Using genetic tools to meet market targets without sacrificing maternal performance

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ABSTRACT: Changes in beef production/marketing systems are creating incentives for beef producers to improve carcass quality. Current grid marketing schemes are characterized by premiums for carcasses that excel for marbling and(or) retail product and by large discounts for noncompliance factors. Economic incentives for producers to select for tenderness may be on the horizon. Effective tools are available for producers to genetically tailor cattle to specific markets. New DNA markers for carcass trait QTL will help cattle producers identify genetically superior animals at younger ages. Markers will be used most efficiently when marker genotype information is incorporated directly into the computation of EPD, and after potential epistatic interactions and genotype × environment interactions are characterized for each QTL. Limited research has not identified risks associated with maternal performance due to selection for increased marbling or tenderness. However, selection for increased lean yield carries risks of older age at puberty, increased mature size, decreased fertility, and possibly increased maternal calving difficulty. Systems research indicates that reduced fertility would have large negative effects on profitability. To avoid detrimental effects on maternal traits, genetic management should consider EPD for multiple traits as part of a systems approach. Managers will deal with increasing amounts of information and detailed monitoring of production costs will become increasingly important to success. Structured crossbreeding, exploiting heterosis and breed strengths, should be used to increase profitability of production systems. Management strategies to reduce phenotypic variation in market groups and to match genetic potential with nutritional management are expected to increase competitiveness in grid marketing schemes.

Key Words: Beef Cattle, Carcasses, Genetics, Maternal Transmission, Systems

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Introduction

U. S. beef production and beef marketing are changing. Beef production systems are becoming more product-oriented rather than commodity-oriented. Value-based marketing is being stimulated by technologies such as electronic identification and Internet commerce. Production segments are becoming more coordinated, sometimes by formal business alliances, sometimes by improved information transfer and measurement of value.

Industry changes are providing new incentives for genetic changes in carcass traits. Developing technologies are providing new genetic tools for making these changes. Cow-calf producers are challenged to genetically tailor cattle to meet new and dynamic markets, yet continue to manage cattle and natural resources in a sustainable manner.

My objectives are 1) to identify the economic aspects of carcass quality and the traits that will likely receive increased attention in future breeding programs, 2) to anticipate how important maternal traits might change in response to selection for different aspects of carcass quality, and 3) to discuss genetic tools and their application in meeting these new carcass targets without sacrificing maternal performance.

Review and Discussion

Economic Incentives for Genetic Change

Grids. Current marketing systems for fed cattle reflect value differences associated with several traits, most of which are measured after slaughter (USDA, 2001). Primary traits include USDA quality grade and USDA yield grade. Quality grade, largely determined by marbling, is intended to be a measure of palatability (USDA, 1997). Yield grade, determined by carcass weight, longissimus muscle area, fat thickness, and kidney, pelvic and heart fat, predicts retail lean yield. Some systems recognize additional indicators of quality grade

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and yield, such as breed identification and muscling. Quality grade and yield grade form the basis of most grid pricing systems (two-dimensional set of premiums and discounts) for individual carcasses and motivate price differentials paid for groups of cattle sold before slaughter. Magnitudes of these premiums and discounts vary seasonally in response to supply and demand factors (LMIC, 2001). Grid prices may also differ among alliances and(or) packers.

Grid marketing schemes normally take into account several compliance factors, measures that largely identify carcasses that cannot be marketed through mainstream channels. Compliance factors include extremes in carcass weight (light or heavy), undesirable levels of maturity, carcasses from bulls or dairy breeds, and dark cutters (USDA, 2001). Essentially, there are no premiums for compliance factors, only discounts. Generally, discounts for the most undesirable quality and yield grades (standard quality grade and yield grades ≥ 4), and for noncompliant carcasses are much larger than premiums paid for desirable quality grades and yield grades. Hence, these carcasses are referred to as "out-cattle" (i.e., cattle that do not fit the grid). Discounts for out-cattle are so severe that it can easily take two or more premium carcasses to balance one noncompliant carcass.

Grid marketing schemes provide incentives for beef producers to genetically improve quality grade and yield grade. In addition, there are strong incentives for producers to avoid marketing out-cattle. Because out-cattle are associated with extreme values for quality grade, yield grade, and carcass weight, the incentive to avoid out-cattle is largely an incentive to market cattle with less phenotypic variability.

