

DEFINING BIOLOGICAL EFFICIENCY OF BEEF PRODUCTION

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Introduction

“Efficiency” is a poorly defined and generally overused term in livestock production. The segmentation present in the beef industry provides wide latitude for limited, and potentially conflicting, definitions and makes achievement of an industry-wide consensus on the definition of efficiency difficult. Much of what we believe today about efficiency of animal production was introduced by Dickerson (1970) in a paper by the same name and was further developed by him and his students in an array of papers on biological and economic efficiency in beef cattle and other species that followed over the next 30+ years.

In ruminants, separate consideration of “biological” and “economic” efficiency is nearly impossible under U.S. conditions. The separate and highly significant contributions of both grazed forages and harvested concentrates to beef production, and the potential substitution of one feed source for the other, dictates that economic considerations must influence our view of biological efficiency. Key economic issues which necessarily influence the definition of biological efficiency include the relative costs of grazed forages versus harvested concentrates and the procedures used to assign costs to grazed forages. Similarly, the U.S. beef marketing system, with simultaneous consideration of quality and yield grades, introduces an element of complexity into any discussion of biological efficiency that is not present in any other species of meat animal.

Issues involving relative feed costs, differential product pricing, and other economic considerations will be gratefully relinquished to other speakers (Tess, 2002). This presentation will focus narrowly on a definition of biological efficiency as:

“the capacity to convert physical inputs (feed) into marketable product (beef) under prevailing production conditions.”

This definition of biological efficiency permits us to consider the basic dichotomy between the efficiency of use of grazed forages (“cow efficiency”) and harvested concentrates (“growth efficiency”). This dichotomy is important, not because of intrinsic differences in efficiency of use of the two feed resources (although such differences certainly do exist), but because the biological traits supporting efficient use of the two resources are markedly different.

This definition of biological efficiency can be applied at both the individual-animal level and at the level of the industry. Consideration of biological efficiency at the industry level

includes issues of genetic diversity, breeding structure, and capacity for short-term adjustments. At the industry level, the definition of biological efficiency may be augmented to include:

“population characteristics that provide the flexibility to rapidly adjust the characteristics of commercial offspring in response to changes in economic conditions.”

This definition allows incorporation of the full array of products and appropriate consideration of genotype x environment interactions. It likewise incorporates consideration of operational issues supporting performance recording programs and achievement of genetic change in chosen biological traits.

Traits that support efficient cow-calf production systems are generally different from those that define efficient postweaning calf growth. For that reason, biological efficiency will be considered separately for the cow herd and for the growing market animal. This approach is consistent with Dickerson's (1970) suggestion that total costs of production be separated into those for the producing and reproducing female population and those for growing progeny to market size.

Cow Efficiency

Biological efficiency in the cow herd is most clearly reflected in the number of calves weaned per cow exposed. The weight of weaned calves is generally of secondary importance in defining biological efficiency in integrated systems, but plays a significant role in defining economic efficiency for the cow-calf producer. If this information could be coupled with an accurate predictor of annual feed intake, a relatively comprehensive measure of cow efficiency could be derived. Additional characteristics of importance to cow efficiency include appropriate transmitted effects to support efficient postweaning growth in crossbred progeny. Achievement of high levels of cow efficiency would be facilitated by high levels of maternal calving ease to support use of terminal sires.

Ample research exists to suggest that cow size and milk production level have intermediate optimum levels appropriate to each production environment, management system, marketing scheme, and crossbreeding program (Notter et al., 1979a,b). Milk production level, in particular, will be dictated almost exclusively on economic grounds involving relative costs of cow and finishing diets and patterns of retained ownership. On solely biological grounds, milk production levels beyond those required to maximize calf survival and health and to set the stage for optimal postweaning growth are generally not needed (Notter et al., 1979a). Access to six to eight breed types representing various combinations of frame size, adult weight, and milk production potential, and with access to within- and across-breed EPDs, seems appropriate to permit prompt (one-generation) adjustments in cow performance traits to meet temporary or unpredictable changes in economic conditions.

