Genetic evaluation of carcass traits in Simmental cattle
by Bruce Cameron Shanks

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Animal Science
Montana State University

Abstract:
Carcass records for this study were provided by the sire evaluation program of the American Simmental Association, and included bulls, heifers, and steers slaughtered from 1971 through August, 1998. To utilize the maximum amount of information available, carcass data were divided into three subgroups: 1) 9,604 measures of hot carcass weight (CW) and percent retail cuts (PRC) representing 696 sires, 2) 6,429 measures of CW, PRC, and marbling score (MS) representing 620 sires, and 3) 1,780 measures of CW, PRC, MS, ribeye area (REA), and fat thickness (FT) representing 354 sires. Weaning weights (WW) from contemporaries of animals with carcass data were included in the analysis. Carcass traits and WW were analyzed jointly with a multiple-trait animal model and REML procedures to estimate genetic parameters and breeding values at an age-, weight-, marbling-, or FT-constant basis. The statistical model for carcass traits included the fixed effect of contemporary group and covariates for the fractional contribution of breed group (10), heterozygosity, and slaughter end-point. Random effects for carcass traits included additive direct genetic (animal) and residual. Weaning weight was preadjusted for founder effects (breed of calf, breed of dam, and year), direct and maternal heterosis, age of dam, and age of calf. The model for WW included the fixed effect of contemporary group and random effects of additive direct genetic (animal), maternal genetic (dam), maternal permanent environment, and residual. Heritability estimates at an age-constant basis were: CW, .34; PRC, .25; MS, .36; REA, .26; and FT, .10. Heritability estimates at a weight- and marbling-constant basis were similar to those estimated at an age-constant basis. Estimates were .25 for PRC, .34 for MS, .22 for REA, and .14 for FT at a weight-constant basis and .33, .25, .28, and .10, for CW, PRC, REA, and FT, respectively at a marbling end-point. Finally, heritabilities estimated at a FT-constant basis were similar for CW (.33) and REA (.29) but were lower for PRC (.17) and MS (.13). Genetic and phenotypic correlations differed in magnitude and sign among trait combinations at different end-points. In general, parameter estimates were within the range of those previously reported in the literature. Pearson product-moment correlations and Spearman rank correlations were calculated to determine the influence of slaughter end-point on carcass trait breeding values and to evaluate the impact of slaughter end-point on ranking of sires. Adjushnent of traits to various end-points resulted in some changes in carcass trait breeding values and some re-ranking of sires depending on the end-point and trait being considered. Results from this study establish that selection for carcass traits should generally be effective in Simmental cattle and indicate that it is possible to select for desirable levels of growth or lean yield without sacrificing carcass quality. Finally, these findings suggest that some consideration should be given to slaughter end-point prior to designing breeding and management plans.

(KEY WORDS: beef cattle, carcass traits, genetic parameters, Simmental)

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APPROVAL

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Bruce Cameron Shanks

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Carcass records for this study were provided by the sire evaluation program of the American Simmental Association, and included bulls, heifers, and steers slaughtered from 1971 through August, 1998. To utilize the maximum amount of information available, carcass data were divided into three subgroups: 1) 9,604 measures of hot carcass weight (**CW**) and percent retail cuts (**PRC**) representing 696 sires, 2) 6,429 measures of CW, PRC, and marbling score (**MS**) representing 620 sires, and 3) 1,780 measures of CW, PRC, MS, ribeye area (**REA**), and fat thickness (**FT**) representing 354 sires. Weaning weights (**WW**) from contemporaries of animals with carcass data were included in the analysis. Carcass traits and WW were analyzed jointly with a multiple-trait animal model and REML procedures to estimate genetic parameters and breeding values at an age-, weight-, marbling-, or FT-constant basis. The statistical model for carcass traits included the fixed effect of contemporary group and covariates for the fractional contribution of breed group (10), heterozygosity, and slaughter end-point. Random effects for carcass traits included additive direct genetic (animal) and residual. Weaning weight was preadjusted for founder effects (breed of calf, breed of dam, and year), direct and maternal heterosis, age of dam, and age of calf. The model for WW included the fixed effect of contemporary group and random effects of additive direct genetic (animal), maternal genetic (dam), maternal permanent environment, and residual. Heritability estimates at an age-constant basis were: CW, .34; PRC, .25; MS, .36; REA, .26; and FT, .10. Heritability estimates at a weight- and marbling-constant basis were similar to those estimated at an age-constant basis. Estimates were .25 for PRC, .34 for MS, .22 for REA, and .14 for FT at a weight-constant basis and .33, .25, .28, and .10, for CW, PRC, REA, and FT, respectively at a marbling end-point. Finally, heritabilities estimated at a FT-constant basis were similar for CW (.33) and REA (.29) but were lower for PRC (.17) and MS (.13). Genetic and phenotypic correlations differed in magnitude and sign among trait combinations at different end-points. In general, parameter estimates were within the range of those previously reported in the literature. Pearson product-moment correlations and Spearman rank correlations were calculated to determine the influence of slaughter end-point on carcass trait breeding values and to evaluate the impact of slaughter end-point on ranking of sires. Adjustment of traits to various end-points resulted in some changes in carcass trait breeding values and some re-ranking of sires depending on the end-point and trait being considered. Results from this study establish that selection for carcass traits should generally be effective in Simmental cattle and indicate that it is possible to select for desirable levels of growth or lean yield without sacrificing carcass quality. Finally, these findings suggest that some consideration should be given to slaughter end-point prior to designing breeding and management plans.

