

Genetic Selection Using Genetic Markers

Gary R. Hansen

Assistant Professor

North Florida Research and Education Center

UF/IFAS

Marianna, FL

With recent advancements in biotechnology, genetic selection of beef cattle has entered the 21st century. Cattle producers now have the ability to assess the genetic makeup of an individual animal through the use of genetic markers. Using a tissue sample (hair, blood, muscle, etc.), cattle can be tested to see if they carry certain genes and whether the allelic combinations within the gene will have a net positive or negative influence when the gene is expressed in the animal. This type of technology will have widespread economic impact on the cattle industry. Using genetic markers will help to speed up selection of animals for traits that are difficult to measure due to expensive data collection as well as traits that are measured only in one sex or measured late in the life of an animal. Basic genetic principles must be understood to have an understanding of the use of genetic markers.

Chromosomes are long thread-like strands of DNA located in the nucleus that contain the code to make proteins, enzymes, hormones, etc. Genes are a discrete segment of a chromosome. The unique nucleotide sequence within a gene determines its specific biological role. Many genes code for protein products while others are involved in metabolic and developmental events. Others genes regulate when different genes will be expressed or not expressed depending upon different metabolic pathways synthesized in the animal. Alleles are alternate forms of genes. Animals that have the same allele at a given locus are homozygotes (BB, bb) while animals with different alleles at the same locus are heterozygotes (Bb). Mutations of a single nucleotide, called a single nucleotide polymorphism (SNP) can affect the expression of a gene, especially if the mutation takes place in a coding region. These types of mutations lead to a specific nucleotide sequence that give rise to easily detectable gene markers that

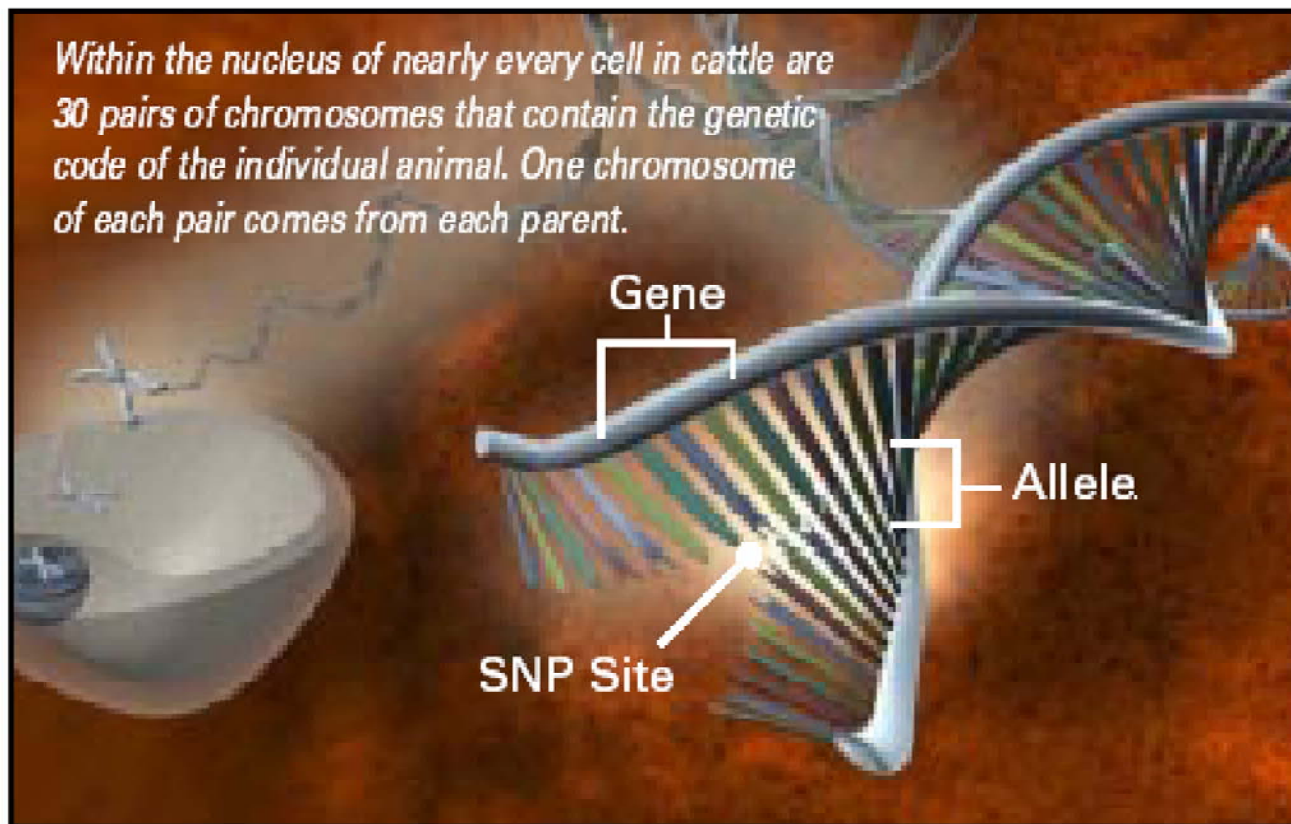
can be used to differentiate between alleles at a locus. Figure 1 illustrates the basic organization of the genetic code for cattle.

Several genes have been identified that account for sufficient variation in specific traits of economic interest to cattle breeders. Traits of economic importance to cattle producers can be classified into two basic classes; qualitative and quantitative traits. Qualitative traits involve the expression of single gene with variation determined by various alleles (black or red coat color, horn versus polled, double muscling) while quantitative traits involve the interaction of several genes (polygenes) and multiple allelic combinations (carcass, growth, production). It appears that almost all economically important beef cattle traits are polygenic traits with 3 to 6 major genes affecting the expression of the trait with each gene having a small effect. This complicates genetic selection for these traits as it difficult to determine how much of the variation can be assigned to a single gene. This is complicated further by the fact that genes affecting the same trait can be antagonist to each other. Genes located close to each other on a chromosome are linked meaning that these genes are almost always passed on from one generation to the next generation together.

