpain (Calpain 316-T2) "C" was related to a decrease in Warner-Bratzler Shear force ranging from 0.4-0.5 (NBCEC, 2005). Complete results from the NBCEC website are given below.

Results

A. Significance of gene effects under an additive model (regression on number of alleles)

Reference Population	Trait	Number Head	Contrast				
			Marker (s)	Coefficient (= 1 star)	DF	F	p
Combined	Warner-Braztler Shear Force (lb)	**662**	**GST** (T1 & T2)**	**-0.39**	**3**	**21.07**	**5.3E-06**
			CAST-T1*	**-0.31**	**1**	**5.63**	**1.8E-02**
			Calpain316 - T2*	**-0.46**	**1**	**15.73**	**8.1E-05**
Charolais x Angus		387	GST** (T1 & T2)	-0.39	3	11.88	6.0E-04
			CAST-T1*	-0.27	1	1.63	0.20
			Calpain316 - T2*	-0.44	1	11.07	1.0E-03
Hereford		285	GST** (T1 & T2)	-0.40	3	8.94	3.1E-03
			CAST-T1*	-0.33	1	3.27	0.07
			Calpain316 - T2*	-0.50	1	5.28	0.02

** GST = GeneSTAR® Tenderness combined marker panel = total number of favorable CAST-T1 and Calpain316 alleles; value of an average star.

*effect of CAST-T1 and Calpain316 estimated separately; Calpain316 has a larger effect than CAST-T1.

B1. Combined Reference Sample Two-marker Genotype Effects (contrasted to CAST-T1 "GG", Calpain316 "GG"), Standard Errors and Frequencies

Reference Population	Trait	No. Head	Allele		Estimated Effect	Standard Error	No.	%
			CAST-T1	Calpain-316				
Combined	Warner-Bratzler Shear Force (lb)	662	2 (CC)	2 (CC)	**-1.5**	0.5	20	3.0
				1 (CG)	**-1.1**	0.4	158	23.9
				0 (GG)	**-0.6**	0.3	250	37.8
			1 (CG)	2 (CC)	**-1.2**	0.4	8	1.2
				1 (CG)	**-0.8**	0.2	64	9.7
				0 (GG)	**-0.3**	0.1	109	16.5
			0 (GG)	2 (CC)	**-0.9**	0.2	1	0.2
				1 (CG)	**-0.5**	0.1	19	2.9
				0 (GG)	**0**	0.0	33	5.0

Source: NBCEC GeneSTAR® Tenderness Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/GeneSTARtenderness/GeneSTAR_tenderness_test_results.htm

B2. Effect of One Star on the Target Trait

Reference Population	Trait	No. Head	No.of Stars	Estimate	SE	N	%
Combined	Warner-Bratzler Shear Force (lb)	662	4	-1.6	0.3	20	3.0
			3	-1.2	0.3	166	25.1
			2	-0.8	0.2	315	47.6
			1	-0.4	0.1	128	19.3
			0	0.0		33	5.0

Source: NBCEC GeneSTAR® Tenderness Validation Study Results
http://animalscience.ucdavis.edu/animalbiotech/ValidationStudies/GeneSTARtenderness/GeneSTAR_tenderness_test_results.htm

Additional Reading:

Molecular approaches to Genetic Improvement. Proceedings of the 8th Genetic Prediction Workshop. Beef Improvement Federation. December 4-6, 2003. Kansas City, Missouri. Available: http://www.beefimprovement.org/GPW_ProceedingsMay212004.pdf

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