

# Can cow adaptability and carcass acceptability both be achieved?

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## Abstract

Beef cattle producers are currently challenged to achieve simultaneous goals of cow adaptability to the production environment and carcass acceptability within the marketing environment. Although this is not an easy task, it is indeed possible with careful attention to design and proper implementation of breeding programs. The information presented in this article is an attempt to achieve the objectives of 1) providing an overview of how to match a beef producer and production system to a specific industry target, 2) discussing current and future tools needed for proper genetic decision-making in beef cattle improvement programs, and 3) providing some perspective on how the beef cattle industry can go about increasing "quality and consistency" while maintaining balances in cow herd efficiency and profitability.

*Key Words: Adaptability, Beef Cattle, Carcasses, Genetics*

## Introduction

Over the past couple of decades, the beef cattle industry has become a confusing place. Messages have been conveyed to producers at a fast and furious pace. This would not be a problem if these messages were consistent and if they were compatible with each other, yet this is far from the real situation.

One could compose a lengthy list of dichotomies in the current beef cattle industry. A partial list might include the following:

- A forage-based production system (low input) vs a concentrate-based feedlot system (high input).
- Fierce pride in producer individuality and independence vs strategic alliances and cooperative relationships.
- Segmentation and resulting inefficiencies vs vertical coordination and(or) integration.
- Traditional purebred cattle-focused seedstock production vs commercially oriented specification seedstock production.
- "Show cattle" vs "performance cattle"
- Commodity-based marketing vs value-based marketing.
- Totally "vested" beef cattle producers vs "less-vested" small land owners.
- Public lands vs private land use for beef production.
- "Artificially selected" cattle vs "naturally selected" cattle.
- "Animal welfare" vs "animal rights."
- Systematic crossbreeding vs mongrelization.
- Purebred breeding vs composite breeding.
- Increased quality and consistency vs increased genetic variation.
- High-tech production vs low-cost production.
- Matching the cow to the production environment vs matching the calf to the marketing environment (i.e., cow adaptability vs carcass acceptability).

The collective concerns and issues listed above, along with a number of others we could further list, have contributed to the confusion for beef cattle producers. Given how quickly these issues can appear, or increase in importance, what is a cow-calf producer to do?

## The Beef Industry Has a #1 Leverage Point

The U.S. National Beef Quality Audit (NBQA), conducted by Colorado State and Texas A&M Universities in 1991, was a wake-up call to the beef cattle industry. The results of the audit of the slaughter cattle population, conducted in 28 plants across the United States, indicated a total of some \$280 in inefficiencies for each fed steer and heifer produced in the beef business. Furthermore, when these inefficiencies were categorized, it became apparent that the majority of losses occurred due to excess fat production with lower consistency in taste than desired. These results indicated that the beef cattle industry needed to achieve change at the carcass level, by implementing a combination of changes in feeding and management practices coupled with genetic improvement.

The executive summary of the 1991 NBQA stated: "Some cattle are born to be misfits. Examples include cattle that are light-muscled, cattle that must be fed to the fattest end of yield grade 3 to grade Select, and cattle that must be fed to 680 kg live weights to reach desirable muscle:bone ratios. The beef industry would be well-served to identify such cattle and eliminate their parents from the breeding herd."

In addition, one of the strategies for improving the quality of beef identified by the consensus panel of the 1991 NBQA strategy workshop was to "eliminate biological types (not breeds per se) of cattle that fail to conform." This statement and philosophy brought the term genetic nonconformance into vogue. Since that time, considerable discussion has taken place regarding how to genetically better hit the industry targets for end product performance. Everything

from eliminating breeds, to combining breeds into composites, to making a new industry standard of 50% British:50% Continental slaughter cattle has been argued.

The NBQA was repeated again in 1995. In comparison to the 1991 audit, a few management effects were different, cattle were marketed earlier due to economic conditions, and, consequently, quality grades had declined. This resulted in a shift in recommendations away from decreasing fat (i.e., 1991) to increasing quality and consistency (i.e., 1995). As a result, the production segment of the industry responded by saying, How can we shoot at a target when it is continually changing?

There are several reasons why little genetic change occurred in the cattle population over those 5 yr, principally: 1) time—5 yr does not quite constitute a single generation interval of beef cattle; 2) most of the necessary genetic tools for identifying specific seedstock animals for specific roles (in relation to end product performance) were still under development; 3) these seedstock genotypes, in most cases, were filling a perceived useful niche in the cow-calf sector; 4) genetics, which was being inappropriately used in 1991 and still being inappropriately used in 1995; 5) the long-standing perception that production of cattle with “value-based genetics” will not receive “value-based rewards”; and 6) there has been concern relative to the effects of genetic change in carcass performance on raising rather than lowering production costs.

### **What About Lowering Costs of Production?**

All changes in a commercial cow-calf operation must be evaluated in terms of their effect on profitability of the whole enterprise. Given the problem that profitability is often, in the short-term, very affected by external market conditions, Dickerson (1970) advocated that these changes be evaluated on the basis of economic efficiency measured as the ratio of input costs per unit of output product value. When one operates under this philosophy, cost of production becomes very important relative to desired increases in product value, mentioned above as industry goals. Furthermore, it is imperative to remember that many of these desired ends are often antagonistically related, meaning that we must be careful to keep the entire production system in perspective.

For example, traditionally we have thought that, in relative economic terms, reproductive efficiency is roughly twice as important as growth performance, which is approximately five times as important as carcass merit (Melton et al., 1979). A few years ago, a reanalysis of the importance of these three types of traits under a more current, value-based kind of marketing system was completed. Under this more current marketing system, the former 10 reproduction:5 growth:1 product ratio was now closer to 2 reproduction:1 growth:1 product (Melton, 1995). A more recent evaluation of these economic weights has been presented from the American Gelbvieh Association’s Gelbvieh Alliance marketing program. After some 110,000 feedlot cattle had gone through that program, the estimated relative importance of these three trait categories was approximately 4:2:1 (Schiefelbein,

1998). There are several things about these relative economic values that are very important. First, under the general assumptions used in their derivation, these results indicate that, although a lot of attention has been given to growth of calves in the past, that will not suffice in the future. In most cases, the problems are in the other two categories: reproductive efficiency, because it has been so difficult to genetically change, and carcass merit, because of a lack of attention to this area.

Second, one should not fall prone to the common error of assuming that these economic weights are universally true. They are applicable to one particular system and environment but may be quite different if the system is changed. One of the universal strengths that makes the beef industry unique is that it uses land resources that cannot be more efficiently utilized by other production systems. Cattle harvest energy from sunlight, soil, and water that is then converted to a higher quality form of protein. They do this from a set of natural resources that cannot be “farmed” any other way. The problem is that those resources exist under such a wide array of ecosystems that we are challenged to come up with one management system that will work for all environments (Hohenboken, 1988). Herein also lies the genetic dilemma of building the best beast to harvest and harness that energy from the environment.

Third, there is a tendency to overgeneralize in the beef industry when talking about “THE TARGET.” As Dell Allen of Excel, Inc. has stated, there are several different target markets in our industry (Allen et al., 1987). The first question that a commercial producer must ask before addressing anything else genetically is, “Which target am I going to aim my production resources toward?” As marketing of cattle in alliance and grid programs has escalated over the past few years, it has become clear that there are major targets in “lean beef,” “high-quality beef,” and “export beef” trade. There are certainly other smaller specialty markets as well. The market may change over time in relation to premiums and discounts for “leanness” vs “quality”. However, a given producer must decide before the genetic decisions are made on a well-defined target that is comfortable. Given the current plethora of alliance marketing programs, one must become educated on where he or she fits and then set their target based on that marketing program. Only then can one truly go about determining the relative importance of these traits.