Niche Markets. Utilizing coordinated networks or integrated systems some beef producers are targeting specialized or niche markets. Generally, these systems market beef products at the retail level with brand name identification. Examples include Laura's Lean Beef (Laura's Lean Beef, 2001), Montana Range (Leachman, 2001), and Coleman Natural Products (Coleman, 2001). Product definition varies among systems but usually focuses on a specific aspect of eating quality (e.g., tenderness or leanness) or food safety (e.g., free of antibiotics). Depending on the market niche, producers participating in these systems experience incentives for genetic change that may be different from those for producers marketing through mainstream channels.

Tenderness is considered a very important heritable palatability trait (Dikeman et al., 2001). Tenderness must be measured on cooked meat, and available technology to measure tenderness in commercial packing plants is considered too expensive (NCBA, 1998a). Therefore, there is currently no industry mechanism to provide information feedback to producers on a large scale. Except for production systems marketing branded retail products (e.g., Montana Range; Leachman, 2001), there is currently little economic incentive for producers to select for tenderness. However, due to the importance of tenderness to beef demand, it seems likely that affordable technology will be soon developed to address this issue, and economic incentives for producers to select for tenderness may be on the horizon.

Genetic Relationships Between Carcass and Maternal Traits

The components of quality grade and yield grade are moderately to highly heritable (Marshall, 1994; Shanks, 1999; Shanks et al., 2001); hence, selection is expected to be effective in changing these traits. Historically, carcass traits have not received much attention in the breeding plans of U.S. beef producers. As beef producers now focus on carcass traits, answers to important questions are needed: 1) Will selection for improved carcass characteristics lead to undesirable correlated responses in important maternal traits and 2) Will breed substitutions to improve carcass quality negatively affect maternal traits? Regrettably, few experiments focusing on selection for carcass quality have been conducted. Therefore, few correlated selection responses have been documented, and we must rely on less direct types of information. I will focus on three traits: marbling, retail product (or yield grade and its components), and tenderness.

Marbling. At the University of Nebraska, Angus sires with high and low EPD for marbling were randomly mated to MARC II composite cows. Progeny were evaluated for growth and carcass traits (Vieselmeyer et al., 1996) and palatability traits (Gwartney et al., 1996). Because heifers were slaughtered, this study provided no information on correlated responses in maternal traits.

Frazier et al. (1999) used field data to evaluate associations of Angus sire marbling score EPD with reproductive performance of females. Marbling score EPD was significantly associated with age at first calving; however, predictors were not consistent across states, even switching signs. Classifying sires into marbling score EPD categories produced inconsistent relationships with age at first calving. The authors concluded that marbling score EPD was not a good predictor of age at first calving or calving interval and suggested that selection for marbling should not affect these maternal traits.

Splan et al. (1998) estimated genetic correlations between male carcass traits and female reproductive traits. Genetic correlations between marbling score and age at puberty, calving rate, and calving difficulty were close to zero (Table 1), suggesting that little change would occur in these maternal traits in response to selection for increased marbling.

As the most popular U.S. beef breed (Taylor and Field, 1999), Angus has served as a benchmark for many breed evaluation studies. Angus cattle have higher marbling scores than most other beef breeds used in the United States (Cundiff et al., 1986). Breed comparisons have not identified problems with age at

Table 1. Genetic correlations between maternal performance traits and carcass traits[a]

Trait	Age at puberty	Conceptions/ service	Calving rate	Calving difficulty	Mature wt
Retail product wt	0.30	0.28		–0.02	0.25
Retail product %	–0.01		–0.13	0.18	
Carcass wt	0.17	0.61	0.05	–0.31	0.21
	0.06			–0.17	
Fat thickness	–0.29	0.21	0.19	–0.36	–0.09
	–0.01			–0.14	
Longissimus muscle area	0.04		0.15	–0.04	
Marbling score	–0.04		–0.05	–0.09	
Warner-Bratzler shear force	0.01		0.11	0.19	
Taste panel tenderness	–0.32		0.07	–0.42	

[a]Correlations involving retail product weight, conceptions/service, and mature weight are from MacNeil et al. (1984). Correlations involving retail product %, longissimus muscle area, marbling score, Warner-Bratzler shear force, and taste panel tenderness are from Splan et al. (1998). When two values are listed, the upper value is from MacNeil et al. (1984) and the lower from Splan et al. (1998). All carcass traits are adjusted to constant age.

puberty, calving difficulty, pregnancy rate, calf crop weaned, or maintenance requirements for beef breeds that rank high in marbling (Ferrell and Jenkins, 1985; Cundiff et al., 1986; Martin et al., 1992).