Progeny tests have been the traditional method to select for economic traits in beef cattle. Animals are evaluated using phenotypic trait comparisons within a contemporary group, followed by statistical analysis to determine genetic differences between individual animals. Recently, the National Cattle Evaluation has used the best linear unbiased prediction (BLUP) model to improve selection by generating expected progeny differences (EPDs).

EPDs have improved the ability of livestock

Figure 1. The basic genetic structure of chromosomes and genes found in beef cattle.



From Merial. Available at: http://us.igenity.com/pdfs/IGN-03-3003-FUNC-GEN_US.pdf, Accessed March 12, 2004.

producers to affect change in their herds; however, caution must be exercised to insure properly balanced trait selection is taking place. Under these types of selection systems, progress is limited due to expense of data collection, time between identification and subsequent gene introduction in the breeding population, and generation interval. This is complicated further in traits that are lowly heritable (fertility, disease resistance), classified only in one sex (milk production, scrotal circumference), measured late in an individual's life (stayability), or evaluated postmortem (carcass traits) (Bourdon, 1988; Hohenboken, 1988). Gene markers allow for identification of animals at birth with the right combination of alleles for traits where selection is difficult. Selection using genetic markers would decrease the time needed to introgress desired genes into a herd of selected animals. Marker assisted selection is used to identify specific regions of chromosomes where genes affecting quantitative traits are located (Davis and DeNise, 1998). Markers closely associate with

a gene (indirect test) or within the gene (direct test) have been identified. Several have become commercially available for cattle producers to use in their genetic selection programs.

Molecular Genetics

Research in molecular genetics has led to techniques that allow for identification and direct manipulation of genes that influence economic traits. Most of the knowledge about gene structure and function has been obtained through recombinant DNA technologies (Snustad and Simmons, 1999). Recombinant DNA approaches begin with cloning the gene through insertion of a DNA sequence into a cloning vector. This allows for multiple copies of the gene to be replicated and allows for other molecular techniques that can determine gene structure and function. Collins (1992) defined two methods to clone genes of interest: functional cloning and positional cloning. Functional cloning identifies a gene through its role

Table 1. Current DNA markers commercially available for use in genetic selection in beef cattle.

Company Name	Available Markers	Gene Identity/ Location	Trait	Cost ^a	Website
Genetic Solutions	GeneSTAR Tenderness	Calpastatin-BTA 7	Meat Tenderness	N/A	www.geneticsolutions.com.au
	GeneSTAR Tenderness 2	Calpastatin-BTA 7 +Calpain 1- BTA29	Meat Tenderness	\$75.00	
Frontier Beef Systems	GeneSTAR Marbling	Thyroglobin-TG5	Meat Quality	\$55.00	www.frontierbeefsystems.com
	TenderGENE	Calpain 1-BTA29	Meat Tenderness	\$35.00	
Genmark	DoubleBLACK	N/A	Black Coat Color	\$38.00	www.genmarkag.com
	Coat Color	N/A	Black Coat Color	\$39.00	
Merial	Myostatin-Peidmontese	Myostatin-BTA2	Retail Yield/ Meat Tenderness	\$25.00	www.igenity.com
			Appetite Regulation/ Energy Utilization	\$60.00	

^aCosts at time of publication and are subject to change. Contact company for current prices and volume discounts.

^bGeneSTAR[®] is a registered trademark of Genetic Solutions.

^cTenderGENE[®] and DoubleBLACK[®] are registered trademarks of Frontier Beef Systems.

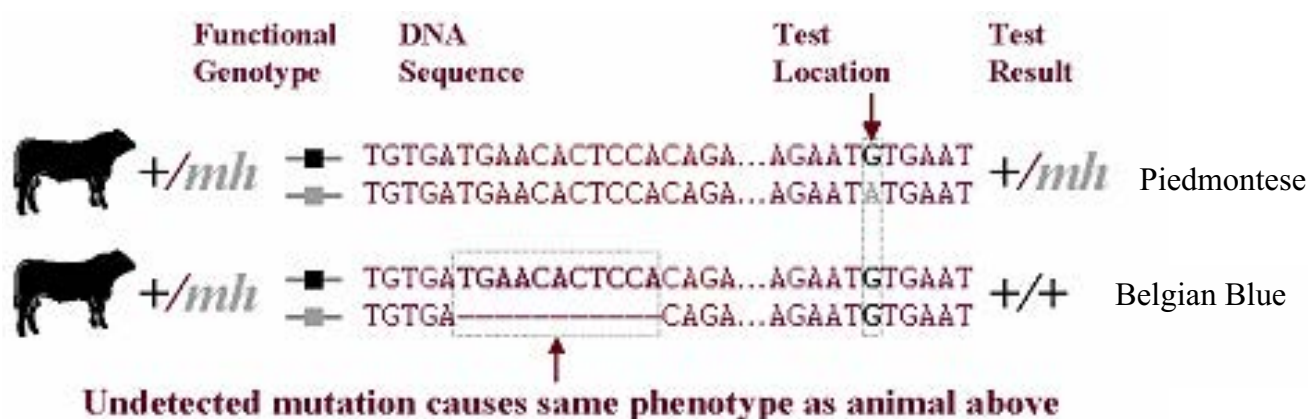
^dIgenity-L[®] is a registered trademark of Merial.

in the biochemical pathways of the organism of interest without regard to chromosomal map position. Positional cloning identifies genes solely by chromosomal map position without knowing gene function (Wicking and Williamson, 1991; Paterson and Wing 1993). Positional cloning makes use of evenly distributed polymorphic markers in the genetic map. Markers are used to locate gene position in a chromosomal region. As new markers are added, map resolution is refined revealing the exact location of the gene. This has led to the discovery of genetic markers to aid in the selection of genes of economic importance.