### **What Should Be in a Commercial Producer’s Want Ad?**

In 1987, the beef cattle symposium program at the annual meeting of the American Society of Animal Science was entitled “Bovine Nirvana.” In that program, Rick Bourdon and Bill Hohenboken discussed different perspectives on how one might describe the “ideal” cow (Bourdon, 1988; Hohenboken, 1988). As they both stated in their remarks, this beast does not really exist, primarily due to the reasons described earlier in this paper. However, we do know that it is possible to provide some general guidelines for the specifications we would look for in performance criteria in the beef cattle production system.

Bob Taylor, our recently deceased animal science colleague, had great foresight in realizing the need to look at “balanced” performance of cattle long before it was popular. A number of years ago, he developed a simple analogy to illustrate the importance of this philosophy to his beef production students. He said that what commercial producers should do is develop a “want ad” for the type of bulls and females they use in their system. This want ad should then be what is used by the seedstock industry to develop “specification seedstock” to address the needs of the commercial production sector of the industry. Although this is a very simple approach, in concept, one is left to wonder just how often it has been applied. Taylor’s generalized want ad, shown in Table 1, provides an excellent overview of the challenge a breeder has to mount in order to “hit the overall” target.

### ***Is It Possible to Genetically Improve Cow Adaptability and Carcass Acceptability?***

***Within-Population Selection.*** Fortunately, collective research results over the past 50 yr have clearly shown that genetic variation exists both between and within breeds for many of the important measures of performance in beef cattle production. Table 2 provides a summary of the average levels of heritability for a variety of reproductive, growth, and carcass traits as provided in an exhaustive analysis of the research literature by Koots et al. (1994a). In general, selection within breed populations is quite effective for carcass traits, moderately effective for growth-related traits, and much slower for reproductive efficiency-related traits.

Until recently, we have believed that there was limited opportunity to genetically improve fertility via direct selection within breeds. Although indicator traits of fertility and age at puberty, such as scrotal circumference, have proven to be quite useful and heritable, they have not been shown to be highly genetically correlated to fertility measured as pregnancy success. Because fertility measures are binary traits (i.e., they are observed as either pregnant or not pregnant), it is quite difficult to use phenotypic information to determine genetic differences (e.g., two females may both get pregnant but may differ widely in their true genetic potential for fertility). This results in traditional analytical methods not being adequate to separate these genetic differences and thus, we have always stated that the heritability of these traits is quite low (Table 2). More appropriate statistical methodology called “threshold modeling” allows appropriate analysis of these types of traits on an underlying continuous probability scale. One of the first applications of this approach was to define a new trait called “stayability” that has been adopted by the Red Angus Association of America and is now being implemented by several other breeds (Snelling et al., 1995). This estimated breeding value is a genetic prediction of the probability of females still being in the herd at a breakeven age of 6 yr given that they were selected as replacements. This measure combines performance differences in fertility, growth, and survivability/adaptability of these females.

In the direct fertility area, an analysis of heifer pregnancy (HP) records from the Hereford herd at the Bell Ranch in

New Mexico has recently been completed (Evans et al., 1999). In that study, the researchers determined that heifer pregnancy was indeed more heritable than previously thought (14%). Furthermore, when the relationship of heifer pregnancy with yearling bull scrotal circumference (SC) was estimated, a nonlinear relationship (i.e., the bulls with low SC EPD had low HP EPD, moderate SC EPD had the highest HP EPD, and highest SC EPD had lower HP EPD) was revealed. A second study conducted a similar analysis using historical data from the Colorado State University Beef Improvement Center Angus population at Saratoga, WY (Doyle et al., 2000). These researchers reported a heritability level for heifer pregnancy of 21%, corroborating the result of Evans et al. (1999). These two studies indicate that it is feasible to produce genetic predictions to enable direct genetic improvement in reproductive rate. The only obstacle is getting breed association national cattle evaluation performance databases to adopt the “whole-herd reporting” format necessary to allow computation of these types of EPD (Golden et al., 1996). Although this is only a start on the whole reproductive efficiency complex, it is a notable improvement over current genetic capabilities in this important area.

***Between-Population Selection.*** Larry Cundiff and co-workers at the U.S. Meat Animal Research Center have conducted the most extensive genetic evaluation of breeds in the world over the past 30 yr (Germ Plasm Evaluation [GPE] program). The design for this project has allowed for the evaluation of a widely diverse set of breeds, as shown grouped by biological type in Table 3 (Cundiff and Gregory, 1999). From the collective results of this effort, they have reported that the magnitude of genetic variability between breeds is roughly equivalent to that within breeds (Table 4) for most performance traits. Although this infers that genetic improvement is possible through proper breed selection implemented in designed crossbreeding programs (i.e., breed complementarity), it also points out that no one breed excels in all characteristics simultaneously, along with a great degree of overlap between various breeds.

The GPE program, along with other studies, has also shown that many genetic antagonisms exist in beef production systems. Koots et al. (1994b) summarized published estimates of genetic and phenotypic correlations between a number of traits of interest (Table 5). These estimates clearly reveal general genetic antagonisms between growth rate and calving ease, growth rate and mature cow size, maternal characteristics and cutability, and carcass quality and cutability. Additionally, the review of these authors pointed out how many genetic relationships between traits of economic importance are poorly understood. An excellent example of the sparseness of information is the lack of any understanding of the relationship between measures of tenderness and other performance criteria.

The most troubling genetic antagonism we must consider when attempting to genetically improve product quality and consistency concerns the relationship between carcass attributes and measures of reproductive efficiency. There is generally a lack of this type of information in the research literature. The best existing data relating actual carcass measures

to reproductive traits comes from a study by MacNeil et al. (1984) at the U. S. Meat Animal Research Center. Table 6 provides a summary of that information and indicates antagonistic relationships between selection to increase retail product weight (at a constant age) and age at puberty, services per conception, and mature size. When one considers these estimates in concert with the experiences of the swine industry with pale, soft, and exudative pork (PSE), potential antagonisms appear to exist and need to be addressed when making selection decisions.

Unfortunately, even though there have been numerous attempts to make one believe otherwise, these antagonisms leave no doubt that no one breed is the answer. Bourdon (1994) used the analogy of “sensible beef stew” to describe the effectiveness of utilizing designed mating systems to “mix and match” strengths and weaknesses of breeds to meet specifications for balanced performance. This fact has been further supported in the analysis of the American Gelbvieh Alliance results, in which a ratio of 50% British to 50% Continental European breeding appears optimal to hit market targets (Schiefelbein, 1998). Cundiff et al. (1994) additionally pointed out the need for alteration of breed inputs in subtropical environments to include either some *Bos indicus* or heat-tolerant *Bos taurus* germplasm.

### **Heterosis: The Final Piece of the Puzzle**

Fortunately, there appears to be a significant amount of heterosis observed in the reproductive efficiency and maternal trait complex to allow breeders to overcome the obstacles of direct selection for fertility and cow adaptability mentioned earlier. Heterosis levels of 20 to 25% are achievable in kilograms of calf weaned per cow exposed to breeding using systems that exploit a terminal sire breed mated to crossbred females of unrelated breeds (Table 7, Cundiff and Gregory, 1999). This amount varies according to the breeds used in the crossing system because heterosis is directly proportional to the difference in gene frequencies affecting the traits between the breeds used in the cross. This is the basis for the success of the *Bos indicus* × *Bos taurus* crosses in the subtropical zones where these females express phenomenal heterosis in maternal and reproductive performance.

Unfortunately, in the attempt to capitalize on the benefits of heterosis, as has too often been the case in animal breeding, there has been too much emphasis on “maximize” and not enough emphasis on “optimize.” When we recall what was mentioned before about evaluating the effects of change on cost per unit of output product value, there is an optimum amount of performance in all traits, even reproductive performance. Beyond that optimum it costs more to achieve than benefits received in return. This is an important concept to keep in check.