(KEY WORDS: beef cattle, carcass traits, genetic parameters, Simmental)

CHAPTER 1

INTRODUCTION

Marketing systems within the cattle industry are currently experiencing rapid change. Areas of change include retained ownership, grids, alliances, formulas, forward pricing, new product development, and branded products. In response to changing marketing systems, there is an increased emphasis on traits which determine carcass merit. This has prompted the American Simmental Association to evaluate and exploit the genetic value of carcass traits in their cattle. Information from the evaluation will be provided to producers in the form of updated carcass Expected Progeny Differences (**EPD**) (EPD = breeding value ÷ 2).

Expected Progeny Differences are considered the most technical method of reporting genetic differences. However, do carcass EPD rank and separate sires the way producers want? Currently, carcass EPD are reported at a common age end-point, which may not match slaughter criteria used in today's production systems. An additional issue is EPD are dependent upon genetic parameter estimates. If genetic parameters are sensitive to slaughter end-point, carcass EPD may rank sires differently based on end-point.

A survey of the literature resulted in several significant findings (Chapter 2). First, there were a large number (n=30) of researchers that reported parameters for carcass traits. Upon summary of these studies, the following characteristics were discovered: 1) large amounts of variation existed for parameter estimates among studies, 2) data were adjusted to various slaughter end-points, 3) there were a small number of records in the majority of studies, 4) few studies utilized field data, and 5) only two published results contained parameter estimates for Simmental cattle. Second, there were a small number (n=7) of United States Breed Associations that reported parameters and EPD for carcass traits. Variation between breed associations indicated that parameter estimates from different breeds are not the same and parameter estimates from one breed cannot be utilized to calculate EPD for another breed. Although the American Simmental Association conducts genetic evaluations for carcass traits, it has not estimated parameters and EPD for ribeye area and fat thickness. Third, the effect of slaughter end-point on carcass trait parameter estimates and EPD has not been adequately addressed in the literature.

Beef producers face the challenge of utilizing diverse resources to produce cattle that are profitable to all segments of the industry and to produce meat products that target consumer demand (Marshall, 1994). To accomplish these goals, breeders need genetic information from a broad spectrum of marketing end-points to implement effective breeding and management plans. Specifically, Simmental producers require an understanding of slaughter end-points and need updated genetic parameter estimates and EPD for carcass traits in order to promote the value of their cattle.

Therefore, the objectives of this project were to 1) estimate genetic parameters for carcass traits in Simmental cattle at different slaughter end-points, and 2) calculate EPD for carcass traits in Simmental cattle at different slaughter end-points and determine their relationships.

CHAPTER 2

LITERATURE REVIEW

Introduction

The intent of this review is to summarize scientific knowledge regarding genetic aspects of carcass and growth measures, and identify strengths and weaknesses of Simmental and Simmental crosses relative to other breeds of cattle in North America. This will first be accomplished by defining those carcass and growth measures considered important by the industry and consumers. Because values of these measures are altered by different slaughter end-points (i.e., harvest criteria), an understanding of these end-points is also necessary. Second, literature estimates of heritabilities of and genetic and phenotypic correlations among carcass and associated growth traits are summarized. These parameters are needed to implement systematic multiple-trait breeding plans. Third, ultrasound technology is introduced, and its relevance in current and future genetic evaluation systems is assessed. Fourth, scientific studies comparing carcass traits of Simmental and Simmental crosses to other breeds of cattle are summarized, and evaluations of Simmental cattle in production systems are reviewed. Finally, current national cattle evaluation procedures are described.