Currently there are several companies that market gene tests to determine the genotype for specific traits in beef cattle. Listed in Table 1 are companies that have genetic tests and the specific genes they are able to test for.

Genetic markers are only tools that can help improve the accuracy of genetic selection. Genetic markers can be used to fix genes within a cow herd, however single trait selection should be avoided as this leads to non-functional cattle. Caution should be exercised when using markers in genetic selection as relationships with other economically important genes is usually unknown.

Figure 2. Mutations in Belgium Blue and Piedmontese cattle resulting in the muscle hypertrophy phenotype.



Source: Pollak, 2004.

Genes Associated with Carcass Traits

Myostatin

Myostatin (Growth-Differentiation-Factor-8 (GDF8)) is a member of the transforming growth β superfamily of secreted growth and differentiation factors that is essential for proper regulation of skeletal muscle mass. GDF8 is a negative regulator of muscle growth allowing for the development of normal muscle size. Mutations in this gene have led to the muscle hypertrophy phenotype found in mice and cattle. Muscle hypertrophy phenotype (double muscling) has been documented in Belgian Blue, Piedmontese, and to a lesser extent in Limousin, Charolais, and Maine-Anjou (Grobet et al., 1998; Kambadur et al., 1997; McPherron and Lee, 1997). In Belgian Blue cattle, a deletion of an 11 nucleotide sequence in the third exon of the myostatin gene causes a frameshift that virtually eliminates all of the mature, active region of the molecule (McPherron and Lee, 1997; Figure 2). In Piedmontese cattle, a single nucleotide polymorphism (SNP) in which adenine is substituted for guanine in the coding region of the myostatin gene causes the muscle hypertrophy phenotype (McPherron and Lee, 1997; Figure 2). This demonstrates the fact that two different mutations resulted in the same phenotype. Casas et al. (2000), showed an interaction between myostatin and chromosome 5 in a Piedmontese X Angus family for meat tenderness measured by Warner-Bratzler shear force at 14 days postmortem. Animals inheriting the inactive myostatin allele from the Angus had higher shear force measurements (less tender) than animals inheriting the Piedmontese allele. Animals with a single copy of the inactivated myostatin gene have greater muscle mass and less fat than normal animals (Casas et al., 2001; Casas, et al., 1998). Tests are currently available to identify those animals segregating the Piedmontese inactive myostatin allele (Genmark).

Calpain and Calpastatin

A chilled carcass should be aged at least 7

days following slaughter to allow for the proteolytic enzymes to break down the myofibrillar structure of the muscle and connective tissue. Most research indicates that the calpain enzymes coupled with their interaction with the calpastatin enzyme are responsible for the increase in meat tenderness during aging (Koochmaraie, 1996). The calcium dependent proteases (calpains) in conjunction with calcium dependent protease inhibitors (calpastatin) appear to have the greatest effects on meat tenderness. The calpains cause degradation of the proteins that maintain myofibrillar structure (Koochmaraie, 1988, 1992, 1996). Calpastatin inhibits calpain activity which reduces the amount of protein degraded in the myofibrillar structure, which leads to less tender meat. *Bos indicus* breeds have more calpastatin activity than *Bos taurus* breeds, which helps to explain some of the differences in meat tenderness between these breed types (Whipple et al., 1990; O'Conner et al., 1997). Studies have shown calpastatin level to be a highly heritable trait which would allow for the selection of animals with low levels of calpastatin activity to increase meat tenderness (Shackelford et al., 1994). Recently, a commercial DNA marker test based on variants of the calpastatin gene located on BTA7 has become available to help predict meat tenderness (GeneNOTE 4, 2003). The test detects different forms of the gene with one form associated with an increase in tenderness and the other form leading to increased toughness (GeneNOTE 4, 2003). However, there is no published quantitative trait locus (QTL) that coincides with the position of calpastatin, so it is unknown how much genetic variation in meat tenderness could be explained by the mutation in calpastatin.

Calpain (CAPN1) has been mapped to a QTL region for WBSF on BTA29, possibly explaining part of the variation in meat tenderness (Smith et al., 2000). Two variant SNP's (SNP316 and SNP530) have been identified to increase meat tenderness (Page et al., 2002). Warner-Bratzler Shear Force (WBSF) was reduced 1.11 lb (greater tenderness) in a set of Simmental and Angus calves when the CC genotype was present at SNP316 when compared to the GG genotype at the same

location. The CG genotype was intermediate indicating that the genotypes are additive. At the same time, WBSF was increased 0.68 lbs when the AA genotype was present at SNP530 when compared to the GG genotype. Animals with the CC genotype for SNP316 and GG genotype for SNP530 had WBSF values that were approximately 1.8 lbs less than animals with the GG genotype for SNP316 and AA genotype for SNP530 (Pollack, 2004). Genetic tests have been developed that identify various variants of calpain (GeneSTAR Tenderness2, *TenderGENE*) and calpastatin (GeneSTAR Tenderness) genes.

Leptin

The leptin protein has been implicated in the regulation of appetite, energy utilization, and fat partitioning in cattle. Leptin is an important part of a negative feedback system that regulates insulin, glucocorticoids, and the sympathetic nervous system.

