

Genotyping: What Applied Economists Should Know

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Introduction

Information drives markets. Buyers and sellers conduct transactions based largely on the attributes of goods or services being exchanged. In some cases, these attributes are easily observed, and goods or services are traded at prices reflecting both buyers' and sellers' valuation of the attributes. In many cases, however, information about the attributes of a product cannot be completely known at the time of transfer, or one party may have greater knowledge of a product's attributes than the other participant in an exchange. A rich literature addresses market characteristics when uncertainty about a product is equally shared or when knowledge about the good or service being exchanged is asymmetric (Stigler 1962; Akerlof 1970; Stiglitz 2000).

Imperfect information affects most markets. Agricultural markets may be especially rife with imperfect information. Markets for wheat (Lambert and Wilson 2003), wine (Fraser 2005), livestock (Ladd and Gibson 1978; Chvosta, Rucker, and Watts 2001), and farm and range land (Miranoski and Hammes 1984; Xu et al. 1993; Elad et al. 1994; Torell et al. 2005), among others, reflect attribute uncertainties for intermediate or final agricultural goods. Uncertainty about the attributes of intermediate goods introduces uncertainties about the quality traits of final products. Various instruments exist to reduce product attribute uncertainties. For example, wheat variety can affect the levels of end use traits desired by processors (Lambert and Wilson 2003). Production contracts are designed so growers produce a specific variety best suited for the end user's needs. Wheat markets also offer premiums and discounts based on various product characteristics. Quality price differentials are found in numerous other markets, such as hogs, beef, milk, corn, oilseeds, and most fruit and vegetable markets.

Cattle genetics are receiving increasing recognition for signaling multiple aspects of animal profitability (Lambert and DeVuyst 2006; DeVuyst et al. 2007; Lusk 2007). Scientific advances are increasing the role of genetic information in determining performance and quality of crop and livestock products. Although tools have long been available to determine the value of information in decision making (e.g., Babcock 1990), few studies have attempted to value information embedded in genetic structure. Valuing genotypic information is only recently becoming possible as research evolves that relates animal genetics to performance or animal quality. The objectives of this paper are to describe recent research relating animal genetics to cattle performance and carcass quality and, ultimately, profitability. We suggest directions for future research relating genetic research to production decisions, discuss current and future data collection and analysis activities, and close with a discussion of how increasing knowledge of genetic structure may affect markets.

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The Economics of Genotypic Information

Most economists are not well-trained in genetics, including a subset of the authors. Therefore, a short course in genetics will set the stage for current research on beef cattle genetics and economic research. A gene is a strand of deoxyribonucleic acid (DNA) that encodes a specific protein. Each gene is a chain of nucleotides. The four nucleotides comprising all DNA are adenine (A), cytosine (C), guanine (G) and thymine (T). The specific order of the chain of nucleotides (A, C, G, and T) instructs cells how to function, including what proteins to produce. The order of a set of three nucleotides dictates which amino acid to place in the protein being made. A mutation, or polymorphism, occurs when one nucleotide occurring within a gene is replaced by another, thus altering the amino acid placed in the newly made protein. When mutations occur, the size, shape and/or efficacy of the protein being produced can be altered. In many cases these changes are minor and have little or no effect on an organism. In other cases, the changes may be significant and alter the organism's biology. In beef cattle, mutations may affect coat color, horned vs. polled, growth, fat deposition, muscling and post-mortem tenderness. In the most extreme cases, proteins essential to life are so severely altered through mutation of the genetic instructions that the animal cannot survive.

Genotype describes the order of nucleotides at a specific location on a gene. Because animals are diploid, they have two copies of each gene or alleles. For example, a "CT" genotype indicates cytosine lies on one gene and thymine on the other, hence it is heterozygous. A homozygous animal would have the same nucleotide on both alleles, such as a "CC" or "TT" genotype. A location on a gene that differs is called a single nucleotide polymorphism (SNP) or a mutation. SNPs are often called genetic markers.

Because genes are formed by nucleotides chained together, multiple mutations are possible at different locations on the same gene. A haplotype is a set of SNPs within a gene. Since protein function can be determined by the influence of multiple amino acids, haplotyping is thought to provide more information than SNPs for complex cell functions.