Retail Product. MacNeil et al. (1984) reported genetic correlations between retail product weight and age at puberty, conceptions/service, maternal calving difficulty, and mature weight (Table 1). Their results suggest that selection for increased retail product weight would lead to older ages at puberty, improved fertility, and increased mature size with no change in maternal calving difficulty.

Retail product percentage and retail product weight are not the same traits but are genetically correlated (0.46, Koch et al., 1982). Splan et al. (1998) computed genetic correlations between female traits and retail product percentage. Correlations reported by Splan et al. (1998) suggest that selection for retail product percentage will lead to no change in age at puberty, a small decline in calving rate, and a slight increase in maternal calving difficulty.

As components of retail product (or yield grade), fat thickness and longissimus muscle area are also of interest. Because breed associations report EPD for these traits, some producers may select for decreased fat thickness or increased longissimus muscle area. Genetic correlations reported by MacNeil et al. (1984) and Splan et al. (1998) indicate that selection for decreased fat thickness would negatively affect age at puberty, fertility, calving rate, and maternal calving difficulty. Selection for increased longissimus muscle area would have no effect on puberty or calving difficulty but would improve calving rate slightly (Table 1). Undesirable associations between maternal traits and retail product appear to be mediated through fat thickness.

Breed comparisons involving breeds that excel for retail product are confounded by the fact that some of these breeds also have high milk production. Restricting comparisons to breeds that have moderate milk but increased growth and lean yield suggests that heifers sired by these breeds tend to be about 1 mo older at puberty and have lower heifer pregnancy rates than breeds with less rapid growth and lean yield (Cundiff et al., 1986; Martin et al., 1992); however, most heifers from these breeds should still reach puberty before their first breeding season under good nutritional management. Means for calving difficulty and calf crop weaned were similar for breeds with moderate vs more rapid growth and lean yield (Cundiff et al., 1986). Bennett and Williams (1994) hypothesized that cows from larger, leaner breeds would require better nutritional management than more moderate types. Nugent et al. (1993) reported that these biological types of cows had shorter postpartum intervals in response to increased feed. Compared to progeny of sires from moderate breeds, progeny of sires from breeds characterized by rapid growth and high lean yield and dams of moderate types are expected to experience more calving difficulty and calf mortality, leading to reduced rebreeding rates in dams (Cundiff et al., 1986).

Feed requirements for maintenance account for over 70% of annual requirements for beef cattle. Many studies have attempted to estimate maintenance requirements for different breeds and biological types (Ferrell and Jenkins, 1985, 1998a,b). In some studies larger, leaner breeds had higher maintenance requirements (Mcal ME/kg$^{0.75}$) than more moderate types, but not in others. Ferrell and Jenkins (1985) concluded that maintenance requirements are positively associated with genetic potential for measures of production such as growth rate and milk yield. However, the relationship between maintenance and milk potential seems to be stronger than that between maintenance and growth potential, and U.S. feeding standards (NRC, 1996) do not adjust maintenance requirements upward for larger, leaner breeds. The lack of independence between estimates of maintenance and the efficiency of energy use for growth, and the change in efficiency of energy use for growth with changing energy intake makes estimation and interpretation of these parameters difficult (Ferrell and Jenkins, 1998a,b).

Although easily classified as high retail product breeds (Wheeler et al., 1996), Belgian Blue and Piedmontese are distinct from other breeds due to their frequent expression of muscle hypertrophy (double-muscling), a condition caused by the effects of alleles at a single locus (inactive myostatin, Casas et al., 1998, 1999). Compared to homozygous normal animals, individuals carrying a single copy weigh more at birth but experience similar calving difficulty, have larger longissimus muscle area, less fat thickness, and greater retail product yield, yet do not express double-muscling (Casas et al., 1998, 1999). Heifers sired by Piedmontese bulls average 15 to 20 d younger at puberty than Angus or Hereford crossbreds (Thallman et al., 1999; Lammoglia et al., 2000). Pregnancy rates, calving and weaning percentages, and postpartum intervals to estrus for Piedmontese- and Belgian Blue-sired heifers appear to be similar to those for Hereford and Angus crossbreds (Freetly and Cundiff, 1998; Thallman et al., 1999).

Tenderness. Splan et al. (1998) reported genetic correlations between two measures of tenderness (Warner-Bratzler shear force and taste panel tenderness) and maternal traits (Table 1). Inconsistencies among correlations for shear force and taste panel tenderness make conclusions difficult; however, their results suggest that selection for increased tenderness should lead to less maternal calving difficulty and possibly younger age at puberty.