Variants (alleles) of a SNP in exon 2 of the leptin gene appear to be associated with variation in carcass traits in beef cattle. One SNP (cc at base pair 130) leads to higher levels of carcass fat while another (tt at base pair 73 and 57) is associated with lean tissue growth. A single nucleotide switch (cytosine versus thymine) leads to an amino acid switch (arginine versus cysteine) which code for different leptin proteins in the animal. When cytosine (cc) is present at a critical point on the DNA of both chromosomes, the leptin protein produced is recognized by specific receptors in the hypothalamus which signals the body to suppress appetite and modify fat metabolism. If thymine (tt) is present at the critical point on the DNA then the leptin protein is structurally different and is largely unrecognized by the normal receptors in the brain. The negative feedback is silenced leading to reduced efficiency in appetite and energy regulation (Merial®, 2004).

Animals with the cc genotype tend to have higher lean tissue growth where as animals with the tt genotype tend to have higher marbling scores. The frequency of the variant alleles in various beef

cattle breeds are listed in Table 2. Notice that British breeds (higher levels of marbling and carcass fat) have a higher frequency of the t allele while Continental breeds (higher levels of lean tissue growth) have a higher frequency of the c allele. The frequency of homozygous animals for the t allele in the British breeds was considerably higher than in the Continental breeds. This would be expected since British breeds tend to have higher marbling scores and higher yield grades than Continental breeds.

Table 2. Frequency of the c and t alleles at the leptin SNP locus in beef breeds.

Breed	t Allele frequency	C Allele frequency	Lepin-tt proportion
Angus	58%	42%	30%
Hereford	55%	45%	32%
Charolais	34%	66%	10%
Simmental	32%	68%	10%

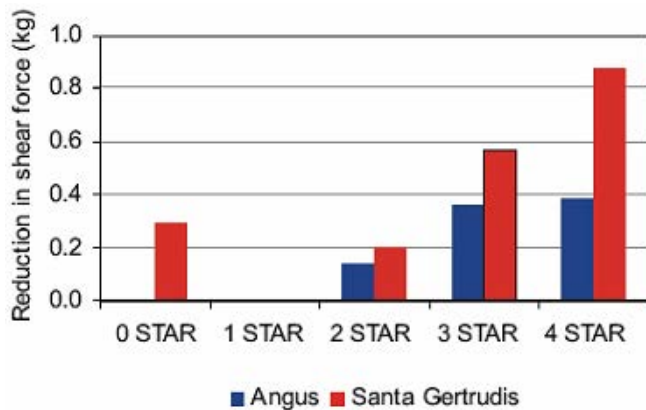
Source: <http://sask.usask.ca/~schmutz/meat.html>, 2004.

Commercially available genetic markers will be briefly discussed. Many of the markers have only recently become available so validation is still an ongoing process. Producers should realize that environment also plays an important role on how genes are expressed. Different genes are expressed at different times in the production environment. Production environment can also affect to what extent a gene is expressed. Producers should also consider which animals to test. Animals that will have a large genetic contribution to the herd (herd sires, donor cows, artificial insemination sires, etc.) should be considered as candidates for genetic testing. Caution should be exercised before culling animals based solely on a single genetic test.

GeneSTAR® Marbling

The GeneSTAR® Marbling test for variants of the thyroglobin TG5 gene. Animals are classified as 0, 1, or 2 STAR animals depending on which alleles are present at the locus. Studies show that animals with 2 versus 0 STAR increased marbling score 9 to 14 points with an accompanying 16-19% increase in animals grading choice. Animals classified as 1 STAR animal were intermediate. Use

Figure 3. Expected reduction in WBSF in Angus and Santa Gertrudis cattle with various levels of favorable alleles.



Source: GeneNOTE 7.

of GeneSTAR® Marbling is dependent on finish end point with the greatest improvement in cattle that are in the Select/Choice transition. Use of this marker would be most beneficial to cattle producers working to supply cattle that will be sold in alliances or on grids that place high premiums on quality grade and it appears to work best in cattle that are fed for a longer duration. Since the genetic component of marbling is controlled by several genes, 0 STAR animals need to be evaluated using other parameters (marbling EPD, %IMF EPD, leptin, etc.) to determine which individuals should be selected as breeding stock. In some instances, bulls with high EPD’s for marbling have genotyped as 0 STAR with the GeneSTAR® Marbling test.

GeneSTAR® Tenderness

GeneStar® Tenderness is commercial DNA marker test marketed by Genetic Solutions and is

based on variants of the calpastatin gene located on chromosome 7. The test detects different forms of the gene with one form associated with an increase in tenderness and the other form leading to increased toughness (GeneNOTE 4, 2003). Calpastatin is a naturally occurring enzyme that inhibits calpain, another naturally occurring enzyme involved with meat tenderization as it ages postmortem. GeneSTAR® Tenderness is now marketed in combination with CAPN1 (calpain SNP316) as GeneSTAR® Tenderness2.

GeneSTAR® Tenderness2

GeneSTAR® Tenderness2 is a second generation DNA marker test that is marketed by Genetic Solution which is a combination of the GeneStar® Tenderness (calpastatin) and a recent test developed by Meat and Animal Research Center (MARC) for CAPN 1 (calpain SNP316). The test measures whether an animal has alleles for the two genes associated with tender or tough muscle. Figure 3 shows that animals with four favorable alleles (4 STAR) for the two genes, will have reduced WBSF when compared to animals with less favorable alleles. Animals with 0 favorable alleles had lower WBSF than animal with 1 or 2 favorable alleles. This could be due to the small sample size of this treatment group as well as other genes with favorable alleles, for WBSF could be being expressed in these animals.