Biology is determined by genotype, environment and the interaction of genotype with environment, so knowledge of genotype may indicate potential animal performance and, consequently, livestock profits. Genetic information may have value if awareness of animal genetic structure affects management, costs, and revenues. Producers and their organizations have utilized other less specific information, such as expected progeny differences (EPDs)² in registered bull markets (Chvosta, Rucker, and Watts 2001), to signal information regarding the genetic potential of individual animals. The need for improved information in beef cattle production and markets was stressed by Hennessy, Miranowski, and Babcock (2004), who noted that efforts to improve beef quality may not succeed until better information is available about individual animal genetic traits. Scientific advances are only now shedding light on the role of specific genes in animal performance and quality. Incorporation of desirable genetic traits can perhaps best be distributed through a cattle herd through selective breeding. Although breeding programs to improve herd genetics may be lengthy due to the biological reproduction process in beef cattle, selective breeding programs using artificial insemination and embryo transfer may decrease the time necessary to achieve desirable genetic structures. Although the effects of genotype on animal performance and quality is still uncertain, several

²Expected progeny differences, or EPDs, are indices to reflect relative differences in progenies' traits, such as marbling, rate of gain, etc.

breed organizations are currently considering adding genetic markers as part of their databases (Shafer 2007).

Most phenotypic traits result from a complex interaction of several genes. For example, EPDs are an aggregate measure of the expression of several genes (Thallman and Hruska 2004), and have been shown to affect breeding stock prices (Chvosta, Rucker, and Watts 2001). Animal scientists suspect that additional genotype information will be used to augment rather than replace EPD measures (Thallman and Hruska 2004). Since it is currently cost prohibitive to identify the genetic structure of all breeding animals, EPDs will probably continue to be used in selecting replacement stock. However, augmenting EPD scores with genetic information would provide greater information to the buyer regarding performance of the breeding stock.

Collecting and analyzing DNA information is costly. DNA testing costs vary with the number of SNPs evaluated, but \$35 per head for a single SNP is common. Producers or technicians can collect required tissue, semen, hair or blood samples. However, data collection for statistical testing of hypotheses relating genotype to animal characteristics requires large-scale data collection and tracking of specific animal performance and quality. The genetic and animal performance and quality data for DeVuyst et al.'s (2007) research on fed cattle were collected over a two-year period. Data collection involved tracking cattle from placement in a feedlot over the approximately 180-day feeding period through post-slaughter carcass evaluation. At placement, blood samples were taken via venous puncture and analyzed for genotype using laboratory facilities at North Dakota State University. Various animal measurements were taken during the feeding phase, at slaughter, and 24 hours after slaughter. The research team, including the faculty, spent several January and February days in a South Dakota feedlot in sub-zero temperatures collecting data. Individual animals were marked using a temporary carcass tag at slaughter and followed through the grading process 24 hours after slaughter. A permanent carcass tag was pinned to each carcass as they were weighed and sent to the cooler. Complete data for each animal from placement through grading required the researchers to be present at each major step in this process.

Economic Analysis of the Leptin Gene

The leptin gene has been associated with animal metabolism, fat deposition, feed conversion, and milk production (Bierman et al.³ 2004; Buchanan et al. 2002, 2003; Kononoff et al. 2004; Larson et al. 2005, 2006). Table 1 summarizes the current state of knowledge concerning leptin genotype, cattle performance and traits, and profitability. Lambert and DeVuyst (2006), DeVuyst et al. (2007), and Lusk (2007) demonstrate that leptin genotype has the potential to affect the value of beef carcasses, feedlot profitability, and ultimately feeder animal markets. Value derives from the grid (or formula) pricing of beef carcasses, where prices are based on weight and discounts or premiums for carcass quality and yield. Mutations in the leptin gene have been shown to affect carcass yield grade (Schenkel et al. 2005; Larson et al. 2005, 2006) and carcass quality grade (Larson et al. 2005, 2006). Consequently, leptin genotypes and haplotypes have the potential to affect feedlot profitability by decreasing lean yields leading to smaller premiums or larger discounts, increasing marbling scores leading to larger premiums or smaller discounts, and possibly affecting time on feed and feed costs.