Differences in Warner-Bratzler shear force and(or) taste panel tenderness have been demonstrated among several breeds (Marshall, 1994; Wheeler et al., 1996). Generally, tenderness measures for F_1 crosses have been within acceptable ranges. *Bos indicus* tend to be less tender than *Bos taurus* breeds. Two breeds that appear to excel for tenderness are Pinzgauer and Piedmontese (Marshall, 1994; Wheeler et al., 1996). The tenderness advantage for Piedmontese does not appear to be associated with the myostatin locus (Casas et al., 1998). Reproductive comparisons involving Piedmontese were reviewed above. Pinzgauer heifers tend to be about 2 wk younger at puberty and have higher pregnancy rates than Hereford and Angus crosses, whereas calving difficulty and calf crop percentages are similar for these breeds (Cundiff et al., 1986; Martin et al., 1992).

Potentially Sensitive Traits in Range Cow-Calf Production Systems. Based on this brief review, there is little evidence to suggest that selection for increased marbling or increased tenderness or that substituting with breeds that excel in these traits will lead to declines in maternal performance. It should be emphasized, however, that direct measures of correlated responses to selection have not been reported. On the other hand, selection for increased retail product is expected to lead to older ages at puberty for heifers, heavier mature weight, and possibly increased maternal calving difficulty. Selection for decreased carcass fat thickness is expected to lead to older ages at puberty, decreased fertility and calving rate, and increased calving difficulty. Breed comparisons suggest that compared to moderate breeds, breeds that excel for growth and lean yield are older at puberty, except for the double-muscled Belgian Blue and Piedmontese, which are younger. Breed comparison studies have not identified important differences in maternal calving difficulty or calf crop weaned due to increased growth or leanness.

It is important to know just how detrimental changes in these maternal traits might be to ranch profitability. Using systems analysis techniques (Tess and Kolstad, 2000a,b), Tess (1999) evaluated the effects of changes in several maternal traits on cow-calf enterprise profitability in a range environment. This study demonstrated that system performance was quite sensitive to performance levels for postpartum interval to estrus and mature cow conception rate (i.e., fertility). Postpartum intervals greater than about 70 d led to precipitous drops in gross margin. Gross margin declined in a nearly linear fashion with mature cow conception rate. Together, postpartum interval and conception rate largely determine calving rate. Profitability was relatively insensitive to calving difficulty rate. Increased age at puberty and decreased heifer conception rate led to higher replacement rates, yet their effects on gross margin depended on marketing strategies for cull heifers. If nonpregnant heifers were sold following the grazing season, gross margin was relatively unaffected, essentially shifting income from calves to yearlings. If nonpregnant heifers were given an additional year to breed, gross margin declined after age at puberty exceeded approximately 420 d. Similarly, if nonpregnant heifers were retained profitability declined in a nearly linear manner as heifer conception rate declined.

Most female reproductive traits have a minimum level of performance below which herd size cannot be maintained without purchasing replacements. The results of Tess (1999) suggest that the relationship between profitability and maternal performance is mirrored by the effects of maternal traits on calf weight weaned per cow exposed, or by weight sold per cow exposed. Any genetic or management change that decreases these measures is likely to be detrimental to ranch profit. Estimates of economic weights for fertility have consistently been positive (Kolstad, 1993; MacNeil et al., 1994; Koots and Gibson, 1998a,b).

Several researchers have studied the effects of mature size on beef enterprise profitability. Using systems analysis techniques, Kolstad (1993) found that increases in mature weight for maternal strains, independent of other growth traits, had negative effects on profit. Similarly, MacNeil et al. (1994) reported that the relative economic value of mature weight was negative for maternal strains and general-purpose strains in all production/marketing scenarios studied. Koots and Gibson (1998a) reported that mature weight had a positive economic value in general-purpose lines; however, in their model mature weight accounted for other growth traits. Further, the economic value of mature weight was sensitive to the marketing assumptions and base trait means (Koots and Gibson, 1998b). Heavier mature weight represents added overhead in terms of feed for maintenance (per cow, Cundiff et al., 1986). For a given feed resource (e.g., rangeland), increasing feed requirements per cow will require reductions in herd size (Tess and Kolstad, 2000b). Cows that excel in rapid early growth but mature at lighter weights should be desirable in most systems.

The Genetic Toolbox

There are a variety of genetic tools currently available to beef producers, and new tools are sure to be developed. Just like a mechanic uses different tools for different jobs, beef producers should use genetic tools based on their effectiveness, ease of application, and cost.

Breed Resources. Breed differences in carcass traits have been reported in several studies (Marshall, 1994; Wheeler et al., 1996). For some producers, exploiting breed differences will be the fastest way to make genetic adjustments in carcass quality. If females will be used as replacements, choices among breeds should be based on maternal as well as growth and carcass traits (Cundiff et al., 1986). For some niche markets, production of animals that carry a single copy of the inactive myostatin allele may form an important component of the breeding strategy (e.g., Montana Range, Leachman, 2001).

Expected Progeny Differences. To practice effective selection within breeds, estimates of breeding value or EPD are needed. Compared to most growth traits, traditional performance and progeny testing for carcass merit is more difficult. Carcass traits cannot be measured directly on potential parents. Carcass measurements on cattle (i.e., progeny or other relatives of potential parents) marketed and harvested through mainstream commercial channels are expensive to collect. Ownership of calves can change several times prior to slaughter and cattle are typically moved to different locations during their lifetime; hence, maintaining animal identification and information feedback to the cow-calf segment (i.e., where breeding decisions are made) are difficult tasks. Nevertheless, carcass traits are moderate to highly heritable (Marshall, 1994; Shanks, 1999; Shanks et al., 2001) and several breed associations currently compute and publish EPD for carcass traits based on direct measures of carcass quality.

Current technology permits computation of adjustment factors for comparing EPD across breeds (across-breed EPD; e.g., Barkhouse et al., 1998) or by computing EPD for animals from different breeds using one multibreed dataset (multiple-breed EPD; Pollak and Quass, 1998). Across-breed EPD adjustments are currently not available for carcass traits.

Ultrasound. Problems associated with direct measures of carcass quality have motivated searches for traits that could be measured on live animals, especially potential parents, that could provide information on carcass quality. Real-time ultrasound has proved to be an effective technology to meet this goal (Wilson, 1992).

An ultrasound measurement made on potential breeding stock raised under ranch conditions (e.g., bulls or heifers at 1 yr) is not the same trait as the direct measurement made on carcasses from animals grown in a feedlot, but a genetically correlated trait that explains (or accounts for) some but not all the variation in the carcass trait. Estimates of genetic correlations between carcass measures and ultrasound measures are needed before EPD for carcass traits can be computed using ultrasound records (e.g., Moser et al., 1998). Hence, breed associations have taken one of four approaches to computing EPD for carcass traits: 1) using carcass data to compute carcass EPD, 2) using ultrasound data to compute ultrasound EPD, 3) computing separate EPD for carcass and ultrasound, or 4) using carcass and ultrasound records to compute a single carcass EPD (i.e., via the genetic correlations).

Due to the fact that ultrasound measurements are made on potential parents, one might predict that future carcass trait EPD will be essentially based on ultrasound measurements. However, developing technology related to source and process verification (i.e., electronic animal identification, animal tracking networks, and Internet data transfer) might facilitate a different course. If this electronic technology is widely adopted, and if the expense is low, direct carcass measures might eventually be the dominant source of genetic information on carcass traits.

Genetic Markers. Molecular genetic markers (i.e., DNA markers) have been reported for QTL affecting several carcass components, including rib bone and dressing percentage (Stone et al., 1999) and marbling score (Casas et al., 2001; GeneStar, 2001). Research also suggests the possibility of QTL for carcass weight, fat depth, longissimus muscle area, and retail product yield (Stone et al., 1999; Casas et al., 2000, 2001). The muscle hypertrophy locus (inactive myostatin allele) found in the Belgian Blue and Piedmontese breeds has been mapped (e.g., Fahrenkrug et al., 1999) and shown to affect longissimus muscle area, retail product yield, marbling, yield grade, fat thickness, and kidney, pelvic, and heart fat. Undoubtedly, additional markers will be discovered and validated for these and other traits (NCBA, 1998b). Markers that prove to be closely linked to important QTL (i.e., QTL having a large economic effect) or markers that actually map to the QTL locus will likely be rapidly commercialized (e.g., GeneStar, 2001).

Due to the part/whole relationship between QTL and the target trait, DNA markers explain a portion, but not all, of the genetic variation in the target trait. In other words (and similar to ultrasound), DNA markers account for part, but not all, of an animal's carcass EPD. The utility of DNA markers is due to the fact that the genotype for the marker, and hence a portion of the EPD, can be determined early in life on potential parents. The most valuable markers will be those that explain a significant portion of one or more EPD and can be economically assayed. Physiological measurements such as blood hormone concentrations could potentially have similar utility in providing early indicators of genetic merit. For example, Davis and Simmen (2000) found that bulls with lower serum IGF-I concentrations had higher marbling scores, quality grades, fat thickness, and yield grades.

In the future, it is likely that marker genotype information will be incorporated into national genetic evaluation programs. In other words, information from DNA markers will supplement performance information in computing EPD. As described for ultrasound, genetic correlations between marker genotype and the trait of interest will be needed in order to incorporate this information into the computation of EPD. If ultrasound and carcass measures are both used to compute EPD, genetic correlations between the QTL and both measures will be needed.

Risks and Questions. Marker-assisted selection will no doubt help beef producers be more competitive in the future. However, like most technology, it is accompanied by risk.

In the future, one can envision several DNA markers and possibly some physiological markers documented for each carcass trait, with private companies conducting assays for the markers. For a given trait, each marker will explain a portion, but not all of the EPD for an animal. To my knowledge no current genetic evaluation system explicitly includes marker genotype information in the analyses, but it is likely that such technology will be soon developed. Nevertheless, current carcass EPD (computed from direct carcass measurements and[or] ultrasound) already account for some of the effects of any QTL that exist for the trait. In other words, QTL affect performance whether we know they are there or not, and performance differences are the basis of EPD.

Consider a beef producer who is considering using semen from a bull based on genetic merit for some carcass trait, and assume that marbling is the trait of interest. It is easy to envision a situation in which the bull under consideration has a marbling EPD, plus one or more known marker genotypes for marbling QTL. Regardless of whether the EPD was calculated using the marker genotype information, the genetic information provided by the EPD and that provided by the marker genotypes overlap (i.e., they are not independent). In such cases the marker genotype information is likely to be overvalued by the beef producer.

As mentioned above, some DNA markers detect alleles at loci that are closely linked to QTL, whereas others detect actual QTL alleles. Using current technology for linked markers, usually only heterozygous animals can be identified (i.e., animals that carry one, but not two, copies of the desirable allele). Hence, it is possible for an animal to carry both desirable QTL alleles but they could be undetectable. In the industry, heterozygous bulls are generating much attention. An obvious problem with heterozygous bulls is that only half their progeny will carry the desirable allele. More important, the danger is that producers will value these bulls highly when it is possible, if not likely, that other bulls within the same breed are genetically superior because they are homozygous for the desirable allele and(or) because their net genetic makeup (EPD) is superior. Because QTL explain only part of the genetic variation for the target trait, it is possible for a bull to carry a desirable QTL allele yet not rank near the top of the breed for the trait.

Research relating to DNA markers has made great progress in a short time. Much effort has been expended to identify potentially useful markers, yet little is known regarding interactions involving QTL. In other words, for many QTL it is not known how or whether the QTL will interact with other QTL or the background genotype (epistasis), or whether the QTL performs the same in all production environments (genotype × environment interaction). For example, Casas et al. (2000, 2001) detected evidence of interactions between the myostatin gene and QTL affecting Warner-Bratzler shear force and fat thickness. Future research will likely address these questions. However, until these questions are answered for each QTL, there will be uncertainty in predicting their effects on performance.

Application of DNA technology in the beef industry faces obstacles and questions beyond the scope of this paper. Statistical procedures to incorporate QTL information into the computation of EPD are currently being developed. The computational complexity of these procedures may restrict the number of QTL that can be incorporated simultaneously. It may be necessary to validate that QTL (and their markers) are segregating in each breed. Private ownership of DNA technology and competition for business will limit information sharing. Cost/benefits of the technology to the beef industry may be difficult to calculate, and marketing of perceived benefits may drive application.

A Systems Approach to Genetics and Management

Similar to other industries, the beef industry is becoming more complex. Managers must deal with increasing amounts of information to be competitive. Coordinated and integrated production systems may need to supply beef products on a weekly basis to meet market demand. Calving in different seasons will make matching forage resources and nutrient demand more difficult (Reisenauer et al., 2001). Detailed monitoring of production costs will become increasingly important. Marketing strategies and genetic tools are just part of beef cattle management systems. Management from a total systems approach will be increasingly important to success.