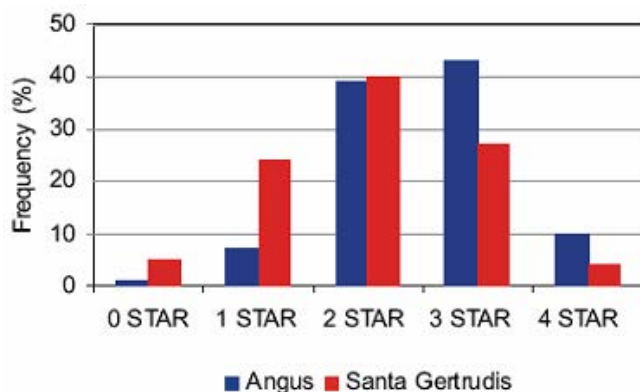
Only two trials, one in straightbred Angus and one in straightbred Santa Gertrudis, have looked at the combined effects of the calpastatin and calpain DNA markers. Further research will be

Table 3. Reduction in WBSF in Santa Gertrudis with various levels of favorable alleles.

	GeneSTAR® Tenderness 2 effects				
Shear force (lb) ³	-0.64 ¹	0	-0.43	-1.24	-1.92 ²
% tough (WBS > 12lb) ⁴	24	33	26	20	8
¹ N=17					
² N=12					
³ Av = -0.62					
⁴ Av = 25%					

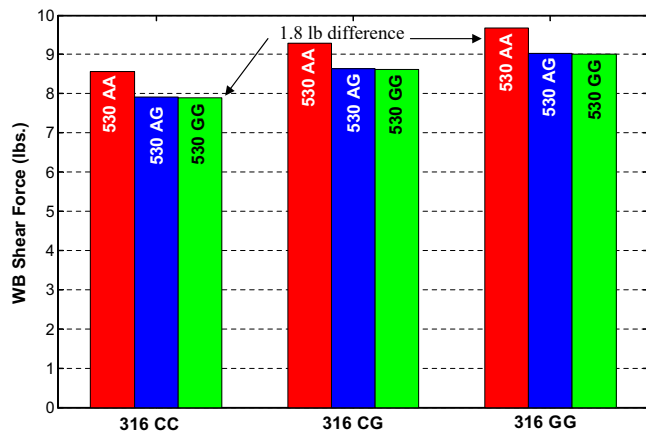
Source: Bovigen Solutions, LLC.

Figure 4. Frequency of Angus and Santa Gertrudis cattle with various levels of favorable alleles (GeneSTAR Tenderness2).



Source: GeneNOTE 7.

Figure 5. Two additive genotypes in Simmental and Angus calf-fed feeder calves.



Source: Pollak, 2004.

needed to validate the combined effects of these markers. The results of the Santa Gertrudis trial are summarized in Table 3.

The Santa Gertrudis trial showed that 4 STAR animals had reduced WBSF by up to 1.92 lbs and also reduced the percentage of tough animals by as much as 25% which translated into three times fewer tough carcasses (BOVIGEN Solutions, LLC). In the Angus trial, less than 2% of the 4 STAR carcasses were classified as tough (> 11 lbs WBSF) compared to 12 % of the 1 STAR and 2 STAR carcasses (BOVIGEN Solutions, LLC). Figure 4 shows the frequency of animals with one, two, three, or four favorable alleles with the Angus

and Santa Gertrudis trials. Assuming that animals within these trials are representative of the population as a whole, one would expect similar results in Angus and Santa Gertrudis herds.

Selection for 4 STAR animals would be possible in both populations, however single trait selection should be avoided.

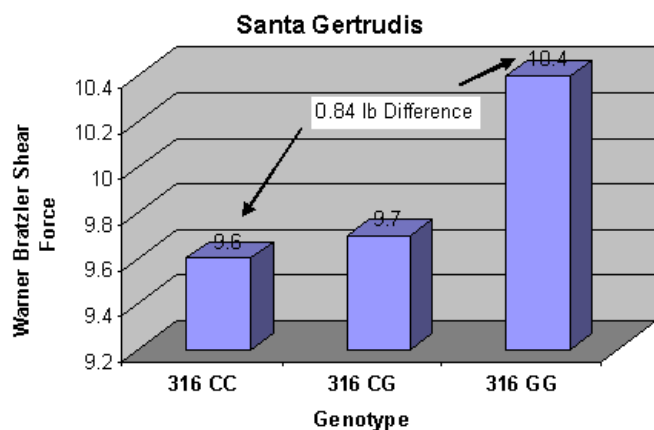
TenderGENE™

TenderGENE™ is a DNA marker test that is marketed by Frontier Beef Systems which test for two variants (SNP316 and SNP530) of the CAPN1 gene. Figure 5 summarizes the effect that each SNP has on WBSF in Simmental/Angus cross cattle. Preliminary results showed reduced WBSF scores in animals with all favorable alleles from CAPN1. Warner-Bratzler Shear Force (WBSF) was reduced 1.11 lb (greater tenderness) in a set of Simmental and Angus calf-feds when the CC genotype was present at SNP316 when compared to the GG genotype at the same location. The CG genotype was intermediate indicating that the genotypes are additive. At the same time, WBSF was increased 0.68 lbs when the AA genotype was present at SNP530 compared to the GG genotype. Animals with the CC genotype for SNP316 and GG genotype for SNP530 had WBSF values that were approximately 1.8 lbs less than animals with the GG genotype for SNP316 and AA genotype for SNP530 (Pollak, 2004).

Currently only the SNP316 variant is used in predicting increased tenderness in *Bos indicus* influenced cattle. In a trial with Santa Gertrudis cattle (Figure 6), WBSF was reduced 0.84 lbs when the CC genotype was present versus the GG genotype.

Animals with different genotypic combinations for the SNP316 and SNP530 are ranked according to the desirability of genotype, 5 being more tender in comparison to 1 (Table 4). Animal rank should indicate which animals would be expected to be more tender due to allelic combinations between the two SNP's.

Figure 6. Difference in WBSF Santa Gertrudis cattle with different genotypes at SNP316.



