GENETIC ASPECTS OF MARBLING IN BEEF CARCASSES

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INTRODUCTION: The goal of this paper is to review the genetic aspects of marbling in beef carcasses and to serve as a reference source. It is not meant to be an exhaustive review of the literature in regard to all relationships involving marbling with other production and carcass traits. However, it is meant to review several of the major studies around the world that could have direct genetic implications on production of beef carcasses in the United States. Historically, fat thickness of fed cattle has been used to estimate carcass quality grade. As a result, this paper focuses on the relationship between subcutaneous fat thickness and marbling. Following an Executive Summary of points, the paper is organized into sections of (1) breed comparison studies, (2) estimates of genetic variation, heritability and correlations of marbling and other carcass traits, (3) evaluation at different carcass end-points, (5) single gene and genetic marker considerations, (6) impacts of selection on marbling, (7) National Beef Quality Audit aspects, and finally (8) cowherd considerations.

EXECUTIVE SUMMARY

- There are substantial differences in marbling ability across breeds of cattle, and within breeds of cattle. Heritability estimates of marbling ability have ranged from .13 to .88 in particular groups, with a mean value of approximately .45. As a result, marbling will respond to selection in all breeds, but the amount of genetic variation is not constant within all breeds, and the relationship of marbling with other traits is probably not constant across all breeds.
- Selection can be utilized to increase marbling ability without increasing external fat, and increased marbling can also be accomplished without causing detrimental effects on other production traits in feedlot animals or in cowherds.
- Where it has been evaluated within proper research trials, effect of carcass end-point-constant basis (age, weight, fat) has a relatively minor impact on heritability estimate for marbling or ranking of individuals for marbling EPD.
- Genetically, the use of external fat thickness alone explains very little in regard to marbling score, and therefore should not be used alone as a predictor of marbling ability because the phenotypic correlation between these two traits will be close to zero in most groups of cattle. The genetic correlation between external fat and marbling is higher, but still not large.
- Expected progeny differences (EPDs) based on carcass data and live animal ultrasound data are important and useful tools for improvement of marbling ability, as are emerging genetic tests. EPDs estimate the genetic potential of an animal as a parent across all gene loci involved, whereas genetic tests are specific to a small number of genes or genetic markers involved in the trait.

- Ultrasound evaluation of body composition provides important information to predict marbling of carcasses from feeder calves and feedlot cattle, as well as to identify genetic potential for marbling among breeding animals.
- More genetic DNA markers and commercial genetic tests will become available in the near future, and will continue to decrease in cost per test. It has been shown that desirable forms of genes will be found in populations of animals not considered to be desirable for the trait; tests are likely to identify animals that are desirable for EPD but do not have favorable genotypes for specific genetic tests, and the reverse is also possible. A high-accuracy (ACC) EPD is more informative than any single genetic test, but genetic test results are available immediately.
- Most breeding and genetics research projects have utilized age-constant basis, and most nutrition research projects have utilized fat-constant basis when evaluating beef carcasses. There need to be more research trials where both are evaluated in the same trial, especially as age-verification programs become more popular.
- There is a need to better evaluate and incorporate calf/herd background information when evaluating marbling ability as well as all carcass traits. Several reports in the literature document the influence of animal age at harvest, age of dam, effects of creep feeding, individual year effects, etc., that may be viewed as "nuisance" variables, and are generally not known on most feedlot cattle. These should receive more attention as source- and age-verified programs become more important, and variation in these types of effects could mask genetic differences if not documented.

Genetic strategies and considerations related to marbling ability

- A large inefficiency in the beef industry comes from managing cattle of different genetic potentials in the same manner because their ultimate potential is not known, or ineffectively projected based on appearances or stereotypes. Therefore, premiums and discounts that are reliably related to end-product differences are needed earlier in the U.S. beef production system. Simply relying on external fat thickness to predict marbling ability is ineffective and inefficient.
- Production supply chains and/or verification programs that have access to individual animal identification, animal age, cowherd management and pedigree information will have distinct advantages over similar programs that do not have these types of information.
- Multiple sources of information should be jointly utilized to genetically change marbling. Crews et al. (2004) found that combination use of live animal ultrasound and carcass data gave a larger range and more accurate EPD estimation than either source did individually.
- There needs to be more focus on evaluation of beef females in regard to improving all carcass traits, although many seedstock producers have been more concerned with obtaining ultrasound information on yearling bulls than heifers. Reverter et al. (2000) found higher genetic correlations between yearling heifer ultrasound IMF and carcass IMF in Australian Angus and Hereford cattle, as compared to yearling bull ultrasound IMF. Crews and Kemp (2001) found much higher genetic correlations between ultrasound fat thickness in yearling heifers and carcass fat in steers than between yearling bulls and steers.

- Relationships between important cowherd traits and end product traits need to be considered in beef production systems. In the attempt to increase genetic ability of marbling, producers need to be careful not to ignore, and thus possibly sacrifice desirable cow functionality and reproduction traits.

Breed comparison studies

Many breed comparison studies have been accomplished through production of crossbred progeny, specifically F_1 calves in many cases where the different breeds evaluated have been different sire breeds bred to the same cows. This procedure yields one-half of the additive genetic breed difference to be expressed in calves sired by different breeds. All F_1 calves produced will have 100% heterosis between the pair of breeds involved; however, some pairs of breeds will show much more heterosis in the F_1 generation than others, most notably *Bos indicus-Bos taurus* combinations may have two to three times as much heterosis as compared to *Bos taurus-Bos taurus* combinations.

One of the most widely known cattle breeding research projects is the USDA-ARS Germplasm Evaluation Program (GPE) conducted at the U.S. Meat Animal Research Center at Clay Center, Neb. This project has been organized into specific cycles where each cycle involved particular sire breeds and particular year. In early cycles (I through IV), Angus and Hereford cows were bred to different sire breeds; however, in more recent cycles (Cycle V and later) Angus, Hereford and MARC III (¼ Angus, ¼ Hereford, ¼ Pinzgauer, ¼ Red Poll) cows have been used to evaluate sire breeds. In each cycle, steers have been serially harvested after three different times on feed so that different carcass end-point adjustments (age, carcass weight, fat thickness, marbling) and comparisons could be made through regression analyses.

Koch et al. (1976) reported the results of sire breed comparisons for carcass traits in steers produced in Cycle I (calves produced 1970-1972). Purebred Hereford and Angus cattle were also produced in addition to the various F_1 crosses. Calves were weaned at seven months of age and fed as calves. These cattle were fed to age constant average basis of 457 d, and the means for carcass weight, fat thickness and marbling score are presented in Table 1. Marbling was significantly higher for purebred Angus than purebred Hereford steers, and the Angus steers were also fatter. Among crossbred steers, Jersey-sired calves had the most marbling and Limousin-sired steers had the least. Both the Jersey crosses and the purebred Angus steers were average Modest for marbling score, but the purebred Angus steer had .66 in of fat whereas the Jersey crosses had .46 in of fat. The Hereford-Angus (HA) crosses had the same fat thickness as the Angus steers, and marbling that was a third of a score lower that purebred Angus. The Jersey, HA, and South Devon had significantly higher quality grades than Limousin, Charolais and Simmental crosses, but they also had more fat cover. There were no fat-constant end-point comparisons made among sire breeds in this report.

Young et al. (1978) reported carcass traits of steers that were produced by Cycle I first-calf heifers by Angus, Hereford, Brahman, Holstein and Devon sires. These calves were born in 1972 and 1973. The means for carcass weight fat thickness and marbling score on age-constant basis of 452 d are presented in Table 2. Steers by Hereford and Angus sires had the most fat cover and most marbling. Steers by Brahman sires had heaviest carcasses and least marbling at similar fat thickness to those sired by Angus and Hereford. Holstein-sired carcasses had the least amount of fat, but intermediate marbling score.

Koch et al. (1979) reported the carcass results from GPE Cycle II, which included sire breeds of Angus, Hereford, Red Poll, Brown Swiss, Gelbvieh, Maine Anjou and Chianina. Contemporary purebred Angus and Hereford calves were produced along with F_1 crosses for this cycle in 1973 and 1974. These steers were weaned at six months of age, and fed as calves. An interesting result reported was that there was a significant sire-breed by dam-breed interaction for fat thickness, but not marbling. The means for the carcass traits for the sire breeds from Angus vs. Hereford dams was not reported though. The means for carcass weight, fat thickness and marbling scores relative to age- and fat-constant end-points are given in Table 3. Purebred Angus steers had the highest average marbling score of all steers at all end-points. These authors stated that adjusted means of these breed types suggested small differences in rate of intramuscular fat deposition relative to total carcass fat. Straightbred Angus, Hereford and HA crosses had the highest degree of fat thickness at the age-constant end-point. Straightbred Angus steers were average Choice with .57 in of fat, straightbred Hereford were high Select (Good) at .56 in fat, and HA crosses were low Choice with .63 in of fat.

Koch et al. (1982) reported results of carcass evaluations from GPE Cycle III. These calves were born in 1975 and 1976. This cycle included sire breeds of Hereford, Angus, Tarentaise, Pinzgauer, Brahman and Sahiwal (*Bos indicus* breed from Pakistan). Calves were weaned at average age of seven months and were fed as calves. The means for carcass weights and marbling scores at age- and fat-constant end-points are presented in Table 4. The HA crosses had the highest marbling scores at age- and weight-constant end-points, but the Pinzgauer crosses had the highest marbling score at a fat-constant end-point. At the age-constant end-point, the *Bos indicus* crosses had intermediate fat thickness, but the lowest marbling scores; HA crosses were the fattest at the average age of 445 d. Based on these data, Tarentaise and Pinzgauer crosses would have been expected to have higher marbling scores than HA crosses at .5 in of fat. Both Tarentaise and Pinzgauer are breeds with fairly high milk production potential.

Wheeler et al. (1996) reported carcass results from GPE Cycle IV. Sire breeds included Hereford, Angus, Charolais, Gelbvieh, Pinzgauer, Shorthorn, Galloway, Longhorn, Nelore, Piedmontese, and Salers. All sire breeds were bred to Angus and Hereford cows. Calves were born 1986-1990 and were weaned at an average of five months of age. Steers were fed as calves. Means for carcass weights, fat, marbling, and percent Choice relative to age and fat end-points are presented in Table 5. At constant age of 426 d, average marbling was higher in Shorthorn, HA, and Pinzgauer crosses than others, and was lowest in Nelore (*Bos indicus* breed originally from India), Charolais and Piedmontese (double muscled from Italy) crosses.

Wheeler et al. (2004) reported results from GPE Cycle VI. These calves were born 1997-1998, and sire breeds included Hereford, Angus, Norwegian Red, Swedish Red and White, Beef Friesian (all three of which are dual purpose *Bos taurus* breeds) and Wagyu (*Bos taurus* breed from Japan). Calves were weaned at an average age of seven months, and all steers were fed as calves. A sire-breed by dam-breed interaction was reported for marbling, but was not discussed in any detail, and means for sire-breed by dam-breed combinations were not given. Table 6 contains means for carcass weight, fat, marbling and percent Choice relative to age- and fat-constant end-points. On an age-constant basis, Angus-sired carcasses had the most fat, most marbling, and highest percent Choice. However, at a fat end-point of .39 in, Wagyu and Norwegian Red and White crosses had the highest marbling.

Gregory et al. (1994) reported fat thickness and marbling scores for steers produced in the Germplasm utilization (GPU) Program at Clay Center, Neb.. This project was designed to study heterosis retention in three composite populations. These steers were born in 1988 to 1991. In three years, calves were weaned at five months of age, and in one year calves were weaned at four months of age. Animals were started on feed immediately after weaning. Mean slaughter age was 438 d. Means for fat thickness and marbling score are presented in Table 7. All of these cattle breed types had means that were quite small for fat thickness, with surprisingly high marbling scores relative to fat thickness in several instances. Perhaps the early weaning and feeding initiation contributed to this.

Chambaz et al. (2003) conducted a study in Switzerland where purebred Angus, Simmental, Charolais and Limousin steers were fed to equal marbling content as estimated by ultrasound evaluation. Steers were harvested when % IMF was estimated to be 3-4%. To reach this target IMF, Angus steers were fed 141 d and produced carcasses that weighed 605 lb; Simmental steers were fed 267 d and had 746 lb carcasses; Charolais steers were fed 281 d and had 869 lb carcasses; Limousin steers were fed 346 d and had 891 lb carcasses.

Adams et al. (1982) compared purebred Longhorn, Hereford, Angus, Brahman, and Holstein steers that were fed to Choice finish, or 186 d. Carcass weight, fat thickness and marbling scores, respectively, were 554 lb, .16 in, Small$^-$ for Longhorn, 622 lb, .66 in, Small$^-$ for Hereford, 594 lb, .70 in, Modest$^-$ for Angus, 492 lb, .31 in, Practically Devoid$^-$ for Brahman, and 635 lb, .17 in, Slight^o for Holstein. These steers were chosen as representative of their breeds (11 each) and fed together, but they were not reared in the same environment.

Table 1. Carcass weight, adjusted fat thickness and marbling means for different sire breeds of steers evaluated in GPE Cycle I (Koch et al., 1976)

Sire breed	Hot carcass weight (lb)	12th rib adjusted fat thickness (in)	Marbling score[1]
Jersey	593	0.46	13.8
South Devon	655	0.49	11.8
Limousin	653	0.41	9.5
Charolais	692	0.39	10.8
Simmental	673	0.40	10.4
Hereford & Angus[2]	637	0.65	11.9
Purebred Hereford	610	0.52	10.1
Purebred Angus	619	0.66	13.1

[1]7-9 = Slight, 10-12 = Small, 13-15 = Modest
[2]Hereford and Angus F_1 crosses reported together

Table 2. Carcass weight, adjusted fat thickness and marbling means of steers born 1972-1973 from different sire breeds out of GPE Cycle I heifers (Young et al., 1978).

Sire breed	Hot carcass weight (lb)	12th rib adjusted fat thickness (in)	Marbling score[1]
HA-CU[2]	603	0.49	11.5
HA-AI[2]	609	0.46	10.9
Brahman	642	0.43	8.5
Holstein	612	0.26	9.6
Devon	587	0.39	10.2

[1]7-9 = Slight, 10-12 = Small, 13-15 = Modest
[2]HA = Hereford and Angus crosses together; CU = cleanup sires, AI = AI sires

Table 3. Carcass weight, fat thickness and marbling means at age-constant (473 d) and fat-constant (0.49 in) end-points of steers in GPE Cycle II (Koch et al., 1979)

	Age constant basis			Fat constant basis	
Sire breed	HCW (lb)	Fat (in)	Marbling[1]	HCW (lb)	Marbling[1]
Hereford & Angus[2]	616	0.63	10.8	552	9.6
Red Poll	598	0.48	10.7	603	10.8
Brown Swiss	658	0.39	9.9	739	11.3
Gelbvieh	667	0.37	9.2	774	10.8
Maine Anjou	684	0.36	9.6	799	11.4
Chianina	669	0.31	8.0	845	10.3
Purebred Hereford	599	0.56	9.1	566	8.5
Purebred Angus	609	0.57	13.3	569	12.3

[1]7-9 = Slight, 10-12 = Small, 13-15 = Modest
[2]Hereford and Angus reported together

Table 4. Carcass weight, fat thickness and marbling means at age-constant (445 d) and fat constant (0.49 in) end-points of steers in GPE Cycle III (Koch et al., 1982)

	Age constant basis			Fat constant basis	
Sire breed	HCW (lb)	Fat (in)	Marbling[1]	HCW (lb)	Marbling[1]
Hereford & Angus[2]	651	0.63	11.4	581	9.8
Tarentaise	653	0.43	10.2	697	11.1
Pinzgauer	645	0.45	10.9	671	11.5
Brahman	678	0.55	9.4	645	8.8
Sahiwal	627	0.53	9.8	603	9.3

[1]7-9 = Slight, 10-12 = Small, 13-15 = Modest
[2]Hereford and Angus reported together

Table 5. Carcass weight, marbling and percentage Choice of steers produced in GPE Cycle IV (Wheeler et al., 1996)

	Age constant basis (426 d)				Fat constant basis (.47 in)		
Sire breed	HCW (lb)	Fat (in)	Marbling[1]	% Choice	HCW (lb)	Marbling[1]	% Choice
AI HA[2]	744	0.61	528	74	680	510	64
CU HA[2]	706	0.54	541	77	671	530	71
AI Charolais	781	0.35	509	63	884	536	77
CU Charolais	746	0.41	490	44	785	500	48
CU Gelbvieh	737	0.37	501	48	812	522	56
CU Pinzgauer	715	0.41	527	65	755	539	71
Shorthorn	744	0.48	551	78	741	551	78
Galloway	669	0.48	515	62	669	515	62
Longhorn	623	0.37	512	60	689	534	71
Nelore	737	0.48	490	48	728	488	47
Piedmontese	722	0.30	496	46	871	537	62
Salers	741	0.39	501	48	796	515	54

[1]400 = Slight 00, 500 = Small 00
[2]Hereford and Angus reported together; AI and CU denote AI vs. cleanup sires

Table 6. Carcass weight, marbling and percentage Choice of steers produced in GPE Cycle VI (Wheeler et al., 2004)

	Age constant (471 d) basis				Fat constant (0.39 in) basis		
Sire breed	HCW (lb)	Fat (in)	Marbling[1]	% Choice	HCW (lb)	Marbling[1]	% Choice
Hereford	836	0.46	509	60	810	492	53
Angus	823	0.52	579	89	774	548	75
Norwegian Red	785	0.31	543	71	838	577	86
Swedish Red and White	774	0.30	518	61	832	555	77
Friesian	772	0.33	514	52	805	536	62
Wagyu	735	0.36	559	85	755	572	91

[1]400 = Slight 00, 500 = Small 00

Table 7. Carcass weight, adjusted fat thickness and marbling means for different purebreds and composites from Germplasm Utilization (GPU) Program (Gregory et al., 1994)

Sire breed	12^{th} rib adjusted fat thickness (in)	Marbling score[1]
Red Poll	0.30	530
Hereford	0.46	524
Angus	0.46	540
Limousin	0.17	446
Braunvieh	0.18	485
Pinzgauer	0.17	516
Gelbvieh	0.14	453
Simmental	0.15	480
Charolais	0.15	471
MARC I[2]	0.22	480
MARC II[3]	0.31	515
MARC III[4]	0.36	530

[1]400 = Slight 00, 500 = Small 00
[2]MARC I = ¼ Charolais, ¼ Braunvieh, ¼ Limousin, 1/8 Angus, 1/8 Hereford
[3]MARC II = ¼ Gelbvieh, ¼ Simmental, ¼ Angus, ¼ Hereford
[4]MARC III = ¼ Pinzgauer, ¼ Red Poll, ¼ Angus, ¼ Hereford

Genetic variation

There are several methods that may be used to study variation in performance traits, and each has a different interpretation. In this section, information is summarized from several reports where genetic variation for marbling and fat thickness have been investigated. One of the most useful measures of genetic variation is heritability (h^2), which expresses the percentage of the total phenotypic variation that is due to additive genetic variation. This in turn relates to how efficiently a trait will respond to selection. In Tables 18 and 19, the mean, genetic standard deviation (σ_A), phenotypic standard deviation (σ_P), heritability and coefficient of variation (CV; (σ_P divided by mean) are presented for subcutaneous adjusted fat thickness and marbling across several studies.

Marbling σ_A has ranged from 1/3 to 2/3 of a marbling score, and σ_P has ranged from ½ to ¾ of a marbling score across several studies with diverse cattle populations (Table 8). If σ_P = .75, then the expected range in the population is six standard deviations or 4.5 marbling scores from top to bottom. Heritability estimates for marbling have been variable across populations. Some of these differences are surely due to different populations possessing different amount of genetic variation, but some of these differences in estimates may also be due to the type of data and/or the analyses employed. Range in h^2 estimates have been from .13 to .88 in recent evaluations. Nonetheless, there is no doubt considerable genetic variation with at least a moderate heritability for marbling (or intramuscular fat), which will respond to selection. When comparing the CV of marbling, it generally appears to be lower than the CV value for IMF, which may be related in part to the scoring used. It also appears that the CV for fat thickness may be larger on average than the CV for marbling or IMF.

Estimates of adjusted fat thickness for σ_A and σ_P seem to be fairly consistent across studies (Table18), even though heritability estimates have varied considerably. Heritability estimates of fat thickness have ranged from .02 to .86 in various studies. Although fat thickness is thought of as a result of feeding management, there are significant genetic differences for subcutaneous fat amount when cattle are subjected to the same environmental influences. In visual evaluation of fed cattle, fat cover has historically been an important consideration in estimating quality grade; however, the phenotypic and genetic correlations involving marbling or IMF with fat thickness are low to moderate.

Phenotypic correlation describes how the performance in one trait is related to the performance in another trait, on average, in the population. Phenotypic correlation estimates between marbling and fat thickness have ranged from -.08 to .30 (Table 10.). This can also be interpreted that fat thickness phenotypes alone may only describe 0.64% to 9.0% of the variation in marbling phenotypes. Genetic correlation describes how the breeding value (additive genetic value) for one trait in an individual is related to the breeding value of another trait in that individual, on average for the population. Additionally, the amount of potential correlated selection response in the secondary trait that is expected is related to the genetic correlation. Estimates of genetic correlation between fat thickness and marbling (Table 9) have been quite variable, ranging from -.13 to .56, but substantially higher than estimates of phenotypic correlation between these two traits. There have been many studies where there was higher genetic correlation reported between ribeye area and marbling than between fat thickness and marbling, although the phenotypic correlation between ribeye area and marbling is very low.

Table 8. Mean values and variation in marbling or percent intramuscular fat

Mean	σ_A	σ_P	h^2	CV	Cattle	Source
SL 94	38	57	0.45	0.12	GPU purebreds	Gregory et al. (1995)
SM 08	45	60	0.55	0.12	GPU composites	Gregory et al. (1995)
SM 30	84	90	0.88	0.16	Shorthorn	Pariacote et al. (2002)
SL 24	35	53	0.44	0.18	Brahman	Riley et al. (2002)
			.13-.23		Angus, Brahman and composites	Elzo et al. (1998)
			.12-.36		Simmental and Simmental-sired	Shanks et al. (2001)
SM 29	59	100	0.35	0.19	GPE Cycles I-IV	Splan et al. (2002)
SM 16	52	61	0.73	0.12	GPE Cycle IV (age constant)	Wheeler et al. (1996)
SM 01	42	55	0.57	0.11	GPE Cycle V (age constant)	Wheeler et al. (2001)
SM 37	42	71	0.35	0.13	GPE Cycle VI (age constant)	Wheeler et al. (2004)
SM 35	50	65	0.59	0.12	GPE Cycle VII (age constant)	Wheeler et al. (2005)
SM 20			0.76		NCBA carcass merit	Thallman et al. (2004)
1.78[a]	0.492	0.683	0.52	0.38	Wagyu 28 months	Mukai et al. (1995)
10.5[b]	1.80	2.84	0.40	0.27	GPE Cycles I-III	Koch et al. (1982)
SM 21	41	70	.35	.13	Hereford steers	Arnold et al. (1991)
SM 07 to 29			.26		Angus steers	Wilson et al. (1993)
3.9[c]	0.63	1.04	0.36	0.27	GPU purebreds	Gregory et al. (1995)
4.1[c]	1.05	1.21	0.75	0.29	GPU composites	Gregory et al. (1995)
4.5[c]	0.59	1.4	0.18	0.31	F1 Bos taurus	Pitchford et al. (2002)
1.25[c]	0.33	0.46	0.51	0.37	Norwegian dual purpose bulls	Aass (1996)

[a]Beef marbling score at 6^{th}-7^{th} rib interface
[b]Slight = 7, 8, 9, Small = 10, 11, 12
[c]Percent IMF

Table 9. Genetic correlations between marbling and other carcass traits

CWT	REA	FAT	KPH	%RP	Shear	Cattle type	Source
.25	-.14	.16	.29	-.37	-.25	GPE Cycles I-III	Koch et al. (1982)
.33	-.01	.19	-	-	-	Hereford steers	Arnold et al. (1991)
-.06	-.04	-.13	-	-	-	Angus field records	Wilson et al. (1993)
-.03	-.37	.01	-	.19[a]	-.55	GPE Cycle IV	Wheeler et al. (1996)
.44	-.36	.42	-	.60a	-.30	GPE Cycle V	Wheeler et al. (2001)
-.98	-.82	.53	-	-.77	-.03	GPE Cycle VI	Wheeler et al. (2004)
.18	-.50	.46	-	-.67	-.46	GPE Cycle VII	Wheeler et al. (2005)
-.27	-.36	.20	-.19	-	-.56	NCBA carcass merit	Thallman et al. (2004)
.36	.02	-.04	-	.09	-	Japanese Wagyu at 28 mo	Mukai et al. (1995)
.01	-.50	.26	-	-.37	-	Australian Angus	Reverter et al. (2000)
-.49	.28	.39	-	-.57	-	Australian Hereford	Reverter et al. (2000)
.27	-.10	.38	-	-	-	Angus steers (age constant)	Kemp et al. (2002)
-	-.26	.29	-	-	-	Angus steers (weight constant)	Kemp et al. (2002)
-.32	-.61	.30				Continental-British steers (age constant)	Devitt and Wilton (2001)
-.03	-.37	-	-	-	-	Continental-British steers (fat constant)	Devitt and Wilton (2001)
-	-.35	.41	-	-	-	Continental-British steers (weight constant)	Devitt and Wilton (2001)
.30	.46	.17	-	.01	-	Simmental and Simmental-sired (age constant)	Shanks et al. (2001)
-	.26	.18	-	.05	-	Simmental and Simmental-sired (weight constant)	Shanks et al. (2001)
.20	.48	-	-	.06		Simmental and Simmental-sired (fat constant)	Shanks et al. (2001)
-.15 to .11	-.11 to -.01	-.03 to .05	.02 to .07	-	-.24 to -.06	Angus, Brahman and composites (fat constant)	Elzo et al. (1998)
.39	.44	.56	.27	-.43	-	Brahman	Riley et al. (2002)
-.10	-.17	.26	.10	.26[a]	-	Shorthorn	Pariacote et al. (1998)
.31	-.02	.44	-	-.60	-1.0	GPU purebreds and composites	Gregory et al. (1995)

[a]Yield grade was reported instead of retail product %

Table 10. Phenotypic correlations between marbling and other carcass traits

CWT	REA	FAT	KPH	%RP	Shear	Cattle type	Source
.13	.03	.24	.18	-.37	-.12	GPE Cycles I-III	Koch et al. (1982)
.08	-.01	.12	-	-	-	Angus field records	Wilson et al. (1993)
.09	-.06	.14	-	.18a	-.11	GPE Cycle IV	Wheeler et al. (1996)
.20	-.10	.29	-	.34a	-.15	GPE Cycle V	Wheeler et al. (2001)
.05	-.09	.28	-	-.49	-.15	GPE Cycle VI	Wheeler et al. (2004)
.14	-.10	.17	-	-.41	-.28	GPE Cycle VII	Wheeler et al. (2005)
.10	-.04	.22	.03	-	-.23	NCBA carcass merit	Thallman et al. (2004)
-.14	.34	-.08	-	.36	-	Japanese Wagyu at 28 mo	Mukai et al. (1995)
			-		-	Australian Angus	Reverter et al. (2000)
			-		-	Australian Hereford	Reverter et al. (2000)
			-	-	-	Angus steers (age constant)	Kemp et al. (2002)
-			-	-	-	Angus steers (weight constant)	Kemp et al. (2002)
.04	-.05	.19	-	-	-	Continental-British steers (age constant)	Devitt and Wilton (2001)
.15	.04	-	-	-	-	Continental-British steers (fat constant)	Devitt and Wilton (2001)
-	-.09	.19	-	-	-	Continental-British steers (weight constant)	Devitt and Wilton (2001)
.09	.02	.11	-	-.16	-	Simmental and Simmental-sired (age constant)	Shanks et al. (2001)
-	-.03	.11	-	-.09	-	Simmental and Simmental-sired (weight constant)	Shanks et al. (2001)
.05	.02	-	-	-.07	-	Simmental and Simmental-sired (fat constant)	Shanks et al. (2001)
.10 to .40	-.26 to .22	.25 to .28	-.22 to .03	-	-.01 to .16	Angus, Brahman and composites (fat constant)	Elzo et al. (1998)
.17	.12	.30	.18	-.19	-	Brahman	Riley et al. (2002)
.09	.20	-.08	.10	.22[a]	-	Shorthorn	Pariacote et al. (1998)
.13	-.05	.25	-	-.43	-.24	GPU purebreds and composites	Gregory et al. (1995)

Evaluation at different carcass end-points

There being a large range in heritability estimates in marbling ability as well as all other carcass traits across studies, it is tempting to compare these estimates across studies where cattle have been fed to different end-point outcomes (age-constant, weight-constant, fat-constant). This should be done carefully, however, because in many cases not only are the end-point bases different, but also breed, feeding regime, geographic region, etc., also differ. To fairly compare the end-points bases, studies that evaluate different bases in the same cattle should receive the most attention. But, there have not been a lot of these types of projects conducted. In studies that have evaluated various end-points comparisons, the relationships involving marbling with carcass weight and ribeye area appear much more variable across end-points as does the relationship of marbling and fat. Shanks et al. (2001) reported r_g between marbling and fat of .17 at age-constant and .18 at weight-constant bases, whereas r_g between marbling and ribeye area was .46, .26, and .48 at age-, weight-, and fat-constant bases, respectively, in Simmental and Simmental-sired cattle. Shanks et al. (2001) also stated that the number of records (and therefore ACC on genetic predictions) was more important for determining rankings of animals than was the end-point of evaluation. Devitt and Wilson (2001) reported r_g between marbling and fat of .30 at age-constant and .41 at weight-constant bases, whereas r_g between marbling and ribeye area was -.61, -.35, and -.37 at age-, weight-, and fat-constant bases, respectively, in Continental-British cross steers. Kemp et al. (2002) reported r_g between marbling and fat to be .38 and .29 at age- and weight-constant end-points, respectively, and found r_g between marbling and ribeye area to be -.10 and -.26 at the same two respective end-points.

Additionally, the heritability estimates of carcass weight seem to vary more that heritability estimates of marbling across end-points. Rios-Utrera et al. (2005) reported heritability of marbling to be .40, .41, and .35 at age-, weight-, and fat-constant end-points, respectively. Heritability of adjusted fat thickness was .20 and .21 at age- and weight-constant end-points, respectively. Carcass weight heritability was .27 at age-constant basis, but .41 at fat-constant basis. Rios-Utera et al. (2006) stated that carcass traits adjusted to different biological end-points should be viewed as different but related traits. Most breeding and genetics research projects have utilized age-constant basis, and most nutrition research projects have utilized fat-constant basis. There needs to be more research trials where both are evaluated, especially as age-verification programs become more popular.

Single gene and genetic marker considerations

Casas et al. (2001) reported results from a study that evaluated the inactive myostatin gene (double muscling) in two populations of cattle. One was produced from an F_1 Belgian Blue-MARC III sire and the other was from an F_1 Piedmontese-Angus sire; both were bred to MARC III females to produce progeny for the analyses. There were three QTL for marbling found on chromosomes (BTA) 3, 8 and 10 in calves from the Belgian Blue sire. The effect of the Belgian Blue allele increased marbling by .29 and .30 scores at the QTL on BTA 3 and 8, respectively, but decreased marbling by .32 score at the QTL on BTA 10 as compared to the allele from MARC III origin. The QTL for fat on BTA 8 was in close proximity to the QTL for marbling, but not the same, and the allele of Belgian Blue origin resulted in slightly increased fat thickness (.06 in) as compared to MARC III-origin allele. No marbling QTL were identified in the

Piedmontese-Angus sire's progeny. However, Casas et al. (2001) found an interaction for fat thickness on BTA 8 where the Piedmontese-origin (P) allele resulted in less fat (.28 in vs. .34 in) than the Angus-origin (AN) allele among animals that did not carry the double muscling allele. Animals that had the P allele on BTA 8 had more fat (.29 in vs. .18 in) than animals with the AN allele when they also were carriers for the double muscling allele.

MacNeil and Grosz (2002) studied genetic regions associated with carcass traits in two large half-sib families made from mating two F_1 Line 1 Hereford-CGC composite (½ Red Angus, ¼ Tarentaise, ¼ Charolais) bulls to both Line 1 Hereford and CGC females. They killed cattle serially to study age, weight and fat carcass end-points. There were four possible QTL identified to affect marbling, one each on chromosome (BTA) 2, 18, 26 and 29. Only the region on BTA 2 seemed to consistently influence marbling at each end-point in both families, and the estimated effect of replacing the CGC allele with the Line 1 Hereford allele was a reduction of .6 of a marbling score on average. This means that the range between alternate homozygotes would be twice this, or 1.2 marbling scores higher for the CGC homozygote than for the Line 1 homozygote. Although other regions on BTA 18, 26 and 29 did not appear to affect marbling at all end-points in both families, the estimated effect of substituting a Line 1 allele was an increase of approximately .5 marbling score at each QTL, indicating that a desirable allele or allelic combination may be present on a breed or population that has a less desirable level of performance. This concept has been documented in several traits.

Casas et al. (2003) reported a study where a large, half-sib family was produced by mating an F_1 Brahman-Hereford bull to Hereford, Angus, F_1 *Bos taurus,* and MARC III cows. A QTL for marbling on BTA 23 showed very strong evidence of influencing marbling, where the effect of the Brahman allele of origin averaged .26 marbling scores higher than the Hereford allele of origin. There was less strong, but suggestive evidence of QTL affecting marbling on BTA 3, 10, 14 and 27, three of which showed the Brahman-origin allele to have favorable effects of .20 to .25 marbling score, but the QTL on BTA 3 showed the Hereford-origin allele to have average of .20 marbling score advantage.

Thallman et al. (2003) reported results from the NCBA Carcass Merit Project on 11 QTL regions that had been previously discovered in the Texas A&M University Angleton project. This was to evaluate progeny of 70 sires (at least 50 progeny per sire) from 13 U.S. breeds. There was one QTL affecting marbling, and two QTL that affected fat thickness. The marbling QTL accounted for 8% of the phenotypic variation seen in marbling, but also accounted for 1-3% of the variation seen in fat thickness, cooking loss, flavor, juiciness, KPH fat, ribeye area, and carcass weight. The two QTL affecting fat thickness accounted for 2-4% of the variation in marbling, and there were two other QTL that each individually accounted for 4% of the variation in marbling.

Casas et al. (2005) used purebred Brahman cattle to evaluate some previously reported markers for two genes (thyroglobulin [TG] and DGAT1) on BTA 14 that have been previously documented to explain marbling variation in *Bos taurus* cattle. Neither was significant in accounting for variation in marbling in these purebred Brahman cattle. The favorable allele for the TG marker in previous studies was only present in the Brahman population at 3% frequency; however, the favorable allele for DGAT1 was present at 90% frequency. Additionally, three markers in the μ-calpain gene were evaluated, all of which were significantly associated with carcass hump height, but only one was associated with sensory panel tenderness. This illustrates the need to investigate the usefulness of genetic markers in a variety of breeds in addition to the population in which they were discovered to prove that they are not simply detecting breed differences at other loci.

Mizoshita et al. (2004) documented potential QTL on BTA 4, 5, 13,and 14 for beef marbling score in Japanese Wagyu steers. They also mapped a QTL for fat thickness on BTA 14 in similar region to that reported in several U.S. studies. The QTL for marbling and fat thickness were in the same region that has been reported to contain thyroglobulin and DGAT1. The QTL for marbling on BTA 4 accounted for 8% of the phenotypic variation in marbling.

Nkrumah et al. (2005) reported on the effects of an SNP in the leptin gene on several traits in *Bos taurus* hybrid cattle in Canada. The additive effect of the gene was calculated to be .68% for ultrasound IMF. Additionally, both feed intake and IMF had a substantial dominance (non-additive) aspect.

Impacts of selection

The reasons behind estimating heritability and genetic correlations are to predict the change in a trait due to selection for that trait and to predict associated changes in other traits, respectively. There is considerable direct and indirect evidence that selection for marbling in cattle is effective.

Vieselmeyer et al. (1996) evaluated high and low marbling EPD Angus bulls from the 1989 American Angus Association Sire Summary. The average marbling EPD for high bulls was +.59, whereas the average marling EPD for low bulls was -.23. These bulls were bred to MARC II cows (1/4 each Angus, Hereford, Gelbvieh, Simmental), and calves were born in 1990 and 1991. In the 1995 sire summary, the high bulls average marbling EPD was +.33 and the low bulls averaged -.35. These sires were very similar for fat thickness EPD. Both steers and heifers were fed, and animals were killed in two groups each year, about 60 days apart. For group 1, progeny of high sires averaged 52% Choice, .33 in fat thickness, 601 lb carcass weight, and 2.4 yield grade. These same traits in progeny of low sires in group 1 were 17%, .35 in, 616 lb and 2.4, respectively. For group 2, these same traits in progeny of high sires were 96%, .52 in, 735 lb, 3.0, respectively, and for progeny of low sires were 78%, .52 in, 750 lb, and 2.9, respectively. For these same cattle, Gwartney et al. (1996) suggested that progeny from high marbling EPD may have faster rate of marbling deposition. No differences were detected for taste panel characteristics in steers from high vs. low sire; however, heifers from high sires had both increased juiciness and tenderness than heifers from low sires.

Sapp et al. (2002) reported a study where Angus bulls were selected on yearling ultrasound IMF (UIMF) and identified as high or low UIMF. The high UIMF bulls averaged 3.75% themselves and 0.18 for UIMF EPD, while the low UIMF bulls averaged 1.70% for UIMF and -0.22 for UIMF EPD. Sires were bred o commercial Angus females and entered the feedlot at 12 to 15 mo of age. Steers from high UIMF sires had more marbling (Small 52) that those from low UIMF sires (Small 08), but did not differ for fat thickness, carcass weight, or yield grade. Sapp et al.

(2002) also predicted that for each 1% difference in sire IMF EPD should result in a difference of .9 marbling score between progeny groups.

May et al. (1995) studied F_1 calves produced from Angus bulls from the 1960s (18 sires) vs. the 1980s (12 sires). These sires were used to produce calves in 1989 and 1990 and were reared as contemporaries and fed as calves. Calves from 1960s sires had carcass traits of 592 lb, .49 in, 12.2 sq in, Small 10, and 2.6 for carcass weight, fat thickness, ribeye area, marbling score, and yield grade, respectively, whereas calves from 1980s sires had average values of 692 lb, .52 in, 12.6 sq in, Slight 86 and 3.0, respectively. The 1980s-sired calves were 10 lb heavier for birth weight (81 lb vs. 71 lb) and 50 lb heavier for weaning weight (488 lb vs. 438 lb). A subset of steers from each type of sire were used to study adipocyte traits, and the calves from 1980s sires had smaller subcutaneous and intramuscular fat cells (more cells per gram of tissue), but no differences in fatness as measured by fat thickness or marbling.

Newman et al. (2002) studied genetic correlations between purebred and crossbred performance for several growth and carcass traits in Australian cattle. Angus, Hereford, Shorthorn, Belmont Red and Santa Gertrudis sires were used to produce purebred calves, and F_1 calves from Brahman cows. The genetic correlation between purebred and crossbred traits was .48, .83, .95, 1.0, and .78 for carcass weight, retail beef yield, IMF (measured by automated camera), rump fat, and ultrasound ribeye area, respectively. The heritability of IMF was .41 in purebreds and .33 in crossbreds.

Crews et al. (2004) evaluated Simmental carcass EPD based on live animal ultrasound data only, carcass data only, and the combination of live and carcass data where the live animal and the carcass data were treated as separate, genetically correlated traits. They found that carcass EPD based on the combined data had a larger range and more accurate values for a larger sample of animals as compared to the analyses that had only ultrasound or only carcass data. Furthermore, sire EPD based solely on ultrasound data differed substantially from EPD based solely on carcass data.

Burrow and Prayaga (2004) stated that selection for reduced rectal temperature in a composite of ¼ each Africander, Brahman, Hereford, and Shorthorn resulted in increased marbling without any change in external fat thickness in high heat stress environment (central Queensland). They also stated that selection such as this might lead to changes in body fat deposition patterns; however, not many details were given about the collection of carcass data.

Aass and Vangen (1997) reported that carcasses from progeny of high milk yield sires tended to have lower IMF (-0.32%) than progeny from low milk yield sires in Norwegian Dual Purpose cattle. These authors also stated that selection for high growth rate in these cattle may lead to changes in muscle structure with negative eating quality, but this seemed very speculative.

National Beef Quality Audits

It would be a fair assumption that cattle should have a combination of some minimal fat thickness as well as time on feed to express their genetic potential for marbling; however, exactly what these levels are remain unknown. Cattle that have the potential to grade Choice and Yield

Grade (YG) 2 should be managed and marketed differently from those that will grade Standard and/or YG 4 given the same circumstances. The problem is that if the genetic and management background and/or genetic potential are not known, it is safest to feed and market the cattle for average values. The main point about cattle that grade Prime is that they have the genetic ability to marble, and it is not because they are fat. In the three NBQA, there are at least twice as many cattle with YG 1-3 that grade Prime as those with YG 4-5. This concept is further illustrated below in Figure 1. Although Prime carcasses are rare, the percentage of carcasses grading Prime varies little across fat thickness levels. Of fat thickness levels over .50 inches, the percentages of Standard and Prime carcasses seem about the same. According to the 2005 NBQA (Smith et al., 2006), carcass weight continues to increase, but the need to increase quality grade and reduce external fat remain priorities. As carcass weight increases, the total amount of excess fat also increases.