³The notation in Bierman et al. (2004) is somewhat confusing relative to current genetics notation. Their "CC" genotype refers to the "TT" genotype discussed here and "RR" is equivalent to the "CC" genotyped discussed here.

Knowledge of the function of specific genes may lead to better predictions of final outcomes, and management strategies can be optimized given likely biological outcomes. For example, if genetic information indicates that a steer is likely to produce less external carcass fat (i.e., a high-yielding carcass⁴), rations might differ from rations for a steer with a genetic disposition towards deposition of more external carcass fat. Optimal feeding periods may differ among genotypes based on optimal times on feed and likely final weight, yield, and quality grade outcomes. Marketing strategies may also differ for animals of different genotype. For example, specific animals may be marketed using lean rather than quality grids.

Three studies analyze beef animal feedlot performance based on the leptin gene (Lambert and DeVuyst 2006; DeVuyst et al. 2007; Lusk 2007). Based on placement and carcass information, Lambert and DeVuyst's research suggested optimal selection of feeder cattle based on genotype. Optimal number of days on feed did not change when genotype was known. However, lean (CC genotype) steers under identical feeding schedules returned between \$13 and \$30 per head more than TT (fat genotype) animals. Net return measures under both models were significantly higher for CC (lean) than CT (mixed or heterozygous) and for CC (and CT) over TT (fat) animals. The difference in returns was not, however, large enough to cover individual animal genotype testing costs.

In contrast, DeVuyst et al. (2007), studying the same SNP as Lambert and DeVuyst (2006), reported an economic advantage from feeding TT (fat) genotype cattle, both steers and heifers. Their results show that optimal days-on-feed varied little by genotype, but advantages from feeding TT cattle vs. CC cattle was over \$20 per head and as large as \$37. Both heifers and steers were considered in their study. As was expected, TT cattle were more likely to grade Choice and Prime but also more likely to yield grade 3 and higher. Given genotype testing costs of around \$35 per sample, DeVuyst et al. (2007) conclude that genotyping is close to breaking even depending on market prices and other factors.

Lusk (2007) analyzed the economic impact of two SNPs on the leptin gene. He analyzed feedlot performance data for 1,668 commercial cattle. He found use of genetic information potentially adds \$23/head for steers and \$28/head for heifers if producers optimally select and feed cattle based on genotype. Upper limits of \$60/head were realized if animals were optimally marketed based on genetic traits. Lusk (2007) concluded that the ultimate gainers from increasing information content of leptin gene characteristics will be owners of fixed assets, such as animal genetic stock, owners of genotyping technology, and perhaps consumers who are able to obtain meat products better matching tastes and preferences.

While the three available economic studies on leptin genotyping show positive returns to genotyping, there are still many unanswered questions. Optimal days on feed varied little when the producer possessed or did not possess genotypic information. Also, unaddressed is how these differences are affected by recent high feed prices. In fact, all three studies ignore potential differences in feed intake and feed efficiency by genotype. The testing of the relevant biological and economic hypotheses would require a feeding trial through the finishing period and collection of relevant carcass traits post-slaughter. These data have not yet been collected.

⁴Some confusion is possible regarding yield. USDA uses yield grades 1 through 5 to indicate leanness. High-yielding carcasses are given low USDA yield grade scores, where the fattest carcasses are given a USDA yield grade 5.

Table 1. Summary of Leptin Genetics Research.