Source: *TenderGene* Fact Sheet, 2004.

DoubleBLACK™

DoubleBLACK™ is a DNA marker for coat color marketed by Frontier Beef Systems®, to determine if an animal is homozygous black. The marker tests for three possible alleles: black, red, and wild type. With the advent of value based programs that are based on black coat color, several breeders are interested in producing animals homozygous for the black coat color. Since the black gene is dominant over red, black animals may carry one or two copies of the black gene. However, homozygous black animals carry two copies of the black gene. The wild type color gene is rare and animals that carry the wild type gene will possess the coat color of the opposite gene the animal is carrying. Therefore, a black animal that carries one copy of the black gene and one copy of the wild type gene is heterozygous even if is not carrying the red gene. Likewise, red animals may possess just one red gene if the other gene is wild type. Again, this is rare, but possible. Almost all red animals will have two copies of the red gene (Frontier Beef Systems, 2004). As with all of the traits previously discussed, caution should be exercised in selecting animal purely on coat color. Production environment should be considered as animals with black coat color can experience considerably more stress in hot, humid environments compared to animals with lighter coat colors.

Igenity™-L

Igenity™-L, marketed by Merial®, is a DNA marker of variant alleles of the leptin protein. Animals homozygous for the L-tt™ genotype have higher marbling scores as well as higher KPH and subcutaneous carcass fat. Animals homozygous for the L-cc™ produce carcasses with higher lean meat yield. Knowing this information would allow producers to sort animals according to what type of grid (quality versus yield grade) the animals will be marketed on prior to entering the production system. Research has proven that, if all other factors are equal, leptin genotype has a significant impact on carcass quality. In a Texas trial of Charolais/Angus steers, only 11% of cattle identified as L-cc™ graded choice, while 62% of L-tt™ cattle earned that grade. In a trial involving Hereford steers, no L-cc™ cattle graded choice, while 48% of L-tt™ cattle achieved that grade. In a trial at the University of Saskatchewan involving Charolais steers, the percent grading choice were 38% and 58%, respectively for L-cc™ and L-tt™ cattle. Cattle with the L-ct™ genotype graded intermediate between the L-cc™ and L-tt™ genotypes (Table 5; Merial®, 2003).

More cattle can grade choice or better if fed long enough. However, producers can unlock increased profit by grouping cattle of similar genotype into properly managed groups. Increased consistency and uniformity of finish will improve precision and reduce discounts for grade and fat (Merial®, 2004).

Table 4. Tenderness rank for different genotype combinations for SNP316 and SNP530.

Rank	SNP316	SNP530	Genotype score
1	CC	GG	5
1	CC	GA	4
3	CC	AA	3
3	GC	GG	3
5	GC	GA	3
5	GG	GG	3
8	GG	GA	2
8	GC	AA	1
9	GG	AA	1

Source: *TenderGENE* Fact Sheet, 2004.

Table 5. Effect of leptin genotype on carcass quality.

	Genotype			P-value
	L-cc TM	L-ct TM	L-tt TM	
Trial 1 ^a - % Choice	11	29	62	0.03
Trial 2 ^b - % Choice	0	19	48	0.01
Trial 3 ^c - % Choice	38	45	58	0.07

^aAzTx Feeders (Charolais/Angus steers).^bDoerksen Feedlot (Hereford steers).^cUniversity of Saskatchewan (Charolais steers).

Parentage Verification and Identification

DNA technology is commonly used for parentage verification and identification of beef cattle. Parentage of calves from multiple sired herds can be determined and inferior sires eliminated. National Cattle Evaluation records have shown that in some instances, misidentification of parentage is as high as 25% of the animals. Using DNA markers to verify parentage allows for a more accurate evaluation. There are several companies that provide DNA technologies for parent verification, but will not be discussed in this paper. DNA markers are also being used to track animals throughout the production chain. This allows producers to track data on an animal from birth to slaughter.

Summary

Several DNA markers are commercially available to assist cattle producers in making genetic selections within their herd. Genetic markers allow for selection of animals early in life. Caution needs to be exercised to properly use these tools with a selection program. Producers need to realize that all of the economically important traits in beef cattle production have a genetic and environmental portion of variance that affects how a gene is expressed. Although an animal may be homozygous for a specific trait, it may not be expressed within the animal due to environmental constraints. All of the economical traits are controlled by several genes, so no one marker will account for all of the genetic variation.

Genetic progress using genetic markers will be faster in the first generations than in succeeding

generations. Phenotypic as well as genotypic correlations of a DNA marker with other genes should be considered before a genetic marker (gene) is fixed within a herd. Genetic selection for one gene could lead to an undesirable correlated response in another gene.

Glossary of Terms

Adapted from BIF Guidelines 1

Alleles - Alternate forms of genes. Because genes occur in pairs in body cells, one gene of a pair may have one effect and another gene of that same pair (allele) may have different effect on the same trait.

Base pair - The complementary bases found within a DNA molecule. There are four different bases: adenine (A), thymine (T), cytosine (C) and guanine (G). A always pairs with T, and C always pairs with G. The base sequence ultimately determines the effect of the gene.

Chromosomes - Chromosomes are paired strands of DNA, with accompanying structural proteins, on which genes are located. Domestic cattle have 30 pairs of chromosomes; one chromosome from of each pair having been inherited from each parent. One random chromosome of each pair is transmitted to each egg or sperm cell produced by a parent.

Codon - A specific three-base sequence in DNA that ultimately codes for a specific amino acid used in the building of a protein.

cM (centimorgan) - The unit of length used to express location of genes on chromosomes. One cM is approximately one million nucleotides long. The length of the DNA within a cattle cell is approximately 3,000 cM. A gene ranges from 0.001-0.005cM in length. A cM corresponds to 1 % recombination between loci.