Opportunities to reduce annual feed requirements for the cow herd or to improve efficiency of utilization of available forages may exist but will be difficult to exploit. Two possibilities involve either the identification of animals with lower maintenance requirements or the identification of animals with enhanced adaptive characteristics that permit them to harvest feed more efficiently in challenging grazing environments or better utilize low-quality feedstuffs. Some evidence for genetic variation in maintenance costs of breeding females exists in several species (see Archer et al., 1999, for review) but without direct measurement of feed intake under controlled (and therefore necessarily artificial) conditions or the identification of highly informative phenotypic indicators or genetic markers, accurate individual-animal evaluation will be difficult. Archer et al. (1999) hypothesize that selection for efficiency of feed use in growing animals, if properly defined and measured, may be feasible and have desirable correlated responses in cow efficiency. Adequate data to address that hypothesis do not now exist but are being collected by Australian scientists (Arthur, 2001).

The second situation involves issues of environmental adaptation and cow efficiency in suboptimal forage environments defined by limitations in either forage quality or availability. In such situations, adaptations that enhance the animals' capacity to harvest and utilize adequate nutrients may have large effects on cow efficiency. Records of reproductive performance, perhaps coupled with information on cow weights and (or) condition scores may be the most appropriate measures of environmental adaptation in such situations.

Reproductive Efficiency. The high proportion of total beef inputs expended on cow maintenance is one of the most significant limitations to increasing biological efficiency of beef production. Costs for cow maintenance, lactation, and growth account for 65 to 70% of the total energy required for beef production but perhaps only 35% of the total cost of production (Notter et al., 1979a), although this last figure can vary widely depending on the cost assigned to grazed forages.

Spreading costs of cow maintenance over larger offspring numbers thus remains the single most important strategy for improving biological efficiency of beef production. This goal can be achieved by:

- maximizing cow fertility,
- increasing cow fecundity by increasing twinning rates.

Options for incorporating measures of reproductive fitness into national genetic evaluation programs include direct measures of fertility such as pregnancy rates and calving dates and indirect measures of indicator traits such as reproductive tract scores in heifers and scrotal circumference in males. Factors limiting widespread emphasis on fertility traits in beef cattle genetic evaluation include the relatively high mean fertility levels already achieved in well-managed herds in favorable environments, the associated low heritabilities of most direct measures of fertility, the difficulty associated with accurate reporting of reproductive events in industry performance recording programs, and insufficient emphasis in most breeds on whole-herd recording.

The dynamics involved in selection to improve fertility are complex, with strong economic as well as biological origins. Nutrients obtained from grazing permanent pastures are commonly assigned low costs, supporting a tendency to correspondingly undervalue cow efficiency. Second, the categorical expression of fertility effectively places a ceiling on realized fertility that makes selection ineffective (and unnecessary) when mean fertility levels are high. The result is a situation in which the contribution of cow fertility to biological efficiency of beef production is paramount at low fertility levels, but trivial as pregnancy rates approach 90 to 100%.

Selection to genetically improve fertility in sub-optimal environments can be effective, as demonstrated by Davis et al. (1993), who documented a genetic response to bidirectional selection for pregnancy rate. More recently, pregnancy rates in Nellore yearling heifers in Brazil were likewise shown to be quite highly heritable ($h^2 = .78$; Eler et al., 2002). Adequate evidence likewise appears to exist to support use of yearling scrotal circumference in males as a useful selection criterion to increase yearling pregnancy rates in late-maturing, but not necessarily in early-maturing, breeds (Brinks et al., 1978; Martins Filho and Lobo, 1991; Notter et al., 1993).

Twinning has clear potential to increase the biological efficiency of beef production. Selection for increased ovulation and twinning rates in cattle has been successful. VanVleck and Gregory (1996) report that the frequency of twinning increased with selection from 3.4% in 1982 to 28.5% in 1993 (Figure 1). Current frequency of twinning in the herd is over 35% (Echternkamp and Gregory, 1999). Modest heritability estimates of .10 and .09 for ovulation and twinning rates, respectively, in that population were leveraged to yield annual rates of genetic change in twinning rates of over 1.8%/yr by an intensive screening process to identify founder animals with a history of twinning, use of A.I. to optimally utilize elite animals, and use of repeated measures of ovulation rate to increase accuracy of evaluation.