### ***How Do We Genetically Manage to Simultaneously Improve End Product Performance and Lower Cost of Production?***

Given that there are hundreds, perhaps thousands, of feed resource and climatic environments used in cattle production, yet end product performance must fit within specification targets, what do we do? Animal breeders have unanimously stated over the past several generations of cattle production that we must achieve this balance by using breed complementarity and heterosis in very carefully designed crossbreeding programs. This must be a several step process to work successfully. First, the proper breeds must be chosen to match maternal performance of the cow herd to a given production environment. Second, the proper lines from within those breeds must be selected to properly hit those environmental targets while also meeting minimum acceptable performance in end product characteristics. Then a terminal sire breed must be selected to bring necessary performance for growth and end product performance to the system. Furthermore, the sires selected from within the terminal breed (or breeds) chosen must have documented performance for growth and carcass traits (i.e., EPD ) in addition to the sires selected for maternal replacements having documented EPD for reproductive and functional soundness. There are several different types of crossbreeding programs available to producers. These have been discussed in detail in the past (Bourdon, 1994; Kress, 1994; Cundiff and Gregory, 1999). There are certainly advantages and disadvantages to each. Unfortunately, a number of the product inconsistency problems our industry is experiencing today are from misuse and abuse of these systems. It has not usually been the choice of the particular crossbreeding program that has gotten breeders into trouble as much as the inability to properly design, implement, and then stay the course in a crossbreeding program. Many programs have been doomed from the start because they were not properly thought out, and yet others have failed because a new breed has come along that tempts the curiosity of the breeder. Furthermore, there are still many breed and tradition loyalties that often get in the way of breeding program objectivity. These facts, coupled with increased selection for extra growth and extra heterosis have resulted in what some have called the “mongrelization” of the U.S. beef cow herd.

### **Is There Any Way to Reduce Crossbreeding Variation?**

Cundiff and Gregory (1999) presented an excellent summary of the effectiveness of various crossbreeding systems in terms of heterosis utilization, use of breed complementarity, and consistency of production. They concluded that the most effective system at doing all three things simultaneously, along with being the easiest to manage effectively, was composite breeding. The theory behind composites has been amply supported by the Germ Plasm Utilization (GPU) Project at the U.S. Meat Animal Research Center under the leadership and guidance of Keith Gregory. The published summary (Gregory et al., 1995) of that work suggests that

composite breeding offers a usable solution to many of the problems being discussed here. Heterosis utilization is high, breed percentages are fixed and do not vary between generations, and breed differences can be used to match breed strengths and weaknesses to the production and marketing environment. Results of the GPU project suggest that the ability to overcome genetic antagonisms and still retain high levels of heterosis in maternal performance is unmatched by any of the other designed systems. Furthermore, once the composite is formed, the breeding system is much simpler to manage than any of the others.

Detractors of the composite approach have argued that composite mating systems will increase rather than decrease variability of production due to increased levels of heterozygosity. The USDA-ARS work has shown that there is not a significant increase in the variability observed in the composite lines as compared with the purebreds (Table 8). Furthermore, compared with other mating systems, such as rotational crosses and rota-terminal systems, the intergenerational variation is eliminated (Figure 1). These same detractors of composites have argued that we cannot afford to give up the consistency that purebreds have worked so hard to develop through their history. They do forget, however, that those purebreds with their consistency have to be the foundation for the composite lines. Just as there is no one breed that offers everything, the beef cattle industry will not be able to develop only one maternal and one terminal composite. Although that may work better for the poultry and swine industries, it will not work for the beef industry. Therefore, the challenge is for the purebred breeds to find where they will fit into various composite lines as they develop.

Reactions to the idea of composite breeding have been very interesting to watch. There have been some pure breeds that have realized that they need to find where they can provide useful germplasm for the formation of these composites. There have been other breeds who have denounced the very idea of such an approach, rather than asking the question of where they, too, can fit. There seems to be the mentality that the pure breeds will disappear from existence because of composites. How can this be true? If one really analyzes the situation, the most likely scenario is for maternal line composites to be developed by geoclimatic zone that will then be mated to terminal or growth/carcass sires to produce market offspring. Many of the breeders who are embracing and implementing the composite idea are doing so because they intend to produce replacement females and sire seedstock for the maternal side while selling purebred or  $F_1$  terminal sires.

There are, however, also a few limitations to the composite approach. One is that in order to develop a composite line, it needs to be done from a relatively large base to avoid inbreeding. The typically cited requirement is 400 to 500 females in the breeding population. Then there has to be intentional avoidance of inbreeding practiced to maintain the heterosis level in the composite line. A second limitation is that genetic evaluation is much more difficult, (i.e., EPD are not readily available, or as accurate, for most composites as they are for pure breeds). We are just beginning to see some movement in the United States to address this problem

through such efforts as the American Simmental Association's multibreed EPD program (Pollak and Quaas, 1998). Another limitation is that composite breeding still cannot overcome poor breeding decisions as is the case with other mating systems. A composite made from the wrong breeds and the wrong lines within those breeds still is a bad product. Composites must be meticulously and carefully developed to be successful.

### How Are We Coming with Carcass EPD?

If the information for end product breeding value is not available, then how can terminal sires be chosen accurately? For example, there is little doubt that the Brahman crossbred female is hard to outperform in the Gulf Coast region of the United States. However, we also know that we need to find a way to make sure that the Brahman sire lines used in that cross do not present the wrong type of end product specifications (particularly for tenderness; Sherbeck et al., 1995; Crouse et al., 1989). If genetic predictions are not available for these carcass traits, the accuracy of selection is surely compromised.

If there is such a need for carcass EPD and the heritability of these traits is relatively high, why are they not widely available? Even though several factors have contributed to this problem, fortunately most of them are being resolved. The largest hindrance to collecting carcass information has been that, until recently, we have had to rely solely on progeny data. This type of information requires time, expense, and labor to collect and also requires cooperation in the packing plant for accurate individual identification of carcasses. The combination of these factors has resulted in somewhat limited amounts of progeny data being placed into breed performance databases in the past. In the United States, the American Angus Association has had the most concerted effort in designed progeny testing of sires. Approximately 50% of their currently published sires have carcass information (2,772 of 5,527 with published EPD; American Angus Association, 1998). Although this illustrates the difficulty of obtaining progeny data for carcass traits, it also emphasizes that useful carcass information can be obtained for a meaningful percentage of the breed. Several other breed programs are attempting to build databases (Table 10).

The second hindrance has been the lack of ability to determine true carcass value differences on live, yearling seedstock cattle to circumvent the need for progeny data. Real-time ultrasound imaging technology has been pursued over the past 10 yr as the primary means to obtain these live animal measures and now appears to be entering the adoption mode. A national consortium of U.S. universities worked together during the early 1990s in a project that had as one of its three objectives "to determine the efficacy of using real-time ultrasound imaging to measure body composition and carcass merit traits in beef cattle" (Bertrand and Kriese, 1995; Green et al., 1994; Wilson, 1995). The conclusions drawn from a compilation of this and other research indicate that: 1) assessment of retail yield amount or percentage on the basis of 12th-rib fat thickness (**FT**) and 12th-rib ribeye

area (REA) is slightly less effective using ultrasonic measures on the live slaughter animal as compared to direct measures on the carcass postmortem (Hamlin et al., 1995; Herring et al., 1994; Perkins et al., 1992); 2) FT is a better predictor of cutability than is REA in the current cattle population (Hamlin et al., 1995; Herring et al., 1994), although not so of retail product weight; 3) ultrasonic measures of these retail yield indicators appear to be under a moderate degree of genetic control (weighted average  $h^2$  of .37 for FT and .26 for REA (Hassen et al., 1999; Robinson et al., 1993; Johnson et al., 1993); 4) genetic correlation estimates between ultrasonic predictors of carcass merit and other economically important traits are sparse but indicate some antagonism between REA and mature size (Shepard et al., 1996; Johnson et al., 1993); 5) prediction of intramuscular fatness and palatability traits is difficult using ultrasound, although high and acceptable levels of accuracy have been achieved in the past few years (Brethour, 1998; I. R. Crouch, personal communication; Wilson, 1995); and 6) data to estimate relationships between ultrasonic measures in yearling bulls and slaughter steer carcass retail yield and palatability have been more limiting (Kriese 1996; Diles et al., 1996a,b; Evans et al., 1995).

The relationship between carcass data EPD vs ultrasound EPD has been the hardest one to resolve in recommending the adoption of ultrasound-generated carcass data for breed improvement programs. As data addressing this issue have been accumulated over the past 5 yr, the conclusions of various researchers have not all agreed. However, as more data have been analyzed in some larger breed databases, the conclusions have become more clearly in favor of the use of real-time ultrasound. Data from the Brangus (Kriese, 1996) and Angus (Crouch, personal communication) breeds have indicated high correlations between ultrasound and actual progeny carcass data in sires for which both types of information have been collected. These conclusions have led to the recent adoption of policy to accept ultrasound data by several breed associations, including Angus, Hereford, Simmental, Brangus, and Gelbvieh (Table 10), with more associations to follow in the next few years. Coupled with actual carcass progeny data, use of real-time ultrasound data should allow great acceleration to occur in the percentage of active sires with carcass EPD for most breeds. For example, the American Angus Association amassed enough ultrasound data in the first 9 mo after adoption to increase the size of its carcass record database by almost 50% (Crouch, personal communication).

### **Do We Have All of the Necessary Information to Genetically Address Carcass Acceptability?**

The only area that may be quite problematic is genetic evaluation of overall meat quality, particularly tenderness. This is a major issue for the beef industry because of estimates that one in five of the steaks produced in the current industry are tougher than desired (Morgan et al., 1991). No industry can afford this kind of defect rate!

There have been numerous debates in the United States over the last few years regarding how marbling can, or cannot, be used to address the meat quality and tenderness issue. This same discussion has also been occurring in Australia as they have begun to implement eating quality assurance grading standards (Cox, 1999). The collective U.S. experience indicates that, although it would be nice to rely on marbling and USDA Quality Grade to ensure palatability, it is simply not good enough. As shown in Figure 2, although the probability of getting an unpalatable steak does significantly decrease when going from Standard up through Choice and Prime grades, there is so much overlap in palatability among the grades that today it is possible to have steaks from carcasses of Prime and Standard grades that will be equally palatable (Smith et al., 1987).

Increasing emphasis is being placed on marbling in breeding programs at the current time, largely due to the marketing success of the Certified Angus Beef program (Marston et al., 1999). Increasing selection intensity for marbling appears to be short-sighted, however, for several reasons: 1) marbling is, at best, an indicator for eating satisfaction of beef; 2) marbling only explains 10 to 15% of the variation in overall palatability of cooked beef product; and 3) just as in any other trait, there are genetic antagonisms with marbling that must be carefully managed (recall the discussion of cutability and marbling earlier in this paper). However, without a more direct, accurate system for assessing true palatability differences, breeders are responding to increased consumer demand for quality and consistency using marbling as their selection criterion because it is the only tool available to them. As long as this selection occurs in a balanced, multitrait configuration, it should net small, yet positive, gains over time (Marston et al., 1999).

### **What About Tenderness?**

It seems as if there has been more discussion about beef tenderness in the past 5yr than in all of the previous century. As reviewed by Tatum (2000), beef is perceived to currently have a toughness problem, particularly in relation to cattle of *Bos indicus* descent (O'Connor et al., 1997; Sherbeck et al., 1995). There are two ways to handle this problem: tenderize the product postmortem and(or) genetically fix it. We know that postmortem aging, electrical stimulation, and calcium chloride injection post-mortem can be used to reduce toughness problems (Tatum et al., 1997). We also know that tenderness, assessed as Warner-Bratzler shear force of loin or rib steaks at a 14-d aging end point is heritable ( $h^2 = .38$ ) and variable (Wulf et al., 1996). Although calpastatin, a primary inhibitor of muscle proteolysis postmortem, appeared to offer a useful selection criterion in early research targeting genetic improvement in tenderness (Wulf et al., 1996; Koohmaraie et al., 1995), genetic polymorphisms in the calpastatin gene have not proved practically usable (Lonergan et al., 1995; Green et al., 1996a,b; Green et al., 1994). However, as pointed out in another presentation in this symposium, application of best management practices postmortem results in a toughness rate that is still unacceptable, leaving the only

remedy long-term through genetic selection (Tatum, 2000). Collectively, this means that breeders must begin addressing the tenderness issue by collecting objective progeny tenderness data (measured as Warner-Bratzler shear force).

This challenge has been taken very seriously by commodity group leaders in the United States and abroad. In 1998, an extensive genetic evaluation project for carcass merit was approved for funding by a consortium of 16 beef cattle breed associations and the beef checkoff (Green et al., 1998). The 42-mo study, referred to as the National Carcass Merit Project, was initiated in June of 1998 and will collect complete carcass data (including ribeye shear force) from 11,000 progeny of sires from these breeds. Each breed is testing a minimum of 10 of their most widely used sires with a minimum of 50 progeny each. Additional sires will be tested with fewer progeny in a majority of the breeds. The objectives of the project include estimation of EPD for shear force and sensory panel assessments of tenderness (as well as all other carcass traits) and an economic analysis of the costs and benefits associated with this type of information. As the planning for this project developed, a particular focal point of the effort became an evaluation of a set of previously identified and promising 11 DNA marker tests for carcass merit. Because DNA technology has been portrayed at times to be the answer in addressing many of the issues surrounding carcass merit and consumer satisfaction, more discussion of this area is warranted.

### DNA to the Rescue

A number of developments over the past 10 yr have led to some DNA testing beginning to be made available to industry. Because I have been discussed tenderness and carcass merit traits at length, it might be helpful to show what is happening in this area as an example.

As pointed out previously, the beef cattle industry in the United States has been attempting to improve consumer demand for beef products by improving carcass merit of the cattle population. In particular, the need has been identified to increase the marbling potential of domestic grain-fed U.S. beef. In response to these needs, a beef checkoff-funded project was initiated at the Angleton research station of Texas A&M University to identify genes, referred to as "quantitative trait loci" (QTL), affecting variation in marbling ability (Taylor et al., 1996). The project was started in 1990 and required the development of resource families that would be expected to be highly heterozygous for gene loci affecting this trait as well as other measures of carcass merit. Based on previous research, the scientists chose a design that utilized Brahman  $\times$  Angus crosses to develop these families due to their divergent performance relative to marbling (Angus high, Brahman low). They first produced reciprocal  $F_1$  crosses between these two breeds. These first crosses were then used to produce full-sib families of backcrosses to either Angus or Brahman through multiple ovulation and embryo transfer. A total of 42 full-sib families were produced representing 16 sires and 19 dams. Life history data on 613 head

of progeny were collected in this project (Taylor and Davis, 1997).

In analyses conducted in this project, the research team identified a number of possible QTL for several traits including five genes that appear to affect marbling, and an additional seven genes that influence either tenderness as assessed by Warner-Bratzler shear force or sensory taste panel. Additionally, the project has allowed identification of five QTL effects on ribeye area and five QTL for dressing percentage. One QTL effect that was detected in the project seemed to influence postweaning growth independent of birth weight variation, a very favorable gene effect. This QTL maps to the same chromosome (bovine chromosome 2) that had been identified to contain the gene causing double-muscling, the so-called myostatin gene (Grobet et al., 1998).

Several things are evident from the experience and results of this project. First, it is clear that these resource families take a great deal of time to develop and collect information from. It is a slow, expensive, and laborious process. Second, the reverse genetics approach (i.e., designing the families to allow detection of differences after the fact) is fairly powerful for detecting these effects, but will likely only yield linked markers in chromosomal regions containing large QTL effects. The researchers still must positionally clone and sequence these gene loci before they can determine the genetic cause of these differences and have more direct genotype tests. This positional cloning requires much finer mapping in order to elucidate the gene of interest. Third, because of the patenting/licensing of any DNA tests that develop from this type of research, much vagueness is observed in the reporting of research results. Instead of knowing the map locations of the QTL effects presented above, the research group can only say that have identified effects rather than elucidating where those are located and in what linkage groups. Unfortunately this slows down overall progress in the field but is a fact of life in any form of today's biotechnology. Fourth, because the reverse genetics approach hopes to identify markers to be used in a marker-assisted selection approach, the linkage relationships identified from a particular set of families may not hold up in other populations due to the phase of the linkage relationship. In other words, the markers linked to QTL effects identified in this particular project may not be useful in other families or breed populations. For example, perhaps the effects being found are breed-specific alleles that we already see in measuring differences between breeds, yet are not segregating within those other breeds (i.e., they are fixed). This last issue can possibly result in the direct application of QTL detected through this approach being difficult to apply beyond the resource population of study.

This research provides an excellent example of the process that the animal industries will face to make usable technology from this approach. Given that it is unknown how useful the markers identified in that project will be across other families and breeds, a second step must be taken. This is where the National Carcass Merit Project mentioned earlier will play a major role. The project has several objectives, one being to validate the DNA markers identified by the Texas A&M project across the major U.S. beef breeds. In

addition to collecting complete carcass data, sensory panel evaluation will be performed on steaks from approximately 3,000 of these progeny. By going through this effort, the question will quickly be answered about whether these markers will be useful in a wide array of germplasm. Additionally, it is hoped that the researchers will at the same time be able to move closer to positionally cloning the actual QTL being "marked." The breeds and numbers of progeny participating in the project are shown in Table 10.

We must note some redundancy in efforts occurring around the world in this area of technology development. One could easily take the Texas A&M and U.S. national project described above and change the names to CRC for Meat Quality and CSIRO Australia and have a parallel story to tell. The same could be done for the University of Saskatchewan and Ag Canada. In my opinion, more cooperation and less competitiveness in this area might do all of our industries a lot of good. Unfortunately, that does not appear likely in the near future.

### What Other QTL Have Been Found?

A number of QTL effects have now been identified through research work at several locations. In addition to the work described above, associations have been reported for myostatin (Georges et al., 1998; Grobet et al., 1998); growth traits (Beever et al., 1992); and carcass attributes, including tenderness (Keele et al., 1999; Stone et al., 1999; Green et al., 1996a,b).

Recently, mapping efforts have begun using complex study populations to identify large QTL effects for traits previously untouchable in genetic improvement programs. The two most exciting of these are both located in Nebraska. The first is a project being led by Daniel Pomp and Merlyn Nielsen at the University of Nebraska, where they are using lines of mice that have been selected divergently for heat production. Heat loss can be used to estimate maintenance energy requirements of an animal through direct calorimetry. The Nebraska project was begun in the early 1980s to determine whether genetic variation existed for maintenance requirements using this approach. They have been successful in changing the heat production between high and low lines by 50% of the average. Earlier this year, this group reported that, in a QTL search of an  $F_2$  intercross of lines of these mice, they were able to identify two major QTL affecting heat production, with another two putative QTL (Moody et al., 1998). This is exciting in that it indicates that it may be possible through marker-assisted selection approaches to identify animals with improved feed efficiency, perhaps our most difficult economic trait to measure.

A second major QTL effort is underway at the USDA-ARS Meat Animal Research Center. In one aspect of that effort, researchers are attempting to use the twinning population, in which selection has been applied over several generations for twinning rate, to detect QTL for ovulation rate and embryo survival. Initial results in that project have been very promising, with at least one major QTL already identified (S. M. Kappes and L. V. Cundiff, personal communication).

### Where Will Marker-Assisted Selection Be of Greatest Benefit?

The resulting QTL that are identified through the ongoing searches of the developing bovine gene map are likely to be most beneficial for the traits that are difficult and expensive to measure, as detailed above. We can expect the following categories of traits to benefit the most from marker-assisted selection (in order of greatest to least degree of benefit): disease resistance and immunocompetence, carcass quality and palatability attributes, fertility and reproductive efficiency, maintenance requirements (i.e., energetic efficiency), carcass quantity and yield, milk production and maternal ability, and growth performance. This ranking is due to a combination of considerations, including 1) the relative difficulty in collecting performance data, 2) the relative magnitude of the heritability and phenotypic variation observed in the traits, 3) the current existing amount of performance information available, and 4) when performance data becomes available in the life-cycle of the cow herd (collected at birth, weaning, yearling, maturity?). Most of the rankings above then become self-explanatory.

To be realistic, however, we must realize that QTL will not solve the industry's problems overnight but rather serve as additional help for producers to make informed selection decisions. As long as we are relying on markers, rather than the QTL themselves, we are still only crudely defining the genotypes across the larger beef cattle population. Once QTL are finely mapped and direct tests are available, then the accuracy of selection will be markedly improved. Until then, however, the marginal gains that marker-assisted selection will give us over selection on polygenic breeding values is not as high as one might think. Charles Smith predicted in the late 1970s that gene-level information would only provide substantial gains for traits when information is lacking for genetic evaluation. Thus, for traits that are currently widely evaluated in national cattle evaluation programs (e.g., growth rate) marker-assisted selection will not help a great deal. His prediction was accurate, and a number of simulation studies now show clearly that he was correct (Haley and Visscher, 1998). The overall conclusion is that markers combined with EPD information will enhance the accuracy of genetic evaluation. The marginal gain, however, is very dependent on the particular trait, the number of markers available for whole genome scans, the availability of performance information, and the availability of marker information from large numbers of animals.

Lastly, in the current climate of the beef cattle industry, where everyone is looking for a quick and magical solution to all that ails us, it is imperative that breeders not overestimate this technology. It is not uncommon to hear statements such as "all we have to do is find the marbling gene and then we will have the problem solved." This is absolutely not going to happen. It must be remembered that economically important quantitative traits are controlled by many genes (i.e., they are polygenic). Although it is also likely true that there are some of those genes that play a larger role than others, there still are many genes in the picture. Put simply,

to place a measure of performance in front of the word gene vastly oversimplifies the true situation.

Although marker-assisted selection is a popular new phrase in academic animal breeding circles, what we really need is "marker-assisted optimum selection." What this means is that markers identifying QTL of large effect can be used to add to EPD for the same trait. This will result in optimal use of information from both the molecular and phenotypic performance levels. In other words, marker-assisted selection or EPD singularly are not great but together they markedly increase the accuracy of genetic evaluation.

### **But How Does One Practice Balanced Trait Selection When There Are So Many Important Traits?**

One of the areas being currently debated by some of the thought leaders in the academic beef cattle breeding community would really help producers in this regard. The ideas being debated relate to how to best combine information on several traits into "selection indexes" for specified breeding objectives. These ideas have been around a long time (since Jay Lush and Lanoy Hazel at Iowa State first proposed them in 1943), but have really become applicable and important as genetic information has been developed on more traits in the past 10 yr. For example, suppose one is looking for a maternal-line bull to produce females for a given production and marketing environment, then these indexes of traits weighted according to their relative amounts of heritable variation, relationships with other traits, and relative economic importance could be very valuable.

The dairy and swine industries have already produced indexes for use in their national genetic evaluation programs and the beef industry should see rapid development of the same in the next few years. In our case, however, the indexes will need to be somewhat "customized" for a given type of production scenario, similar to the discussion earlier in this paper about the importance of defining and sticking to a particular market target before deciding what to do genetically. Fortunately, tools are being developed to help in this area, such as the recently released Decision Evaluator for the Cattle Industry (DECI) model developed by USDA scientists at the U.S. Meat Animal Research Center (Bourdon, 1998; Jenkins and Williams, 1999). This simulation model is an attempt to give producers a baseline picture of their production systems so that changes in economic scenarios (i.e., marketing avenues), biological and environmental components of their production systems (i.e., cattle and forage), and management can be evaluated. This customizable simulation tool allows a producer to ask many "what if" questions with readily available answers. This is a critical area where a great deal of research and development is needed.

### **Conclusions**

The following are unavoidable conclusions from experiences over the past 30 yr. 1) Beef is losing market share relative to poultry and pork. 2) A large portion of the reason

for lost market share is due to higher costs of production. Reproductive efficiency and other aspects of maternal performance in the environment cannot be sacrificed. 3) We can genetically alter cattle for end product performance. 4) The most feasible way to approach the end product nonconformance problem genetically is to use properly designed and implemented crossing systems that match maternal production to environmental feed resources with sire selection based on growth and carcass performance. 5) The benefits of heterosis on overall performance of a cow herd (as much as 25% improvement in weight of calf weaned per cow exposed) cannot be ignored. 6) Proper terminal sire selection for growth and carcass performance is unachievable in the absence of end product EPD and proper maternal sire selection for reproductive and maternal performance is unachievable in the absence of appropriate EPD. 7) Single-trait selection has never been and will never be a wise breeding philosophy.

Given these conclusions, we have several possible approaches for achieving both cow adaptability and carcass acceptability. Each of these has merit and should therefore be attempted. In order of priority, they are as follows. 1) Immediately demand that end product performance data be gathered and utilized in national cattle evaluation programs. This must be done by amassing the necessary progeny data (either carcass or ultrasound) for lean yield and objectively measured meat quality attributes. Additionally, implementation of whole-herd reporting formats for breed performance data collection to enable calculation of EPD for fertility and longevity-related traits must occur. 2) Educational plans should be developed, by geoclimatic region, for matching of breed resources to environments. 3) Breeders must more willingly evaluate the alternative of using "composite" breeding program when applicable. Breeds need to be working today to determine where their germplasm fits into composite cattle breeding, which is inevitable. 4) A high-integrity system of identification must be developed for every animal produced in the beef production system. This system must then be used to provide information feedback and true value discovery and pricing. 5) All available resources should be used to identify new DNA-based technologies to assist in making genetic improvement in problematic traits (e.g., maintenance energy cost and disease resistance).

Several of these items are much more politically difficult to achieve than others, which are physically more challenging. The political acceptance may, or may not, ever happen. This entirely depends on whether groups and people within the industry are committed to the good of the whole industry or the good of their portion of the industry. The physical challenges, however, are ones over which breeders and scientists have direct control. We can make those happen with the right resources directed in the right directions (e.g., carcass EPD, individual animal ID and feedback, and whole-herd reporting). What happens if every commercial bull buyer starts demanding reproductive/fertility and end product EPD specifications before buying a bull? What happens if a feedlotter requires an electronic identification (or better yet, a DNA bar code) on every incoming feeder or yearling before

they will purchase and(or) feed them? What happens if, on the basis of that identification, the industry provides direct pricing (with information feedback) on every animal? What happens if seedstock suppliers develop systems to analyze the needs of their customers followed by production of specification seedstock rather than producing first and then trying to find customers? What happens if animal breeding scientists take a more active role in education and technology adoption? The beef industry would universally benefit in the long term.

### Implications

Beef cattle production systems will continue to increase in sophistication and complexity. Many of the challenges that currently exist relative to overcoming antagonisms between cow adaptability and carcass acceptability could be met today if the available knowledge and technology in beef cattle breeding were universally applied. As the industry evolves in the part of the 21st century, it has clear opportunity to increase demand for beef products by improving efficiency through application of the knowledge gained from a very productive past 75 yr of beef cattle breeding and genetics research. Additionally, with the dawning of a new “technological age,” the future gains in efficiency of production are likely to move the industry further than anyone can envision. Clearly, however, we must first put into use what we already know to move the beef cattle industry forward.

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### Notes

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**Table 1.** Production and marketing specifications for beef cattle<sup>a</sup>

Trait	Optimum range <sup>b</sup>	Industry target <sup>c</sup>
Reproduction		
Age at puberty, mo	12–16	14
Scrotal circumference, cm	32–40	36
Reproductive tract score, 14 mo	4–5	5
Weight at puberty, kg		
Heifers	270–360	320
Bulls	400–500	450
Age at first calving, mo	23–25	24
Birth weight		
Calves from cows, kg	35–45	39
Calves from heifers, kg	27–36	32
Body condition score, BCS, 1–9	4–6	5
Postpartum interval, d	55–95	75
Calving interval, d	365–390	365
Calving season, d	45–90	65
Calf crop weaned, % cows exposed	80–95	85
Cow longevity, yr of age	9–15	12
Growth		
Mature cow weight, kg at BCS 5	400–600	500
Weaning weight, kg; steer at 7 mo	200–275	240
Yearling weight, kg; steer at 365 d		
Grazed and(or) backgrounded	275–365	320
Weaning to feedlot	400–500	450
Feedlot gain, kg/d	1.1–1.6	1.4
Feedlot feed efficiency, steer	5–7 <sup>d</sup>	6 <sup>d</sup>
Days on feed, high-energy ration	60–120	90
Carcass		
Carcass weight, kg	275–365	320
Quality grade	Select <sup>+</sup> to Choice <sup>+</sup>	Choice <sup>-</sup>
USDA yield grade	1.5–3.5	2.5
Fat thickness, mm	2.5–15.2	7.5
Ribeye area, cm <sup>2</sup>	71–97	84
Palatability, % fat in retail cuts	3–7	5
Warner-Bratzler shear force, kg	Below 3.65	Below 3.65
Muscle to bone, kg muscle to kg bone		
	3.5–4.5	4.0
Lean yield/day age, kg		
Weaned steer to feedlot	0.35–0.45	0.40
Grazed yearling steer to lot	0.20–0.30	0.25
Frame score		
Steers	4–6	5
Cows	4–6	5
Bulls – Maternal	4–6	5
Terminal	5–7	6

<sup>a</sup>Adapted from Taylor and Field (1999).

<sup>b</sup>Range will include most commercial beef operations where an optimum combination of productivity and profitability is desired.

<sup>c</sup>Target gives central focus applicable to many commercial beef operations. Deviation from this target and optimum range is dependent on market, economic, and environmental conditions in specific commercial beef operations.

<sup>d</sup>High-energy diet, kg feed per kg gain.

**Table 2.** Heritabilities ( $h^2$ ) for beef cattle performance traits<sup>a</sup>

Trait	Number of studies <sup>b</sup>	Weighted mean $h^2$ <sup>c</sup>
<b>Reproduction</b>		
Age at first calving, direct	7	6
Age at first calving, maternal	1	19
Calving date	7	8
Calving interval, cows	3	1
Calving interval, heifers	7	6
Calving ease, direct	19	10
Calving ease, maternal	11	9
Calving rate	9	17
Scrotal circumference	25	48
Heifer conception rate, direct	9	5
Heifer conception rate, maternal	1	2
Cow conception rate, direct	21	17
Cow conception rate, maternal	1	2
<b>Growth</b>		
Birth weight, direct	167	31
Birth weight, maternal	34	14
Weaning weight, direct	234	24
Weaning weight, maternal	38	13
Yearling weight, direct	147	33
Yearling weight, maternal	6	6
Mature cow weight	24	50
Feed efficiency	25	32
Feed intake	21	34
Relative growth rate	12	22
<b>Carcass</b>		
Backfat thickness	26	44
Ribeye area	16	42
Slaughter weight	52	41
Carcass weight	19	23
Dressing percentage	13	39
Cutability	12	47
Lean:bone ratio	4	63
Marbling score <sup>d</sup>	12	38
Warner-Bratzler shear force	12	29
Sensory panel tenderness	3	13
Yearling frame score	27	61

<sup>a</sup>Adapted from Koots et al. (1994a) and Green (1999a).

<sup>b</sup>Number of research studies represented.

<sup>c</sup>Average heritability of trait, weighted by number of observations in studies. Expressed as a percentage.

<sup>d</sup>Recent review of Marston et al. (1999) reported average of 43% heritability for marbling.

<sup>e</sup>All traits are expressed on an age constant basis where applicable.

**Table 3.** Breeds evaluated in USDA-ARS Germ Plasm Evaluation Program grouped into biological type (Cundiff and Gregory, 1999)

Breed group	Growth rate / mature size	Lean to fat ratio	Age at puberty	Milk production
Jersey	X	X	X	XXXXXX
Longhorn	X	XXX	XXX	XX
Hereford-Angus	XXX	XX	XXX	XX
Red Poll	XX	XX	XX	XXX
Devon	XX	XX	XXX	XX
Shorthorn	XXX	XX	XXX	XXX
Galloway	XX	XXX	XXX	XX
South Devon	XXX	XXX	XX	XXX
Tarentaise	XXX	XXX	XX	XXX
Pinzgauer	XXX	XXX	XX	XXX
Brangus	XXX	XX	XXXX	XX
Santa Gertrudis	XXX	XX	XXXX	XX
Sahiwal	XX	XXX	XXXXXX	XXX
Brahman	XXXX	XXX	XXXXXX	XXX
Nellore	XXXX	XXX	XXXXXX	XXX
Braunvieh	XXXX	XXXX	XX	XXXX
Gelbvieh	XXXX	XXXX	XX	XXXX
Holstein	XXXX	XXXX	XX	XXXXXX
Simmental	XXXXXX	XXXX	XXX	XXXX
Maine Anjou	XXXXXX	XXXX	XXX	XXX
Salers	XXXXXX	XXXX	XXX	XXX
Piedmontese	XXX	XXXXXXX	XX	XX
Limousin	XXX	XXXXXX	XXXX	X
Charolais	XXXXXX	XXXXXX	XXXX	X
Chianina	XXXXXX	XXXXXX	XXXX	X

<sup>a</sup>Increasing number of X's indicates relatively higher values.

**Table 4.** Relativity of variation within and between breeds for various performance criteria

Trait	Number of additive genetic standard deviations <sup>b</sup>
Age at puberty, d	8.5
Slaughter weight, 450 d	8.0
Retail product weight, 450 d	8.2
Retail product %, 450 d	6.6
Marbling score, 450 d	6.1
Warner-Bratzler shear force, kg	5.1

<sup>a</sup>Adapted from Cundiff and Gregory (1999).

<sup>b</sup>Assumption is made here that within a breed approximately six genetic standard deviations of variation exist in any trait.

**Table 5.** Weighted mean literature estimates of genetic correlations between various performance traits<sup>a</sup>

Trait <sup>b</sup>	Phenotypic correlation	Genetic correlation
Calving ease / birth weight	-0.28	-0.74
Birth wt / feed efficiency	-0.12	-0.46
Yearling wt / feed efficiency	-0.46	-0.60
Feed intake / feed efficiency	–	0.71
Wean maternal / feedintake	–	0.80
Scrotal circumference / feed efficiency	0.12	0.61
Birth wt / weaning wt	0.46	0.50
Birth wt / yearling wt	0.38	0.55
Weaning wt / yearling wt	0.71	0.81
Weaning wt / mature wt	0.45	0.57
Weaning wt / slaughter wt	0.65	0.79
Yearling wt / slaughter wt	0.65	0.56
Yearling wt / scrotal circumference	0.36	0.39
Backfat / feed intake	0.29	0.44
Backfat / scrotal circumference	0.27	0.78
Carcass wt / birth wt	0.41	0.60
Carcass wt / yearling wt	0.85	0.91
Cutability / yearling wt	0.85	0.87
Marbling / yearling wt	0.14	-0.33
Marbling / feed intake	0.24	0.90
Marbling / cutability	-0.25	-0.35
Ribeye area / weaning wt	0.23	0.49
Ribeye area / yearling wt	0.35	0.51
Ribeye area / slaughter weight	0.33	0.43
Ribeye area / cutability	0.33	0.45
Ribeye area / marbling	0.06	-0.21

<sup>a</sup>Estimates shown are taken from Koots et al. (1994b) and represent the weighted mean of available literature estimates.

<sup>b</sup>Traits represented are expressed on an age constant basis where appropriate and represent direct genetic effects.

**Table 6.** Genetic correlations between measures of carcass merit and reproductive efficiency (MacNeil et al., 1984)

Female trait	Postweaning gain, kg	Carcass weight, kg	Fat trim, kg	Retail product, kg
Age at puberty, d	.16	.17	-.29	.30
Weight at puberty, kg	.07	.07	-.31	.08
Services/conception	1.33	.61	.21	.28
Gestation length, d	-.10	.03	-.07	.13
Calving difficulty	-.60	-.31	-.31	-.02
Birth weight, kg	.34	.37	-.07	.30
Mature weight, kg	.07	.21	-.09	.25

**Table 7.** Heterosis effects in crosses of *Bos taurus* × *Bos taurus* breeds and in crosses of *Bos indicus* × *Bos taurus* breeds from diallel crossing experiments<sup>a</sup>

Trait	<i>Bos taurus</i> × <i>Bos taurus</i>			<i>Bos indicus</i> × <i>Bos taurus</i>		
	n	Units	%	n	Units	%
Crossbred calves (individual heterosis)						
Calving rate, %	11	3.2	4.4	-	-	-
Survival to weaning, %	16	1.4	1.9	-	-	-
Birth weight, kg	16	0.8	2.4	4	3.3	11.1
Weaning weight, kg	16	7.4	3.9	10	21.7	12.6
Postweaning ADG, kg/d	19	.034	2.6	6	.116	16.2
Yearling weight, kg	27	13.2	3.8	-	-	-
Cutability, %	24	-.3	-.6	-	-	-
Quality grade, 1/3 grade	24	.12	-	6	.3	-
Crossbred cows (maternal heterosis)						
Calving rate, %	13	3.5	3.7	7	9.9	13.4
Survival to weaning	13	.8	1.5	7	4.7	5.1
Birth weight, kg	13	0.7	1.8	6	1.9	5.8
Weaning weight, kg	13	8.2	3.9	12	31.1	16.0
Longevity, yr	3	1.36	16.2	-	-	-
Lifetime production						
No. of calves	3	.97	17.0	-	-	-
Cumulative weaning weight	3	272	25.3	-	-	-

<sup>a</sup>Estimates are from experiments contributing to North Central Regional Project NC-1 (Iowa, Indiana, Missouri, Ohio, USDA-ARS and Nebraska), Southern Regional Project S-10 (Virginia, Florida, Louisiana, Texas, USDA-ARS and Louisiana, USDA-ARS and Florida) as reported by Cundiff and Gregory (1999).