Author(s) / SNP location	Result (Significance)
Bierman et al. 2004 Exon 2 SNP 305	T allele decreases cutability ($p < 0.10$), marbling ($p < 0.05$) and increases % Choice ($p < 0.10$)
Buchanan et al. 2002 Exon 2 SNP 305	T allele increases fat deposition ($p \leq 0.023$) T allele more frequent in Angus than in Charolais and Simmental ($p < 0.05$)
Buchanan et al. 2003 Exon 2 SNP 305	TT Holstein cows milk 1.5 kg/d more than CC cows ($p = 0.04$)
DeVuyst et al. 2007 Exon 2 SNP 305	T allele in fed cattle reduces ribeye area ($p < 0.05$) TT cattle fatter than CC ($p < 0.05$), heavier than CC ($p < 0.10$) and \$14-\$48/hd more profitable than CT and CC cattle (NA)
Kononoff et al. 2005 Exon 2 SNP 305	T allele associated with higher yield grade scores ($p \leq 0.06$) and not associated with carcass weights ($p = 0.03$) TT cattle have higher quality grades than CT (NA) No difference between TT and CC quality grade and yield grade (NA)
Lambert & DeVuyst 2006 Exon 2 SNP 305	CC cattle \$6-\$8 more profitable than CT (NA) CC cattle \$13-\$31 more profitable than TT (NA)
Larson et al. 2005 Exon 2 SNP 305	TT cattle have thicker backfat than CT or CC ($p = 0.04$) TT cattle have smaller ribeye than CT or CC ($p = 0.02$) TT cattle have higher yield grade scores than CC ($p = 0.03$) No differences in average daily gain by genotype (NA)
Larson et al. 2006 Exon 2 SNP 305	CC cattle have larger ribeye than CT or TT ($p < 0.001$) TT cattle have higher yield grade scores than CT or CC ($p < 0.001$) TT cattle have higher marbling scores than CC or CT ($p = 0.01$)
Lusk 2007 Exon 2 SNP 305 + USASMS2	Difference cattle value varies by genotype by as much as \$60/hd (NA)
Nkrumah et al. 2005 USASMS2	T allele increases backfat thickness ($p = 0.001$), marbling score ($p = 0.01$), dry matter intake ($p = 0.001$), final live weight ($p = 0.1$), dry matter intake ($p = 0.001$) T allele does not affect feed efficiency ($p = 0.81$), ribeye area ($p = 0.40$)
Nkrumah et al. 2005 USASMS3	G allele increases final live weight ($p = 0.04$), backfat thickness ($p = 0.04$) G allele does not affect feed efficiency ($p = 0.29$), marbling score ($p = 0.36$), or ribeye area ($p = 0.64$)

*Not available or reported.

Markets and Genetic Information

The three studies quantified the relationship of genotype with feedlot performance and carcass quality and value. All three found an economic value to the genetic information. While management strategies did not always differ by genotype,⁵ genotype did affect the value of the finished animals. Consequently, if genetic information could be collected at low cost, producers may pay more for feeder cattle with preferred genetics. As DeVuyst et al. (2007) demonstrate, the benefits of individual animal testing are, at best, about equal to the costs. Can the benefits be realized by reducing testing costs? One possible solution may be to reduce the fixed cost of genetic testing through selective breeding programs. Thallman and Hruska (2004) thus argue for using DNA markers to assist breeding stock selection. Selection and mating criteria may include phenotype, EPDs, and known DNA markers. Mating of cattle with known genotype would result in a predictable distribution of calf genotypes from a cow-calf producer. Further, if both dam and sire are homozygous (CC or TT, for example), the genotype of offspring is predetermined. As each cow is expected to wean multiple calves over her life and each bull may sire hundreds or even thousands of calves, the fixed costs of genotyping just the breeding stock would be spread over numerous calves. If calves from these matings are retained for breeding purposes, the costs of genotyping could be spread over generations of cattle.