Correlation - A numerical measure, ranging between -1.00 and +1.00, describing how two traits are related. A high positive correlation means that

as one trait increases, the other one usually does as well. For example, cattle with higher than average yearling weight generally will have larger mature size as well. When traits are negatively correlated, if one is above average, the other is likely to be below the average. For example, as birth weight of a calf increases, calving ease is likely to decrease. A near zero correlation between traits means there is no particular relationship between them.

DNA - Deoxyribonucleic acid a long double-stranded nucleic acid molecule arranged as a double helix: the main constituent of the chromosome, it carries genes as segments along its strands.

Exon - Those regions of a gene in which the nucleotide sequence actually codes for a biological relevant product.

Gene - A gene is a discrete segment of the DNA molecule, located at a specific site (its locus) on a specific chromosome pair. It is the basic physical unit of heredity, a linear sequence of nucleotides along a segment of DNA that provides the coded instructions for synthesis of RNA. Which, when translated into protein, leads to the expression of hereditary character. Two copies of each gene exist in each nucleated diploid cell in an animal. Only one gene of each pair is randomly transmitted to the offspring through the gamete. The unique nucleotide sequence of each gene determines its specific biological role. Many genes specify the amino acid sequence of a protein product. Others produce gene products that are involved in controlling metabolic and developmental events.

Gene Marker - A specific sequence of nucleotides that is easily detectable and can be used to differentiate among alleles at a locus. A small unique sequence of DNA whose specific location on a chromosome is known.

Genetic Antagonism - A genetic correlation in which desirable genetic change in one of the traits is accompanied by an undesirable change in the other. For example, because of the positive genetic

correlation between milk yield potential and cow maintenance requirement, selection for increased milk would also lead to increased feed cost for maintenance.

Genetic Correlations - Correlations between breeding values for two traits that arise because some of the same genes affect both of them. When two traits (weaning and yearling weight for example) are positively genetically correlated, successful selection for one trait will result in an increase in the other trait as well. When two traits are negatively genetically correlated (birth weight and calving ease for example) successful selection for one trait will result in a decrease in the other. This is sometimes referred to as a genetic antagonism between traits.

Genetic Map - The order of DNA markers on a chromosome and distance between them.

Genome - The entire complement of DNA characteristic to individuals of a species.

Genotype - The two alleles present at a locus in an individual, for a locus with only two alleles, three genotypes are possible. For example, at the polled/horned locus in cattle, two common alleles are P (the dominant allele preventing growth of horns) and p (the recessive allele allowing horn growth). The three possible genotypes are PP (homozygous dominant), Pp (heterozygous or carrier) and pp (homozygous recessive).

Heritability - The proportion of the differences among cattle, measured or observed, that is transmitted, on average, to their offspring. Heritability of different traits may vary from zero to one. The higher the heritability of a trait, the more accurately individual performance predicts breeding value and the more rapid should be the response to selection of that trait.

Heritability estimate - An estimate of the proportion of the total phenotypic variation between individuals for a certain trait that is due to transmissible genetic merit. It is the proportion of

total variation for a trait caused by differences among individuals in breeding value.

Indicator trait - Traits that do not have direct economic importance, but aid in the prediction of economically important traits.

Intron - DNA whose nucleotide sequence does not code for a product. An intron is transcribed but is excised and not translated. Therefore, it does not affect the sequence of sub-units in the gene product.

Linkage - The occurrence of two or more loci of interest on the same chromosome within 50 cM linkage distance of one another.

Locus - The specific location of a gene on a chromosome.

Marker Assisted Selection (MAS) - The use of genetic markers to select for specific alleles at linked QTL's and therefore specific traits.

Microsatellite - A type of genetic marker. It is composed of repeating nucleotide sequences with DNA that are locus specific and variable in the number of times the sequence is repeated.

Nucleotide - The subunit of DNA composed of a five carbon sugar, one of four nitrogenous bases (adenine, thymine, cytosine, or guanine) and a phosphate group.

Phenotype - The visible or measurable expression of a character; weaning weight, postweaning gain, or reproduction for example. For most traits, phenotype is influenced by both genotype and environment. The relative degree to which phenotypic variation among individuals is caused by transmissible genetic effects is the heritability of a trait.

Phenotypic Correlation - The net correlation between two traits caused both by genetic factors and environmental factors simultaneously influencing both traits.

Qualitative Traits - Those traits in which there is sharp distinction between phenotypes, such as black versus red or polled versus horned. Only one or a few pairs of genes are involved in the expression of many qualitative traits.

Quantitative Traits - Those traits, such as weaning weight, in which there is no sharp distinction in the range of phenotype, with a gradual variation from one extreme to the other. Usually, many gene pairs are involved as well as environmental influences affect variation in such traits.

Quantitative Trait Loci (QTL) - A gene locus that has an effect on a quantitative trait. Often the actual nucleotide sequence is unknown, so selection is based upon genotype at a linked gene marker.

Transcription - The process by which an RNA copy is made from a gene.

Translation - The process by which ribosomes use the nucleotide sequence in RNA to synthesize protein.

Variance - Variance is a statistic that numerically describes the differences among individuals for a trait in a population. Without variation, no genetic progress would be possible, since genetically superior animals would not be distinguishable from genetically inferior ones.

Literature Cited

BIF Guideline 1. 1996. Available at <http://www.beefimprovement.org/guidelines.html>. Accessed August 24, 2003.

Bovigen Solution, LLC. GeneSTAR Tenderness Marker. Available at <http://www.bovigensolutions.com/html/tender.html>.