**Table 8.** Genetic standard deviations ( $s_g$ ) and phenotypic coefficients of variation (CV) for purebreds and composites (castrated males)<sup>a</sup>

Trait	Purebreds		Composites	
	$s_g$	CV	$s_g$	CV
200-d weight, kg	13.3	.10	14.2	.11
Slaughter weight, kg	21.7	.08	28.7	.08
Carcass weight, kg	12.4	.08	17.9	.09
12th-rib fat, mm	1.3	.48	2.0	.44
Retail product, %	2.2	.04	2.3	.06
Carcass lean weight, kg	8.1	.08	10.7	.09
Carcass fat weight, kg	8.6	.18	6.3	.19
Carcass bone weight, kg	2.8	.08	2.1	.10
Longissimus muscle fat, %	.6	.27	1.0	.29
Shear force, kg	.18	.22	0.59	.21

<sup>a</sup>Cundiff and Gregory (1999) and Gregory et al. (1995).

**Table 9.** Current U.S. National Cattle Evaluation Programs – Carcass Merit (as of 1 January 1999)

Breed	Total Sires	Total published sires	Sires with carcass data	Sires with carcass EPD	Traits evaluated <sup>a</sup>	Ultrasound accepted?
Angus	95,995	5,527	1,944	2,772	1,2,3,4,5	Yes
Beefmaster	10,756	401	180	Not released	2,3,4	Yes
Brangus	8,999	982	150	Not released	2,3,4	Yes
Charolais	21,453	1,650	27	0	2,3,4,5	Yes
Gelbvieh	5,173	1,800	363	219	1,2,3,4	Evaluating
Hereford	94,221	4,261	4,986	1,010	2,3,4	Yes
Maine-Anjou	1,240	348	55	0	1,2,3,4	Evaluating
Red Angus	16,910	1,145	829	293	2,3,4	No
Salers	10,827	657	–	85	1,2,3,4	No
Shorthorn	11,788	862	565	115	1,2,3,4	No
Simmental	80,804	2,804	–	372	1,4,5	Yes

<sup>a</sup>Traits: 1 = carcass weight, 2 = ribeye area, 3 = fat thickness, 4 = marbling, 5 = % retail cuts.

**Table 10.** Distribution of progeny across breeds in the National Carcass Genetic Merit Project (Green et al., 1998)

Breed	No. DNA sires at 50 progeny each	No. Additional EPD sires at 25 progeny each <sup>a</sup>	Total no. sires
Angus	10	20	30
Brahman	10	5	15
Brangus	10	0	10
Braunvieh	10	0	10
Charolais	10	9	19
Gelbvieh	10	7	17
Hereford	10	23	33
Limousin	10	15	25
Maine-Anjou	10	5	15
Piedmontese	10	5	15
Red Angus	10	10	20
Salers	10	0	10
Shorthorn	10	5	15
Simbrah	10	5	15
Simmental	10	15	25
South Devon	10	0	10
Total no. sires	160	124	284
Total no. progeny	8,000	3,100	11,100

<sup>a</sup>EPD sires are to calculate EPD only (no DNA analyses will be performed).

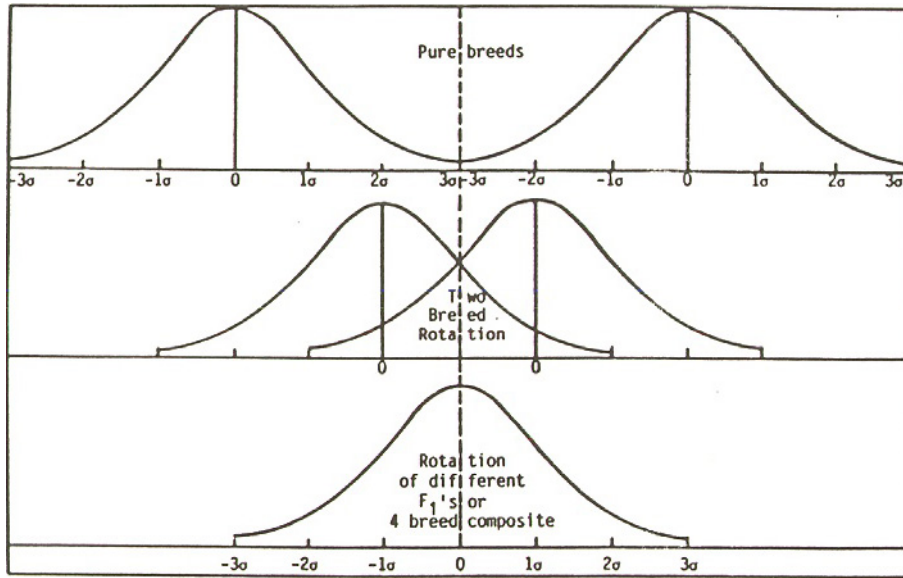


Figure 1. Variation resulting from various mating systems (Cundiff and Gregory, 1999).

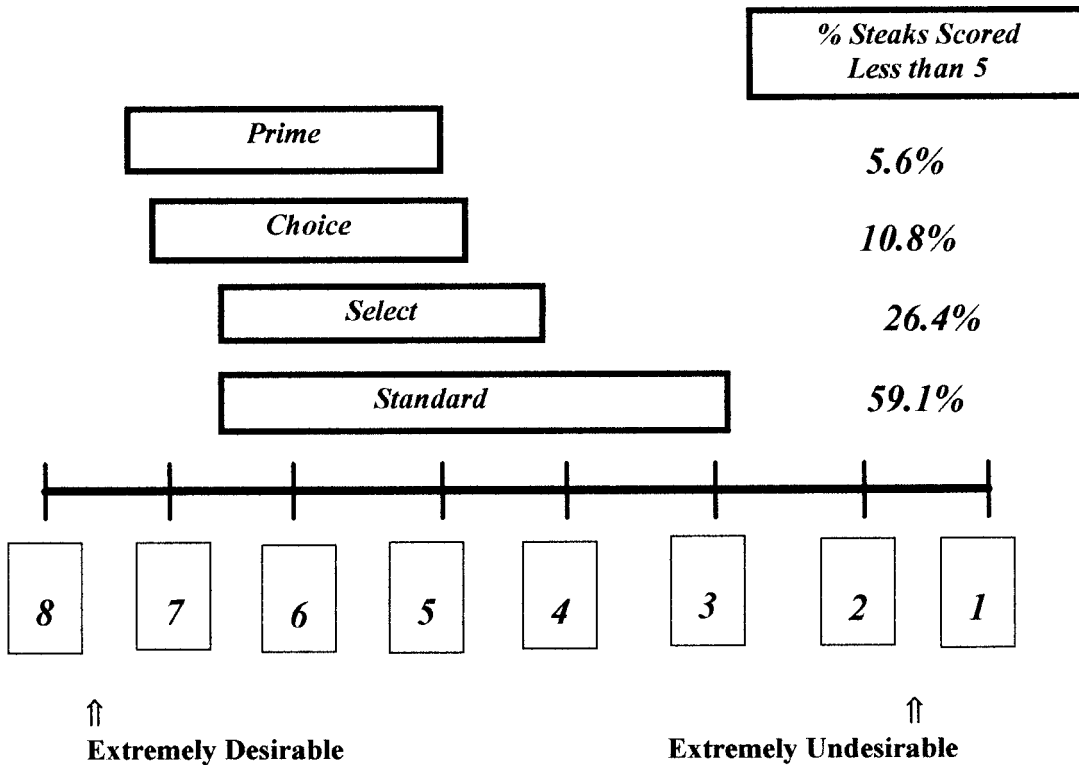


Figure 2. Relationship between palatability and USDA quality grade (Smith et al., 1987).