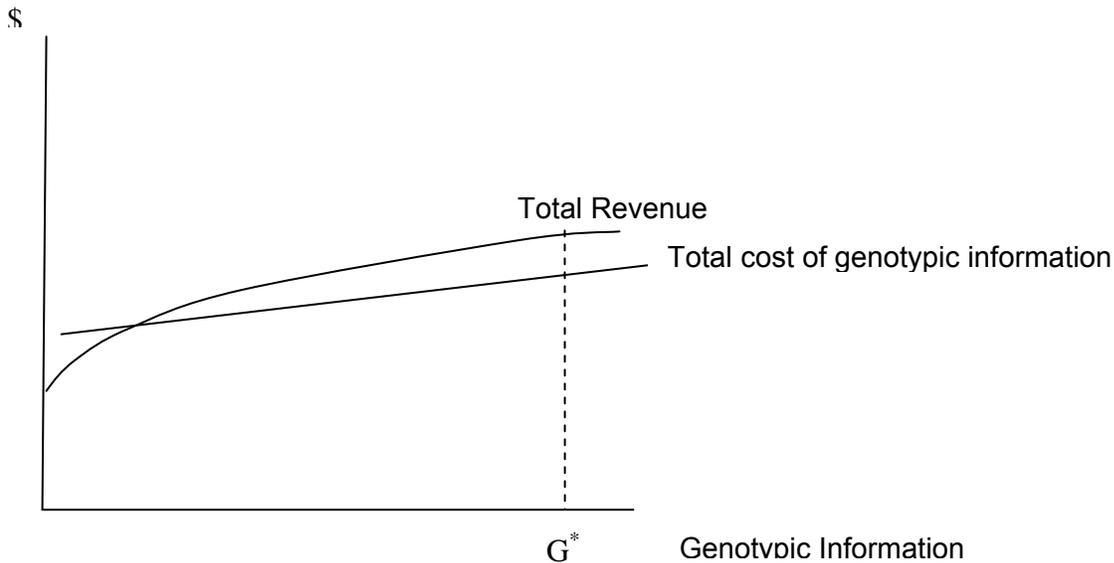
Utilizing genetic information throughout the supply-demand chain and across generations of cattle requires that mechanisms be developed to reliably collect, store, and transmit information. For breeding stock, breed registries have been established to relay information. Pedigree, EPDs and progeny data are usually maintained in these registries. Adding relevant genotypic information should be low cost (after the cost of collecting the DNA data), though occasional verification of genetic data will be necessary given common mating practices (e.g., multiple bulls in a pasture or lot) and errors. Transmission of data beyond the cow-calf operation becomes more difficult. Consider data that may be relayed to consumers, such as a genetic index measuring tenderness. These data must be maintained and relayed for individual animals from cow-calf producer to the supermarket shelf or restaurant menu. Current data collection and maintenance methods are not established, at least on an industry level, to allow for that level of identity preservation. Read-write identification tags could aid in these collection, maintenance and transmission efforts. The costs of these information services and who pays for these services have not yet been determined. What can be stated with confidence is that, if there is significant value in collecting, maintaining and transmitting genotypic information, mechanisms will eventually be developed to capture that value.

In figure 1, we show total producer revenue as a function of genotypic information. Concavity of the total revenue function implies diminishing marginal value as information increases. If, for example, there are 100 SNPs affecting marbling, the value of the additional information contained in knowledge of the last SNP is likely relatively small, especially since each SNP explains a very small percentage of biological variability. The total cost of collecting genotypic information has a high fixed cost associated with collecting a DNA sample and preparing it for

⁵None of the studies were based on feeding trials. Thus, the relationship between genotype, feed intake, and metabolism remain unanswered.

analysis. For illustration, marginal costs of genotypic information are assumed constant in figure 1. With high-throughput DNA analysis, assessing additional SNPs does not require additional analysis time. Hundreds of SNPs can be evaluated simultaneously for each sample.

Figure 1. Total revenue vs. total costs of genotypic information.



A profit-maximizing producer would choose to maximize the difference between total benefits and total costs. In figure 1, this occurs at G^* . At this time, however, additional research is necessary to quantify the benefits and costs of genotyping. DeVuyst et al. (2007) report the value of a single SNP ranges from about \$0.01 to over \$48 per head, depending on how the information was utilized. Lusk (2007) reports that knowledge of two SNPs adds between \$22 and \$66 in additional revenue per head. The costs of acquiring genotypic information are also difficult to estimate. A panel of leptin markers costs about \$37.50 (Lusk 2007), but that does not include the costs of collecting the DNA sample.

The final observation depends upon the organization of the cattle industry. The expected value of the information initially represents unclaimed rents. Rent distribution will depend upon the relative market power of market participants. Research has identified the potential for increasing market power by livestock processors resulting in part from increasing concentration (Schroeter 1988; Sexton 2000). Reliance by processors on production contracts might result in a greater share of the rents accruing to processors. Conversely, were significant numbers of animals to enter the market without contracts, sufficient incentives must be provided to suppliers to provide the optimal mix of animals with differing levels of genotypic information. Incentives would require at least some sharing of the potential rents between buyers and sellers in the market. Further, given that collection and maintenance of genomic information is costly, the costs of producing animals with known genetic markers are likely higher than for animals with unknown genetic markers. There will likely be a need to share rents between economic agents in the livestock production sector in order to provide incentives to all participants to collect and maintain the genetic data.