As reviewed above, evidence suggests that producers breeding for increased lean growth risk loss of performance for some maternal traits, including age at puberty, fertility, calving ease, and mature size. Yet, the

Table 2. Reduction in phenotypic standard deviation (%) due to the production of various types of related calves[a]

Mating scheme	Additive genetic variance: 20.00 / Dominance variance: 20.00	Additive genetic variance: 40.00 / Dominance variance: 20.00	Additive genetic variance: 40.00 / Dominance variance: 40.00
Multiple unrelated sires	0.00	0.00	0.00
Sires = ½ sibs	0.63	1.26	1.26
Sires = ¾ sibs	0.78	1.57	1.57
Sires = full sibs	1.26	2.53	2.56
Sires = inbred full sibs (F = 0.25)	1.51	3.05	3.05
Single sire	2.53	5.13	5.13
Single inbred sire (F = 0.25)	3.18	6.46	6.46
Full-sib embryo transfer calves	7.80	13.40	16.33
Calves = clones	22.54	36.75	55.28

[a]Phenotypic variance = 100.00. No maternal effects.

research available regarding the relationships between maternal traits and marbling or tenderness is not extensive. Hence, uncertainty exists regarding how genetic emphasis on carcass performance will affect maternal performance. How do genetic tools fit into the management system to meet future markets?

Multiple Trait Genetic Management. First, it is important to emphasize that effective genetic management will be *multiple* trait management. In coordinated or integrated production systems profitability is determined by production efficiency in each production segment (cow-calf, background or stocker, and feedlot), plus end-product value. Carcass traits should never be the sole focus of genetic decisions. Markers (and possibly other indicator traits) will provide valuable early indicators of genetic merit. The industry will use markers most efficiently when information from marker genotypes is incorporated directly into the computation of EPD.

Fortunately, EPD are available for many important beef cattle traits. Widespread whole-herd reporting could facilitate genetic evaluation of additional maternal traits (Tess, 1999). Monitoring an array of traits in making selection decisions can prevent undesirable correlated responses. Most breed associations compute EPD for calving ease or birth weight, which can be used to avoid increases in calving difficulty. Some breeds compute EPD for mature weight, and most compute EPD for weaning weight, yearling weight, and carcass weight. These growth traits are highly correlated (Bullock et al., 1993; Northcutt and Wilson, 1993; Kaps et al., 1999); hence, monitoring EPD for these traits will help producers avoid unwanted increases in mature size. Grid discounts for extremely heavy carcasses provide further incentive to constrain mature size. Development of EPD for scrotal size and stayability will be useful in maintaining or improving age at puberty and fertility (Tess, 1999).

Heterosis. Second, the economic value of heterosis should be exploited, especially in reproductive females. Favorable heterosis effects for reproductive traits are well documented (Long, 1980; Cundiff et al., 1986; Gregory et al., 1992). Crossbreeding is an effective way of counteracting the potential increase in age at puberty expected from using breeds that excel for lean growth. Crossbred heifers reach puberty 1 to 3 wk earlier than purebreds (Gregory et al., 1991; Martin et al., 1992). Heterosis effects are desirable for most carcass traits except fat thickness and retail product percentage (Cundiff et al., 1986; Marshall, 1994).

Practical, structured crossbreeding systems and well-designed composite breeds permit breed differences and heterosis to be combined in a complementary manner and manage trade-offs due to genetic antagonisms (Gregory and Cundiff, 1980; Kress and MacNeil, 1999). Using systems analysis techniques, Lamb and Tess (1989) reported that two- and three-breed rotational crossbreeding systems produced about 11% more income than purebred systems in small herds. Davis et al. (1994) determined that maternal heterosis improved profit \$70·cow^{-1}·yr^{-1} for range-based cow-calf enterprises. Lamb et al. (1992a) found that rotational crossbreeding systems improved economic efficiency by an average of 16 to 17% over purebred systems. Tess and Kolstad (2000b) reported that a rotation of three composite breeds improved annual net income per cow by 12% and ranch gross margin by 6% when compared to the average of the same composite breeds managed as purebreds. Adding a composite terminal sire breed improved net income per cow and gross margin by 18 and 19%, respectively. Lamb et al. (1992b,c; 1993) found that rotational crossbreeding systems were economically more efficient than purebred systems in the feedlot segment and in integrated systems, regardless of the marketing end point.