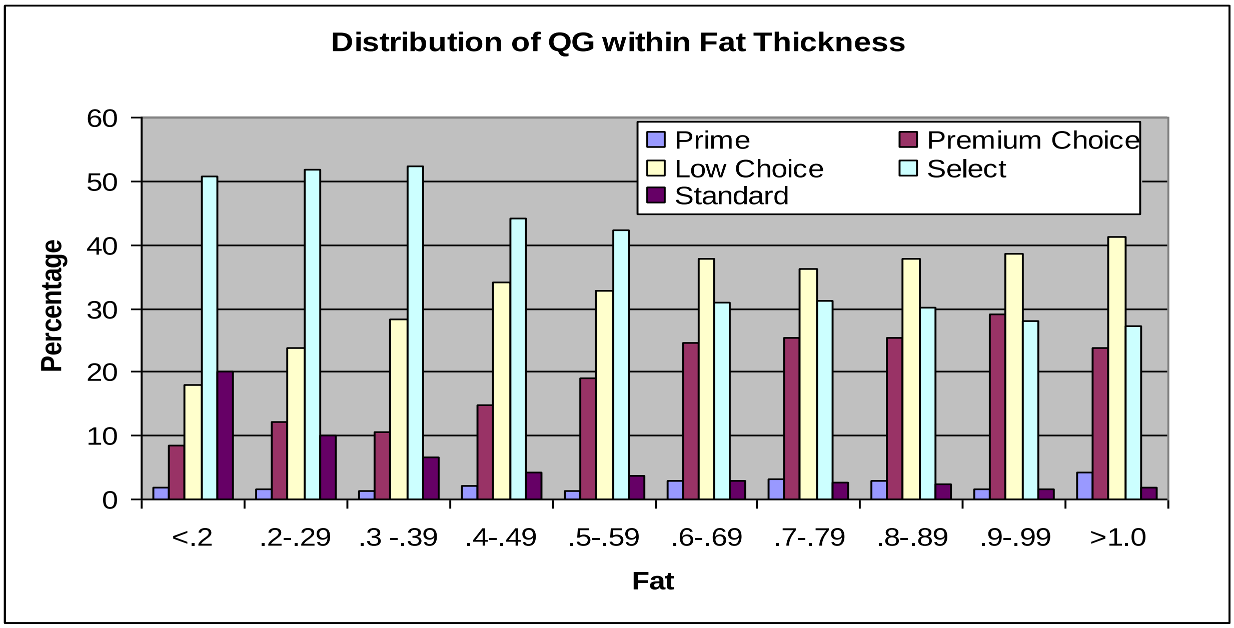

Figure 1. Distribution of quality grade percentages within each level of fat thickness from 2000 NBQA (Summarized by Dan Hale, Texas Cooperative Extension).

Cowherd considerations

There is a shortage of research that relates carcass traits with mature cow traits in contemporary females. Nephawe et al. (2004) evaluated these relationships in cattle produced in the first four cycles of GPE. Mature cow weight and height were very lowly, negatively genetically correlated with marbling score in steer mates (-.15 and -.17, respectively), and cow body condition score was not correlated at all (-.03). Cow body condition score was moderately genetically correlated with adjusted fat thickness of steers however (.30). Mature weights of cows were very highly genetically correlated to carcass weights whether or not they were adjusted for body condition score (.81 and .82). Cow body condition score only had .23 genetic correlation with carcass weight. In these analyses, carcass data were on an age-constant basis. The continual increase in carcass weight is not independent of cow size. Figure 2 shows weights at five years of age of cows produced in 1970s vs. late 1990s in the GPE program at MARC.

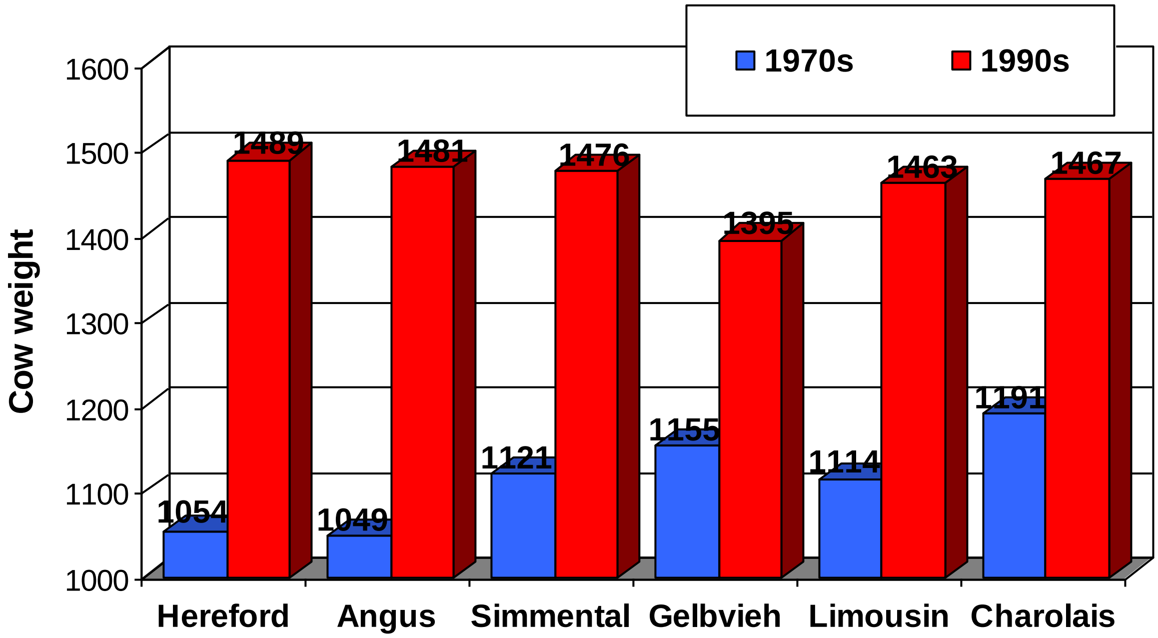

Figure 2. Average cow weights at five years of age from breeds evaluated in Germplasm Evaluation (GPE) Program at Clay Center, Neb..

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