Performance of cows producing twins and of twin-born calves in this project (Table 1 and 2) were reviewed by Gregory et al. (1996) and by Echternkamp and Gregory (1999a,b). Twin-born calves had 13% lower survival rates in the first 3 d of life (81 vs 94%) but only 2% higher death losses from 3 d of age to weaning. Surviving twin-born calves grew 15% less rapidly to 200 d. Twin-born males grew 3% less rapidly postweaning, averaged 2% lighter at slaughter, and required an extra 20 d to reach slaughter weight. Number and weight of calves at weaning were increased by 65 and 58%, respectively, in cows producing twins. Twinning significantly increased the incidence of dystocia, which was 22% higher (42 vs 20%) in cows with twins, primarily due to malpresentation of one or more offspring (Echternkamp and Gregory, 1999a). In terms of postpartum reproductive performance (Echternkamp and Gregory, 1999b), conception rates in a 60- to 70-d breeding season were 77% for cows that produced singles but only 67% for cows that produced twins. Among cows that conceived, those that produced twins required, on average, an additional 9 d to conceive. Adjustment for effects on cow fertility and calving date in an annual calving season would reduce the advantage of twinning to approximately 42% for number of calves produced and to

about 30% for weight of calf weaned. Guerra-Martinez et al. (1990), in a study of cows that twinned after ET, similarly concluded that input costs per unit of beef output could be reduced by 24% in the proportion of the herd that produces twins.

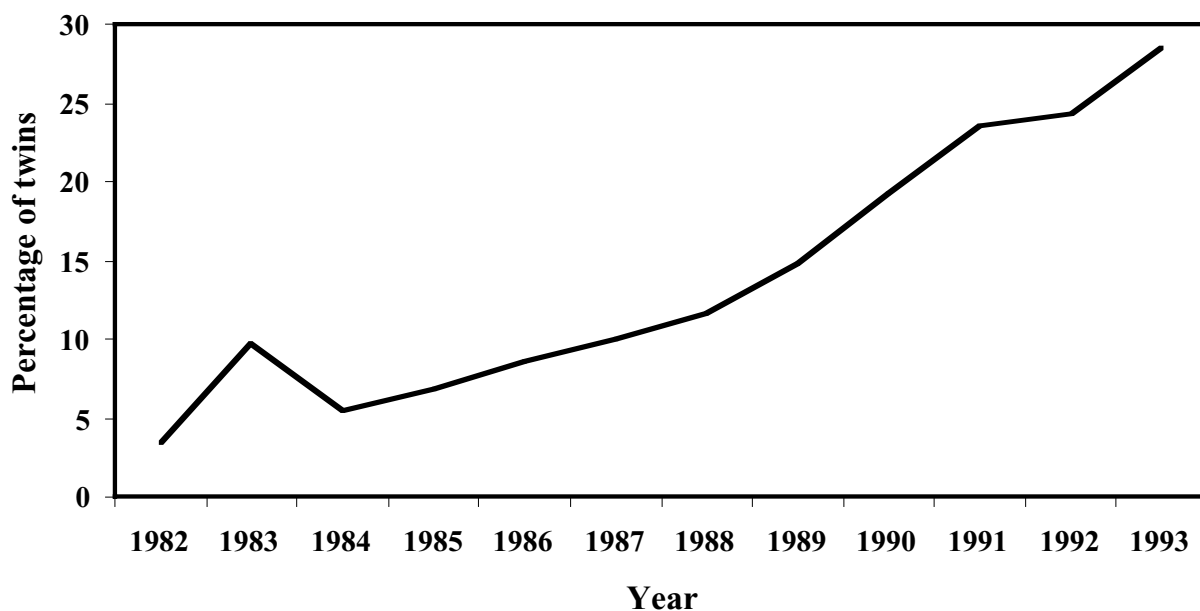


Figure 1. Percentage of twin births in a line of cattle selected for twinning (Van Vleck and Gregory, 1996).

An opportunity to increase output from the cow herd by perhaps 15% (a 42% increase in output with a 35% twinning rate) is hard to ignore, but there are mitigating economic factors. A high frequency of twinning would require more labor at calving to manage dystocia. Estrus synchronization and ultrasonic detection of twin births could assist in focusing additional labor on short periods of time. Spring and fall calving seasons could enhance realized annual fertility, but at a cost of additional management, feed, and labor. Creep feeding and possible early weaning of at least some calves would increase feed costs per calf, but would also be expected to enhance calf performance. Results in sheep suggest that twinning rates can only be increased to perhaps 60 to 70% before the incidence of triplet and larger litters becomes high enough to introduce a new level of potentially adverse effects on dystocia and calf survival.

Growth Efficiency

The biological traits influencing efficiency in the growing market animal, and particularly in the feedlot, differ considerably from those desired in the cow herd. Issues of appetite (positive and negative), lean growth potential, maintenance requirements, growth efficiency, and carcass fat level and distribution become primary. At best, most of these traits are largely independent of the traits defining cow efficiency. Some antagonisms may exist, but none are well documented. Nor are any of the antagonisms that may

exist apparently large enough to seriously compromise an integrated program of genetic improvement.

Table 1. Performance of cows producing twins^a

Item	Singles	Twins
Incidence of dystocia, %		
2-yr-old cows	41	52
≥3-yr-old cows ^b	16	45
Postpartum conception rate, % ^c	77	67
Days to conception ^c	89	98
Calves weaned/cow calving	.92	1.52
Wt of calf weaned/cow calving, lb	513	811

^aGregory et al. (1996), Echterkamp and Gregory (1999a,b).

^bWeighted average of cow age classes.

^cWeighted average of type of birth x number of calves suckled classes.

Table 2. Performance of single- and twin-born calves^a

Item	Singles	Twins
Birth wt, lb	103	84
Perinatal survival, % ^b	96	83
200-day wt, lb ^c	570	510
Slaughter age, d ^d	448	468
Slaughter wt, lb ^d	1,320	1,296

^aGregory et al. (1996).

^bWeighted by calving difficulty score.

^cWeighted by number of calves nursed (0 or 1 for singles; 0, 1, or 2 for twins).

^dMales calves only.

Feed Efficiency. Efficiency of feed use will be addressed by several speakers in this year's BIF proceedings, building upon the comprehensive analysis of feed efficiency in beef cattle conducted by Dickerson et al. (1974). Recent advances in methods for evaluation of efficiency of feed use have come from Australian studies (e.g., Arthur et al., 2001) using the concept of selection for reduced residual feed intake (RFI). Residual feed intake is the difference between actual feed intake and some predicted intake based either on tabular values or regression analysis. As applied by Arthur et al. (2001), RFI is the deviation of the actual feed intake from that predicted (by regression) for animals of the same average metabolic weight and ADG. This concept of RFI was used in beef cattle by Koch et al. (1963), who reported a heritability of the trait of .28, somewhat lower than the value of $.39 \pm .03$ reported by Arthur et al. (2001), but still indicative of opportunity for genetic change. Analyses of RFI have also been conducted for layer chickens, pigs, and dairy cattle, with variable results (Emmans and Kyriazakis, 2000).

Residual feed intake is presented as an alternative to the more widely used feed conversion ratio (FCR, the feed:gain ratio) as a measure of biological efficiency of growth. It is thought to be more indicative of the intrinsic efficiency of feed use, and particularly of maintenance. The RFI likewise avoids some of the problems involved in the use of ratios as selection criteria. However, as pointed out by Dickerson (1970), RFI alone is unlikely to be a sufficient indicator of growth efficiency. Efficient growth involves the combined effects of rapid growth (to dilute maintenance requirements), desirable composition of gain, and efficient utilization of consumed feed. Alternatives to FCR must recognize all these determinants of efficient growth.

The dynamics of the feed conversion ratio are well known: rapid growth, with associated dilution of maintenance requirements, has the most important impact (phenotypically and genetically) on FCR and is effectively a prerequisite for lowering FCR. The impact of appetite (voluntary feed intake) and composition are variable, depending upon the stage of growth and the breed. In early life, when lean tissue growth predominates, appetite may be associated with desirable FCR, but at higher degrees of maturity, appetite and propensity to fatten commonly combine to yield an undesirable association between appetite and FCR. It seems clear that selection for FCR may result in less than optimal lean tissue growth efficiency and that selection for FCR should be combined with negative emphasis on measures of fatness (likely measured by ultrasonic BF thickness) to maximize biological efficiency of lean tissue production. Imposition of quality standards (minimum fatness levels) on the final product could favor unadjusted FCR as a selection criterion, but selection involving an index of ADG and residual feed index may be superior to direct selection on feed conversion ratio.

The picture that emerges favors high feed intake and associated rapid growth provided the appetite and lean growth potential are synchronized to prevent excessive fat gain. Lower appetite is acceptable and may be favored when lean growth potential is more limited. Leanness is favored, but only in animals of high growth potential. The concept of RFI attempts to account for these interactions among appetite, lean growth potentials, and growth rate. RFI also places more emphasis on potential differences in intrinsic maintenance requirements and may have a favorable association with maintenance costs in the breeding herd (Arthur et al., 2001). Genetic associations among efficiency traits in Australian Angus cattle (Table 3) reveal that RFI has a substantial genetic association with FCR and feed intake. FCR is much less closely associated with intake but is more closely associated with ADG. Associations of backfat thickness with both RFI and FCR are less than might be anticipated. RFI is nothing more (and nothing less!) than a linear index of mean metabolic weight, ADG, and feed intake and in that sense may be, in some ways, superior to FCR. But the index weightings implicit in RFI are likely not optimal for prediction of growth efficiency.

Table 3. Genetic correlations among residual feed intake (RFI), feed conversion ratio (FCR), mean weight, average daily gain (ADG), feed intake (FI), and backfat thickness (BF) in Australian Angus cattle^a

Trait	Trait				
	FCR	Mean wt	ADG	FI	BF
RFI	.66	-.06	-.04	.69	.17
FCR		-.01	-.62	.31	.03
Mean wt			.53	.65	n/a ^b
ADG				.54	n/a ^b
FI					.27

^aArthur et al. (2001).

^bNot reported.

Modification of the Growth Curve. Intense interest in potential to modify the growth curve arose in the 1970's (e.g., Brown et al., 1976) but was largely dismissed as impractical, at least under conditions emphasizing use of field records in selection. However, an historical analysis of weight:age relationships in broiler chickens (Emmans and Kyriazakis, 2000) provides compelling evidence of genetic change in the growth curve. Over the period 1950 to 2000, adult weights of broiler males were estimated to have increased by 75%, whereas their maturing rate increased by over 150%. Since maturing rate is anticipated to decline with increases in mature size, this pattern represents a clear modification of the growth curve. Knap (2000) provides similar evidence that mature lean body mass in pig sire lines has remained relatively stable over time, whereas rate of protein deposition has clearly increased. The persistence of high lean growth rate in pigs appears to also have been extended to later ages (accounting for increases in slaughter weights). Interestingly, this pattern is much less clear in dam lines where increases in growth rate appear more likely to be accompanied by the expected increases in mature size.

Results from broiler chickens and from mouse experiments confirm that selection for body weight at a fixed age is expected to have substantial effects on appetite and fatness unless there is corresponding negative selection emphasis on these traits. Results from the most recent cycle of the U.S. MARC Germplasm Evaluation Program (Cundiff et al., 2002) show remarkable uniformity among U.S. breeds in postweaning ADG of steers and 400-d weight of heifers (Table 4) despite significant differences favoring calves sired by continental European breeds in measures of fatness and yield of retail product. Conclusions involving appetite-driven effects on growth and on the shape of the growth curve for these breeds will be intriguing but must await data on adult body weights and frame scores for the various types. Appetite-driven changes in growth rate would not be expected to have a positive effect on biological efficiency of lean tissue deposition but could influence the growth curve and have a positive effect on economic efficiency by increasing the percentage of animals in the USDA Choice quality grade.

Table 4. Means for growth and composition traits of cattle sired by various breeds^a

Sire Breed	Weaning weight, lb	Postweaning ADG, lb/d ^b	400-d wt, lb ^c	% Retail product ^b	Yield grade ^b
Hereford	524	3.46	829	59.5	3.35
Angus	533	3.40	877	58.8	3.32
Red Angus	526	3.40	872	57.7	3.76
Simmental	553	3.47	848	62.1	2.95
Gelbvieh	534	3.33	812	62.3	2.80
Limousin	519	3.30	835	63.0	2.63
Charolais	540	3.43	830	62.2	2.77

^aCundiff et al. (2002).

^bOf steers.

^cOf heifers.

Use of the Myostatin Gene? The recent discovery that two different mutant forms of the myostatin gene are responsible for muscular hyperplasia (“double muscling”) in the Piedmontese and Belgian Blue breeds (Kambadur et al., 1997) leads to new opportunities to manage and use muscular hyperplasia. Individuals carrying one copy of either of the alleles associated with double muscling are superior to noncarriers in muscularity and leanness, though substantially less extreme than homozygous double-muscled individuals (Table 5). Casas et al. (1998) reported that a single copy of a mutant *mh* allele increased retail product yield by 4.4% and reduced mean yield grade by 0.7 units. However, marbling score was also reduced by about 10%. Short et al. (2002) reported that a single copy of mutant *mh* increased percentage of primal cuts by 2.1%, but also reduced marbling score from 6.0 to 5.4. Birth weights were consistently increased in calves carrying a single copy of *mh*, but estimates of the magnitude of increase have been inconsistent, ranging from 2.9 (Short et al., 2002) to 7.0 (Casas et al., 1999) and 10.0 lb (Casas et al., 1998). In all these studies, the incidence of calving difficulty was not significantly increased in adult cows producing calves that carry the *mh* allele. However, the incidence of calving difficulty was increased from 13 to 43% in heifers delivering calves carrying one copy of *mh* (Short et al., 2002).