- Bourdon, R. M. 1988. Bovine Nirvana- From the alternative forms of the myostatin gene. *J. Anim. Sci.* 79:845-860.
- Casas, E., S. D. Shackelford, J. W. Keele, R. T. Stone, S. M. Kappes, and M. Koohmaraie. 2000. Quantitative trait loci affecting growth and carcass composition of cattle segregating alternate forms of myostatin. *J. Anim. Sci.* 78:560-569.
- Casas, E, J. W. Keele, S. D. Shackelford, M. Koohmaraie, T. S. Sonstegard, T. P. L. Smith, S. M. Kappes, and R. T. Stone. 1998. Association of the muscle hypertrophy locus with carcass traits in beef cattle. *J. Anim. Sci.* 76:468-473.
- Collins, F. S. 1992. Positional cloning: Let's not call it reverse anymore. *Nature Genet.* 1:3-6.
- Davis, G. P., and S. K. DeNise. 1998. The impact of genetic markers on selection. *J. Anim. Sci.* 76:2331-2339.
- Frontier Beef Systems. *DoubleBLACK™*. Available <http://www.frontierbeefsystems.com>. Accessed March 12, 2004.
- GeneNOTE 4, 2003. GeneSTAR® Tenderness - The first commercial gene marker test for beef tenderness. Available at http://www.geneticsolutions.com.au/content/products_c1.asp?name=NavPH_GeneSTAR. Accessed Jan. 17, 2003.
- GeneNOTE 7, 2004. GeneSTAR® Tenderness2 - A new, enhanced DNA marker test for two important tenderness genes. Available at http://www.geneticsolutions.com.au/content/gproducts_c1.asp?name=NavPH_GeneSTAR. Accessed March 12, 2004.
- Grobet, L., D. Poncelet, L. J. Royo, B. Brouwers, D. Pirottin, C. Michaux, F. Menissier, M. Zanotti, S. Dunner, and M. Georges. 1998. Molecular definition of allelic series of mutations disrupting the myostatin function and causing double-muscling in cattle. *Mamm. Genome* 9:210-213.
- Hohenboken, W. D. 1988. Bovine Nirvana-From the perspective of an experimentalist. *J. Anim. Sci.* 66:1885-1891.
- Kambadur, R., M. Sharma, T. P. L. Smith, and J. J. Bass. 1997. Mutations in myostatin (GDF8) in double-muscléd Belgian Blue and Piedmontese cattle. 1997. *Genome Research* 7:910-915.
- Koohmaraie, M. 1996. Biochemical factors regulating the toughening and tenderization process of meat. *Meat Sci.* 43:S193-S201.
- Koohmaraie, M. 1992. Role of neutral proteinases in postmortem muscle protein degradation and meat tenderness. *Proc. Recip. Meat Conf.* 45:63-71.
- Koohmaraie, M. 1988. The role of endogenous protease in meat tenderness. *Proc. Recip. Meat Conf.* 41:89-100.
- McPherron, A. C., and S-J. Lee. 1997. Double muscling in cattle due to mutations in the myostatin gene. *Proc. Natl. Acad. Sci. (USA)* 94:12457-12461.
- Merial®. 2004. Available at: http://us.igenity.com/pdfs/IGN-03-3003-FUNC-GEN_US.pdf. Accessed March 12, 2004.
- Merial®. 2004. IGENITY™ L test results for the beef producer. Available at <http://www.igenity.com>. Accessed March 12, 2004.
- Merial®. 2003. IGENITY testing services. Available at <http://www.igenity.com>. Accessed. March 12, 2004.

- O'Conner, S. F., J. D. Tatum, D. M. Wulf, R. D. Green, and G. C. Smith. 1997. Genetic effects on beef tenderness in *Bos indicus* and *Bos taurus* cattle. *J. Anim. Sci.* 75:1822-1830.
- Page, B. T., E. Casas, M. P. Heaton, N. G. Cullen, D. L. Hyndman, C. A. Morris, A. M. Crawford, T. L. Wheeler, M. Koohmaraie, J. W. Keele, and T. P. L. Smith. 2002. Evaluation of single-nucleotide polymorphisms in *CAPN1* for association with meat tenderness in cattle. *J. Anim. Sci.* 80:3077-3085.
- Paterson, A. H., and R. A. Wing. 1993. Genome mapping in plants. *Current Opin. Biotech* - no 1. 4:142-147.
- Pollak, E. J. 2004. Validation of DNA testing for carcass traits. Powerpoint presentation, Brown Bagger Series, National Beef Cattle Evaluation Consortium. February, 9, 2004.
- Shackelford, S. D., M. Koohmaraie, L. V. Cundiff, K. E. Gregory, G. A. Rohrer, and J. W. Savell. 1994. Heritabilities and phenotypic and genetic correlations for bovine postrigor calpastatin activity, intramuscular fat content, Warner-Bratzler shear force, retail product yield and growth rate. *J. Anim. Sci.* 72:857-863.
- Smith, T. P. L., E. Casas, C. E. Rexroad, III, S. M. Kappes, and J. W. Keele. 2000. Bovine *CAPN1* maps to a region of BTA29 containing a quantitative trait locus for meat tenderness. *J. Anim. Sci.* 78:2589-2594.
- Snustad, D.P., and M. J. Simmons. 1999. *Principles of Genetics*. 2nd ed. John Wiley & Sons, Inc., New York, NY.
- TenderGENE* Fact Sheet. 2004. Available at <http://www.frontierbeefsystems.com/tendergene.html>. Accessed March 12, 2004.
- Wicking, C., and B. Williamson. 1991. From linked marker to gene. *Trends Genet.* 7:288-293.
- Whipple, G., M. Koohmaraie, M. E. Dikeman, J. D. Crouse, M. C. Hunt, and R. D. Klemm. 1990. Evaluation of attributes that affect longissimus muscle tenderness in *Bos taurus* and *Bos indicus* Cattle. *J. Anim. Sci.* 68:2716-2728.

Notes: