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INTRODUCTION

Beef cattle production in the United States remains largely a segmented rather than integrated industry. The needs and goals of the various segments of the production chain, with respect to production specification targets, are often different and sometimes conflicting. The resulting inadequate response of the industry to consumer needs has occurred at the same time as intensified competition from pork and poultry products, each of which has contributed to the decline of beef consumption.

Seedstock and commercial cow-calf producers represent particularly important links in the beef production chain because they have primary control of the genetics and produce the "raw material" used by all sectors of the industry. Producers have been told that they must produce cattle that are profitable to the entire industry. However, Melton (1995, 1997) has shown that economic incentives have generally been considerably different for a producer selling calves at weaning than for an enterprise which fully integrates all aspects of production from conception to consumption. Thus, when contemplating changes in breeding programs to benefit other sectors of the industry, producers must question the effects of such changes on their own economic well-being. Variation can be thought of as the raw material with which to make change in production, and its control is a topic of much interest in today's beef industry. This paper will discuss the potential and limitations for control of variation, and address some of the issues that should be considered with respect to the design of breeding programs and impact of genetic decisions.

INHERENT STRENGTHS AND WEAKNESSES

In order to improve the competitive position of beef, it is useful to assess strengths and weaknesses of beef production relative to those of primary competitors. Undoubtedly, the ability of cattle to convert grass to meat is their greatest inherent competitive strength. Thus, cattle make use of vast areas of marginal and non-arable land. Many consumers view grazing as a preferred method of livestock production as compared to confinement methods which are prevalent for swine and poultry. The ability of cattle to utilize other lower cost feeds, such as crop residues and food industry by-products, helps compensate for poorer feed conversion rates as compared to swine and poultry. Another positive factor is that some cattle products are unique and preferred by many consumers for taste or others characteristics.

There are several biological factors that tend to limit inherent production efficiency for cattle as compared to swine or poultry. Longer generation intervals of cattle limit genetic improvement from selection per unit of time. Lower female reproductive rates are associated with lower selection intensities and reduced ratios of market animals per breeding animal. A related consequence is that a greater fraction of marketed beef is from animals of maternal breed-type, thus limiting the fraction from breed-types that may be better suited to market animal production. The need to match cow type to local environmental and resource constraints sometimes necessitates the use of breed-types that are not optimal for other industry segments and contributes to industry-wide variation in beef products. The industry does have an array of market categories to accommodate variable products, but the ability to accurately classify live animals or even carcasses according to market is limited.

VARIATION

Variation can be viewed in either a positive or negative context. On the negative side, a lack of product consistency is a major concern of the beef industry. From a positive viewpoint, genetic diversity is needed to match production potential to environment and resource base, to meet the different target specifications of alternative markets, and to make future genetic change. Genetic variation is the raw material that the breeder has to work with, and so it seems wise to maintain genetic variation in some form, such as between breeds, lines, or families within a breed. Genetic types that are not useful today, but may have future value, could possibly be retained as frozen germ plasm. The real key, it would seem, is control of variation, exploiting it to our advantage while avoiding unwanted consequences. However, there are certain limitations and misconceptions regarding our ability to control variation which are important to consider.

The measurable or observable variation among individuals in a population for a given characteristic is called phenotypic variation. Phenotypic differences can arise from a combination of genetic and non-genetic factors. For convenience, geneticists tend to lump all non-genetic factors together and call them environmental effects. Variation from genetic effects can be further subdivided into additive and non-additive components. According to genetic theory, production traits can be genetically controlled by either additive or non-additive effects or a combination of both. Additive and non-additive sources of variation in the population, respectively, can be exploited by selection and crossbreeding.

Some knowledge of statistics is helpful to develop a better understanding of how much variation exists in cattle populations. The standard deviation is a mathematical measurement of variation among individuals in a group. Though technically not quite correct, the standard deviation can sort of be thought of as how much individuals differ, on average, from the overall group or population mean (average). For traits that tend to follow a bell-shaped (normal) frequency distribution (as many cattle production traits do), we can estimate that approximately 68.3% of the individuals in the population will have trait values within one standard deviation (plus or minus) of the overall mean. Similarly, about 95.5% will have trait values within two standard deviations and 99.7% within three standard deviations of the overall mean.

Consider, for example, birth weight in Table 1 (from Gregory et al., 1995) which has a mean of 96 lb. and phenotypic standard deviation of 11.9 lb. Based on expectations of a normally distributed trait, we expect about 4.5% of the birth weights to be at least two standard deviations away from the mean, about evenly split between the two tails of the bell-shaped curve. That is, we expect about 2.25% of the birth weights will be 72 lb. or less and a similar proportion will be 120 lb. or heavier. About 99.7% of the calves would be expected to weigh from 61 to 131 lb. spanning a range of 6 standard deviations.

The coefficient of variation (CV) expresses the standard deviation as a percentage of the mean. Phenotypic CV values for beef production traits are often in the neighborhood of 5 to 20%. In the study of Gregory et al. (1995), phenotypic CV values ranged from 3% (dressing percentage) to 47% (fat thickness) and averaged 13% across 26 traits related to growth and(or) carcass composition (seven of the 26 traits are included in Table 1).

Heritability is based on the ratio of genetic variation to phenotypic variation. Most estimates of heritability for beef cattle traits are less than .5, which suggests that non-genetic factors account for a significant degree of phenotypic variation. This implies that moderate reductions in genetic variability will have modest impact on phenotypic variability. The large amount of non-genetic variation suggests that current management practices are often not conducive to enhancing uniformity. Sometimes uniform management will have differential animal-to-animal effects, because animals often respond differently to environmental stimuli due to physiological differences caused by factors such as age, sex, maturity, genetic makeup, etc. Methods to reduce such differences among animals within a management group (e.g., reduced calving season, appropriate sorting into management groups) could help reduce phenotypic variation.

Table 1. Measures of Variation for Selected Traits in a U.S. MARC Study[a]

Trait	Mean	Genetic standard deviation	Phenotypic standard deviation	Coefficient of variation, %	Heritability
Birth wt, lb	96	6.0	11.9	12	.25
Carcass wt, lb	736	30.2	62.8	8	.23
Fat thickness, mm	6.5	1.5	3.07	47	.25
Fat wt, lb	174	17.1	31.6	18	.29
Marbling score[b]	4.97	.40	.59	12	.48
Shear force, kg	5.08	.38	1.12	22	.12
Panel tenderness[c]	5.08	.30	.65	13	.22

[a] Source: Gregory et al. (1995).
[b] 4.0 to 4.9 = slight; 5.0 to 5.9 = small.
[c] 4 = slightly tough, 5 = slightly tender.

There is little question that a large amount of genetic variation exists for most biological traits important to beef production. A common question concerns how the degree of variation within a breed compares to variation between breeds. The answer depends on which breeds you wish to compare and on the trait of interest. In a study of diverse breeds at U.S. MARC (Wheeler et al. 1997), the mean difference between breeds with the lowest versus highest percentage of retail product equated to 7.87 genetic standard deviations. Other highest-versus-lowest breed mean differences were 13.87 genetic standard deviations for carcass weight (adjusted to 426 days of age) and 4. 14 genetic standard deviations for percentage of bone in the carcass. Of course, the differences between means of similar breeds were much smaller. Keep in mind that, on a within-breed basis, a range spanning six standard deviations will incorporate over 99% of the animals. Previous MARC research (Cundiff et al., 1986) indicated that the range in breed means was similar to the range in within-breed breeding values (i.e., six genetic standard deviations) for many traits among the breeds evaluated. For many traits important to beef production, it can be concluded that there is considerable overlap among many breeds in terms of individual animal breeding values, although breeds that are at opposite extremes for a trait may have few, if any, animals with overlapping breeding values.

Can selection be used as a tool to remove genetic variation?

Continued selection in the same direction for a given trait will rend to decrease within-population genetic variation over time. In a broadly defined population (e.g., an entire breed), it would likely take many generations of intense selection to substantially reduce genetic variability for most cattle production traits. A "closed" population developed from a narrow genetic base could provide relative genetic uniformity, although the effects of inbreeding could be a problem, and the time to expand a closed population to the point of serving retail markets would be prohibitive. Perhaps technologies such as cloning and embryo transfer, if they become cost-efficient on a large scale basis, will become useful for this purpose.

Can sire selection or EPDs be used to improve uniformity?

Using bulls of the same breed (or composite) should result in improved genetic uniformity as compared to using bulls of different breeds. The use of bulls from the same family may result in some additional genetic uniformity. In predicting how successful these practices might be, it is again worth pointing out that moderate reductions in genetic variability will likely have relatively minor impact on phenotypic variability. As a note of caution, it is important to choose the right family when using related sires, because the risks associated with sampling are not being spread as widely.

EPDs can be used to improve uniformity with certain limitations. Using a battery of sires of the same breed with similar EPDs should result in improved uniformity as compared to using bulls with a wide range of EPDs. However, trying to improve uniformity by matching EPDs of the sire and dam may well be frustrating and often ineffective, as will be demonstrated below. Also, the Accuracy value that accompanies an EPD should not be interpreted as a measure of expected progeny variability. The Accuracy value reflects the amount of information used to calculate the EPD, and indicates the confidence one should have that the EPD closely approximates the true mean progeny performance.

Can within-breed mating systems be used to improve uniformity?

Matings between animals with similar performance or EPDs will result in improved uniformity under some conditions, but not others. To demonstrate, consider an example in which animals have the same gene combinations at all but two loci (gene pairs) affecting birth weight. Assume that the values given in Table 2 are the relative contributions to birth weight of alternative genotypes of these two loci (excluding environmental and epistatic effects) expressed as deviations from the population mean, and that the overall average birth weight is 90 lb. To simplify things, we'll assume constant environmental effects for all animals so that differences in genotype completely determine phenotypic differences. Table 3 shows all possible two-locus genotypes along with corresponding phenotype (birth weight). Note that different genotypes can sometimes produce the same phenotype. There are a total of nine possible genotypes and 5 possible phenotypes in this example.

Table 2. Example of the Effect of Individual Genetic Loci on Calf Birth Weight.

Locus	Possible genotypes	Relative expression, lb	Type of gene action
	AA	+5	
1	Aa	+5	Complete dominance
	aa	-5	
	BB	+10	
2	Bb	0	Additive gene action
	bb	-10	

Table 3. All Possible Genotypes and Phenotypes for Birth Weight Example.

Genotype	Relative expression, lb	Calf birth wt , lb
AABB	+15	105
AABb	+5	95
Aabb	-5	85
AaBB	+15	105
AaBb	+5	95
Aabb	-5	85
AaBB	+5	95
AaBb	-5	85
Aabb	-15	75

Next let's consider some specific matings, again keeping in mind that the results do not include environmental effects. In each of the first four matings shown in Table 4, both parents have the same phenotype. Progeny uniformity ranges from complete uniformity in Mating 1 to extreme variability in Mating 3. It is clear that some, but certainly not all, "like-to-like" matings result in uniformity. Furthermore. one of the matings between extreme opposites (Mating 5, AABB x aabb) resulted in highly uniform progeny. Mating opposites will not in general consistently improve uniformity, but such (corrective) matings need not be avoided because of variability. One generality that is apparent is that progeny variability increases as degree of heterozygosity in the parents increases. Conversely, highly homozygous parents tend to produce progeny that are more uniform.

Table 4. Possible Outcomes of Selected Matings.

Mating	Sire		Dam		Progeny	
	genotype	birth wt, lb.	genotype	birth wt, lb.	genotypes	birth wt, lb.
1	AABB	105	AABB	105	AABB only	105
2	AABb	95	AaBb	95	6 types	85 to 105
3	AaBb	95	AaBb	95	9 types	75 to 105
4	AAbb	85	aaBb	85	2 types	85 to 95
5	AABB	105	aabb	75	AaBb only	95
6	AaBB	105	Aabb	85	3 types	85 to 95

One principle illustrated by the example is that it is sometimes possible for phenotypically similar animals to be quite different genetically, even in the same environment. Secondly, progeny uniformity will depend on the degree of homozygosity versus heterozygosity in the parents. An obvious question, then, is how to produce highly homozygous animals. Matings between related animals (inbreeding) will increase homozygosity over time, but may not be a practical alternative because inbreeding will increase the frequency of both desirable and undesirable homozygous gene pairs in the progeny (e.g., Mating 3 in Table 4). Over time, the frequency of the undesirable homozygous gene pairs can be reduced by selection, but the negative consequences in the interim tend to be too severe to justify inbreeding.

Breeding systems for commercial production.

A common question in the beef industry is the extent to which crossbreeding has contributed to increased variability. While it is true that some crossing systems do increase variability, others will have variation that is similar to the contributing straightbreds. Therefore, variability *per se* is probably not a logical reason to not crossbreed, because the potential advantages of heterosis and possibly genetic complementarity would also be missed. Furthermore, in cases where dramatic genetic change is desired, between-bred selection is generally more efficient than within-breed selection.

The use of straightbreeding (sire and dam are of the same breed or composite) for commercial production might be justified when a single breed (or composite) provides both the optimal cow type and calf type. Straightbreeding requires only one breeding pasture which could be an advantage in small single-sire herds. A composite might be preferred over a pure breed when a blending of two or more breeds is preferred over a single breed and when heterosis is thought to be important. Composites formed from divergent breeds, at least in early generations of inter se matings, might be expected to have more variability than a highly uniform pure breed. However, variability within composites at U.S. MARC was similar to variability within contributing purebreds on average (Gregory et al.. 1995). Unlike rotational systems, composites do not have significant between-generation variability.

In rotational crossing systems, there is somewhat of a tradeoff between heterosis and between-generation variability, because each of these increases as the number of, and genetic distance between, contributing breeds increases. Like composites, rotational systems do not allow breed composition of market animals to differ from that of the cow herd.

Terminal matings provide an opportunity to derive maximum potential benefits from crossbreeding while maintaining relative genetic uniformity. Optimal terminal systems for commercial production take advantage of maternal and individual heterosis, and allow the opportunity to use complementary "specialized" sire and dam breed-types. From an industry point of view, the use of such matings for commercial production allows seedstock producers to focus on a narrower range of traits, thus allowing a greater rate of genetic improvement per trait, and genetic antagonisms are less of a concern. Despite these apparent advantages, terminal matings are not especially widely utilized for beef production, largely because of issues related to production of replacement females.

DESIGNING A BREEDING PROGRAM

It is critical that producers, both seedstock and commercial, identify which market(s) they intend to serve and the corresponding desired production specifications. If the producer knows specifically what the economic rewards and discounts are for various levels of production, then the design of an appropriate breeding program becomes much easier. Unfortunately, general recommendations are not always particularly helpful to the individual producer because relative economic values for production traits tend to vary among producers (due to different resources, environments, markets, etc.) and can be vastly different across segments of the production chain.

A logical approach is to determine an optimum economic balance between cow-calf production efficiency and traits that are of more importance to other industry sectors, including postweaning performance and carcass value. Thus, the common suggestion to the cow-calf producer is to match the cow to the environment and the calf to the market. Factors such as climate, feed resources, and level of intensity of management are important when choosing cow breed-types. Choosing an appropriate breeding system depends on such factors as herd size, availability of breeding stock, and the extent to which cow breed-type provides the desired characteristics in the market calf. Between-breed differences tend to be highly heritable, and so between-breed selection is generally more efficient than within-population selection if dramatic genetic change is warranted. With the large array of cattle breeds available, it should be feasible to find, at least in a mixture of breeds, the right combination of trait production levels to fit most selection objectives. With regards to post-weaning traits, general conclusions from breed evaluation research (Cundiff, 1997) indicate that :

breed-types that excel in growth potential and cutability often produce heavier than optimum carcasses with less than optimum marbling;

breed-types of moderate growth potential and higher marbling potential tend to produce fatter than optimum carcasses with lower cutability; and

certain breed crosses with 50:50 ratios of British to Continental inheritance are more likely to produce optimal levels of carcass weight, cutability, and marbling than most single breeds.

In addition to choosing a breeding system and breed-type(s), sire selection is also an important consideration, and the development of EPDs have significantly improved selection accuracy. Today, in several breeds, EPDs are available for any registered animal in the breed, and so commercial breeders often have access to bulls with EPDs. Even though the accuracy of an individual young (non-parent) bull may be low, the accuracy of the average EPD of several young bulls is usually much higher.

Compared to sire selection, selection of individual cows is much less important from a genetic standpoint for commercial producers. Cow selection is important in seedstock herds because the cow may produce bull progeny that will be used for breeding. In commercial herds, cow evaluation should be based more on expected production and convenience traits of the cow herself rather than on her expected genetic contribution to future generations.

SUMMARY AND IMPLICATIONS

Seedstock and commercial cow-calf producers have primary control of the genetics used by all sectors of the beef industry. If genetic change is needed by other sectors in the production chain, they need to provide feedback and economic incentives to the breeding herd sector. Genetic decisions should take into account resource constraints and marketing considerations, which tend to be specific to the individual enterprise. Thus, producers must pick and choose from general recommendations and fine tune those most applicable to them, while maintaining the flexibility to adapt as constraints change.

A lack of product consistency is a major concern to the beef industry. Consequently, there has been much interest in sources and manipulation of variability. There is little question that considerable genetic and non-genetic variation exists within and between breeds for many cattle production traits. Environmental and resource constraints vary among producers and require that different cow breed-types and production methods be used in different herds, thus contributing to industry-wide variation. There are some methods of genetic control which could reduce within-herd genetic variability, although in many cases the reduction would be relatively small compared to phenotypic variation. Uniform management will not necessarily reduce phenotypic variation if the animals within a management group have variable requirements. Thus, it is important to reduce differences (in age, weight, maturity, etc.) among animals within a management group.

Decisions to make in the design of a breeding program include selection of breeding system, breed-type(s), and individual breeding stock. The impact of genetic decisions can be difficult to predict. For example, a given bull could produce, on average, weaning weights of 500 lb. in one herd and 550 lb. in another herd with the difference due to different dams and environment. Over time, through trial and error, a producer can develop a better sense of expected production levels based on factors such as breed and EPD. To attain feedback on postweaning and carcass traits, cow-calf producers may need to develop alliances with feeders, and make use of programs such as steer feed-outs and carcass data collection services.

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