The *mh* allele appears to have little effect on appetite or postweaning gain and therefore does not improve feed conversion ratio. However, efficiency of lean tissue gain is clearly improved (Short et al., 2002). Negative effects of *mh* on marbling score and quality grades will likely limit realization of the advantages of improved lean gain efficiency in traditional markets. However, several studies indicate that Warner-Bratzler shear measures and tenderness scores of cattle that carry the *mh* allele are at least equal to those of noncarrier despite their lower marbling scores (Wheeler et al., 2001; Short et al., 2002). Use of the *mh* allele will thus require development of new marketing options that do not rely on the U.S.D.A. grading scale to indicate quality characteristics (Keele and Fahrenhrug, 2001).

Table 5. Effect of 1 copy or 2 copies of an inactivated myostatin allele on performance to traits in beef cattle^a. Tabular values are expressed as a percentage change relative to normal cattle

Trait	Study ^b		
	1 ^a	2	3
Birth wt, lb	+2.9 (+9.7)	+7.0	+10.0
Dystocia incidence, %:			
Heifers	+30.2 (+36.7)		
Cows	-0.7 (+7.1)	+5.0	
Weaning wt, lb	-2 (-8)	+20	
Postweaning gain, lb	0 (-4)	+24	
Final wt, lb	+2 (-6)		
Dressing %	+1.8 (+5.3)		
Lean yield, %	+2.1 (+6.1)		+4.4
Marbling score	-0.6 (-2.0)		-0.5
Yield grade	-0.6 (-2.0)		-0.7
Gain efficiency, % ^c	-2.7 (-3.0)		
Lean gain efficiency, % ^c	+4.8 (+20.6)		

^aTabular values show the mean difference between calves that carry 1 or 2 copies of the inactive allele and those that do not. Effect of 2 copies of the mutant allele are shown (in parentheses) only for study 1.

^bStudy 1 is Short et al. (2002); study 2 is Casas et al. (1999); study 3 is Casas et al. (1998).

^cEfficiency was measured as grams of gain (or lean gain) per Mcal of feed consumed.

The most likely use of the *mh* allele would be through the production of heterozygous market animals by mating homozygous *mh/mh* sires to noncarrier cows. However, the opportunity to use DNA testing to discriminate between carrier and noncarrier animals provides additional options for managing this allele. Thus Short et al. (2002) envision the possibility of maintaining a herd of *mh/+* carrier females which would be mated to homozygous *mh/mh* sires. Offspring would be 50% carriers and 50% double muscled. All double-muscled offspring would be marketed. Females would be genotyped and only heterozygous individuals retained as replacements. Advantages in lean gain efficiency from this system could, however, only be realized in a marketing system that does not place emphasis on marbling scores.

Interesting options also exist for introgression of *mh* alleles into different genetic backgrounds, particularly those with high genetic merit for appetite and marbling score. Short et al. (2002) report that Piedmontese-sired calves lacking the *mh* allele grew less rapidly postweaning than Hereford-sired calves, but had similar marbling scores. These results suggest that supplemental selection for leanness (represented by both low appetite and high lean growth potential) has occurred in the Piedmontese (and also likely in the Belgian Blue) to augment effects of *mh*. These effects could potentially be modified by placing *mh* in a different genetic background.

Conclusions

The biological efficiency of beef production is best viewed as a characteristic of the industry rather than the individual. Biological efficiency reflects options as much as optimums. Efficient cows are those that produce calves regularly and easily; most of the other biological characteristics of the cow herd are negotiable, depending upon markets and production environments. But if they don't calve regularly and easily, they won't be efficient.

The biological efficiency of the growing calf is more directly about balance: high lean growth potential, with an appetite in synchrony, is the basis for high biological efficiency. But the filter of the market, with an association between intramuscular fat and quality, adds art to the science, along with a healthy dose of unpredictability. Economic efficiency always trumps biological efficiency, so we arrive at the conclusion that biological efficiency is the servant of economic efficiency. And that master is best served by having the biological diversity to rapidly accommodate changes in markets and economic variables. We regularly act in ways that fail to maximize biological efficiency of lean tissue production. We need not apologize for that, since the success of the commercial cattleman is measured in profit, not efficiency. But neither should we forget it.

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