Use of terminal sires probably gives producers the greatest flexibility in genetically tailoring cattle to specific market end points (Bennett and Williams, 1994). Terminal sire systems will be the most practical way of exploiting the advantages of animals that are heterozygous for single copies of QTL such as the inactive myostatin allele. Many producers, especially those managing small herds, find terminal sire systems difficult to implement due to problems associated with bull/cow ratios, generation of replacement heifers, and variation in performance between progeny of terminal sires

Table 3. Effects of breed variation and sorting on the range in sale weights (kg)[a]

Scenario	No sort	Sort off 5%	Sort off 10%
Uniform crossbreeding system	121	94	83
Inconsistent crossbreeding, maximum performance difference among breeds	137	107	93

[a]Steer calves sold at weaning. 60-d calving season. Calves removed are those with extreme heavy or light weights.

and maternal-line sires. It seems likely that economic incentives created by some markets may motivate more producers to purchase replacement heifers.

Reducing Variation. The large discounts associated with nonconforming carcasses in most grid-marketing systems can be avoided by marketing phenotypically uniform groups of cattle. Hence, managers have incentive to limit genetic variation as well as variation caused by management and environmental factors.

Related animals are genetically more similar than unrelated animals. Table 2 shows the expected reduction in phenotypic variation (i.e., the range in phenotypic values or the standard deviation) by producing different types of related calves. Using related sires has relatively little effect on phenotypic variation, even when heritability is high. The production of full-sib calves (i.e., through embryo transfer) or clones could reduce phenotypic variation for traits exhibiting much genetic variation (additive and dominance variance) (Lamberson, 1994), but it is doubtful that either will be practical in the near future in beef cattle. Inbreeding helps reduce variation, but the loss of performance associated with inbreeding is too great for this to be a useful tool (Brinks and Knapp, 1975). Within-family variation does not appear to be affected by differences in EPD between parents (Bullock et al., 2000). Unfortunately, there are few practical tools to significantly reduce genetic variation within breeds.

Genetic variation associated with breeds and mating systems also can add to variation among calves. Table 3 illustrates the expected weight variation among calves from herds using what could be called "uniform" crossbreeding vs herds using "inconsistent" crossbreeding. Predictions in Table 3 were simulated based on performance differences among British and Continental beef breeds reported by the U.S. Meat Animal Research Center (Cundiff et al., 1986). Herds using rotational crossbreeding based on breeds with similar performance levels (i.e., the same biological type) will produce variation similar to purebred herds. Similarly, well-planned terminal-sire crossbreeding systems and straight-breeding systems based on composite breeds will also exploit heterosis without increasing calf variation. Across-breed EPD and multiple-breed EPD can be used to choose bulls with similar EPD from breeds that might have quite different performance means, although these tools are not yet available for carcass traits. Crossbreeding systems that indiscriminately use sires from different biological types and switch sire breeds frequently will produce more variable calves.

Variation in calf age contributes greatly to variation in phenotype. Table 4 summarizes expected differences in variation associated with differences in the length of calving season. The range in weaning weights expected among steers born over a 45-d period is approximately 118 kg. This difference increases by another 36 kg for calves born over a 120-d calving period. The obvious way to restrict the calving period is to restrict the breeding season. However, the real issue is the length of the calving period rather than the number of days bulls run with the cows.

Sorting off extreme animals prior to sale or shipment can be an effective tool to reduce phenotypic variation. Tables 3 and 4 illustrate the effects of sorting on weaning weight variation. Just as ultrasound is used in feedlots to sort animals into management/marketing groups, it seems possible that DNA markers might also be used this way. For example, knowing whether cattle are expressing a major allele affecting marbling might help beef producers better match cattle with specific pricing grids, or knowing whether or not cattle are expressing a major allele for tenderness might reduce the risk of guaranteeing branded products as tender. The utility of using DNA markers as management/marketing tools will depend on the cost/benefit of the information.

Table 4. Effects of calving season length and sorting on the range in sale weights (kg)[a]

Calving season	No sort	Sort off 5%	Sort off 10%
45 d	116	90	78
60 d	121	94	83
90 d	136	108	94
120 d	152	118	103

[a]Steer calves sold at weaning. Uniform crossbreeding system. Calves removed are those with extremely heavy or light weights.

Implications

Information from DNA markers for carcass trait QTL will help cattle producers identify genetically superior animals at younger ages. Markers will be used most efficiently when marker genotype information is incorporated directly into the computation of EPD, and after potential epistatic interactions and genotype × environment interactions are characterized for each QTL. To avoid detrimental effects on maternal traits, genetic management needs to consider multiple traits as part of a systems approach. Structured crossbreeding, exploiting heterosis and breed strengths, should be used to increase profitability of production systems. Management strategies to reduce phenotypic variation in market groups are expected to increase competitiveness in grid marketing schemes.

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