Additional research is necessary to quantify demands for different information sets, a necessary component to determine the expected value of genetic information underlying figure 1. Industry studies should also project rent distribution and possibly contract design to ensure sufficient incentives exist for suppliers to provide the optimal levels of genetic information collected.

We have discussed how genetic markers affect producers and processors. There are also, however, consumer effects. Beef demand is affected by prices and quality attributes of competing meats. If genetic information can be used to increase the quality and consistency of beef products, there may be an outward shift in consumer demand for beef (Hennessy, Miranowski, and Babcock 2004). More genetic markers for marbling and tenderness are becoming known, though a large number of genes are involved in determining these traits. MMI Genomics utilizes 128 SNPs to predict marbling and 11 SNPs for tenderness (Ishmael 2007). Consumer willingness to pay for higher quality and more consistent quality meat will determine the economic viability of testing large numbers of markers. Until lower cost methods of testing for these markers are available and markets develop to reward desirable genomic structure, rent capture associated with this genetic information will be elusive.

Promising Genetic Research and Economics

On-going biological research programs, both privately and publicly funded, are identifying SNPs and their biological impact on livestock. Hocquette et al. (2007) report that an EU-funded project to identify SNPs in cattle genes has found 710 SNPs in 209 genes. Hocquette et al. (2007) also list commercial testing services currently being offered for marbling, tenderness, milk fat yield, milk yield, feed efficiency and other beef and dairy animal traits. These tests are in addition to the MMI tests for marbling (89 markers), tenderness (11 markers) and daily gain (92 markers) (Ishmael 2007). Economists have considered few of these markers and their impact on profitability for seed stock producers, cow-calf producers, feedlot operators, meat processors and retailers.

Although tenderness and other desirable attributes have been the subject of several experimental economics studies (e.g., Melton, Huffman, and Shogren 1996; Lusk et al. 2001), two important points are yet to be addressed. The first point is the effectiveness of the link between profitability in the various steps of production and consumer demand. If consumers are willing to pay for desirable attributes, how will profits be divided among supply chain agents? The second point concerns signaling of product quality (e.g., tenderness) to the consumer. Testing of individual carcasses and cuts is unlikely to prove profitable. However, DNA-based information might provide evidence of likely tenderness and other desirable attributes. Since genomic testing of individual animals is currently cost prohibitive, testing for various markers may best occur at the seed stock level. If genomic information relating to end product quality can be credibly relayed from seed stock producers to cow-calf producers to feedlot operators to processors to retailers to consumers, markets may reward testing for these markers and to credibly relay the production-related genomic information among agents in the supply chain.

Scientists are quickly unraveling the genetic code of animals and plants. Applied scientists are finding important pathways between genotype and crop and livestock growth and metabolism. Economists have long used both traditional (e.g., Babcock 1990) and more innovative methods (e.g., Hennessey et al. 2004) to assess the expected value of information embedded in the biological relationships. Vast research needs exist. Much still needs to be learned about how various SNPs influence economically-relevant biology. Collaboration among animal scientists

and economists is essential to realize the economic benefits embedded in an animal's genes. In order to realize those benefits, economists and their biological sciences colleagues must develop an improved understanding of

- The relationships between genetic markers and cattle performance factors (i.e., feed intake and feed efficiency);
- The relationships between genetic markers and yield grade factors;
- The relationship between genetic markers and quality grade (i.e., marbling);
- The relationship between genetic markers, desirable consumer attributes (e.g., tenderness, flavor, texture, and juiciness) and consumer willingness-to-pay;
- How markers contribute to seed-stock producers', cow-calf producers', feedlot operators' and packers' profitability; and
- The costs of obtaining genotypic information and credibly relaying that information through the supply-demand chain.

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