Carcass and associated growth traits

Yield grade factors

Yield grade (**YG**) indicates the amount of closely trimmed (½ inch fat or less), boneless retail cuts expected from the major wholesale cuts (round, sirloin, short loin, rib, and square-cut chuck) of a carcass (USDA, 1997). There are five yield grades applicable to all classes of beef denoted by numbers 1 through 5, with YG 1 representing the highest degree of cutability (USDA, 1997), or estimation of the percentage of salable meat from a carcass (BIF, 1996). Yield grade is determined by four factors: (1) thickness of external fat (**FT**), (2) percentage of kidney, pelvic, and heart fat (**KPH**), (3) area of the ribeye or longissimus muscle (**REA**), and (4) carcass weight (**CW**) (USDA, 1997). External fat is measured at the 12th rib at a point three-fourths of the length of the longissimus muscle. It may be adjusted up or down to compensate for any visible differences in fat in other portions of the carcass (Tatum, 1997). Amount of KPH is estimated subjectively and is expressed as a percent of the CW (AMSA, 1997). Ribeye area is determined between the twelfth and thirteenth ribs. It is usually measured subjectively or by use of a grid. Carcass weight is usually determined soon after slaughter, or may be estimated as 102% of the chilled CW. Yield grade is calculated by the following mathematical equation (BIF, 1996):

$$\begin{aligned} YG = 2.50 &+ (2.5 \text{ x Adj. FT, in.}) \\ &+ (0.2 \text{ x KPH, \%}) \\ &+ (0.0038 \text{ x Hot CW, lb.}) \\ &- (0.32 \text{ x REA, sq. in.}). \end{aligned}$$

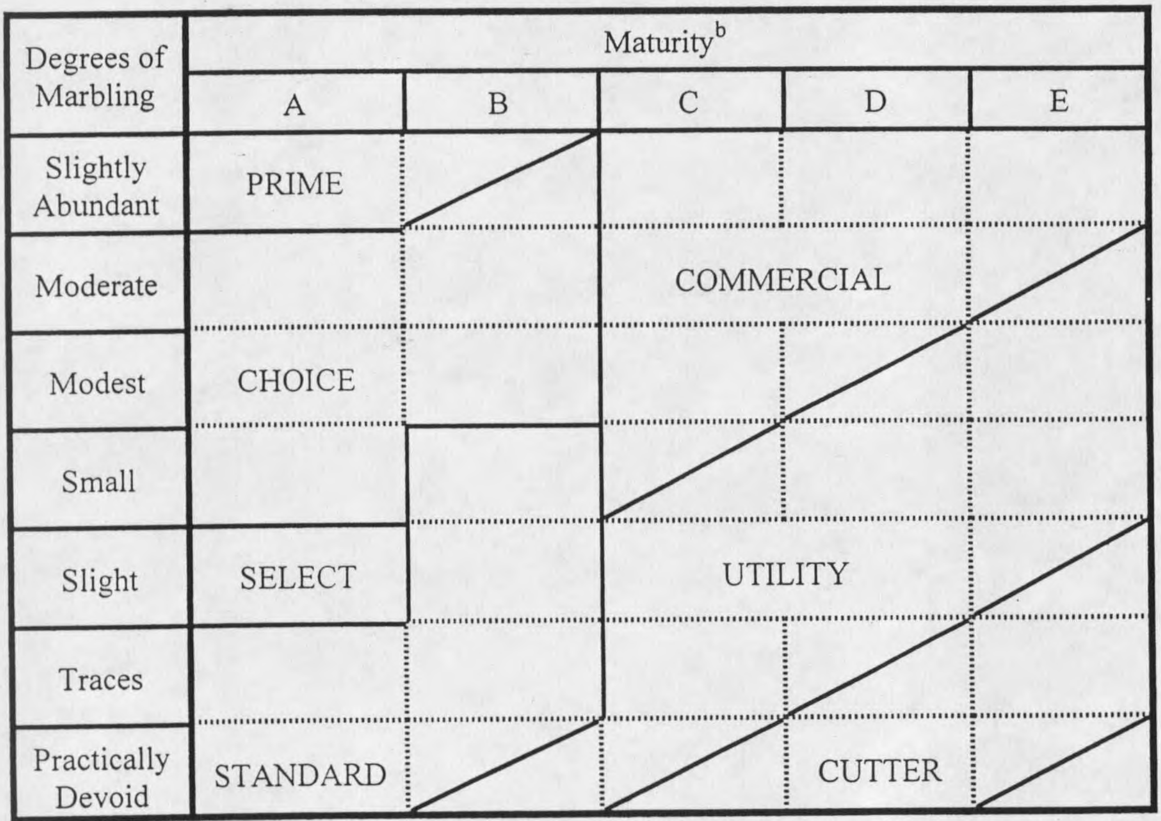
Quality grade factors

Quality grade (**QG**) refers to the overall palatability of the edible portion of the carcass (BIF, 1996). Quality grades assigned to beef carcasses include prime, choice, select, standard, commercial, utility, cutter, and canner (USDA, 1997). Primary factors of QG are maturity and marbling score (**MS**); but texture, firmness, and color of the lean are also considered (BIF, 1996). Maturity is an estimation of the physiological age of the carcass determined by evaluating the size, shape, and ossification of bones and cartilages, and the color and texture of the lean. There are five degrees of maturity - A, B, C, D, and E (USDA, 1997) corresponding to the following ages (Tatum, 1997):

A— 9 to 30 months
B— 30 to 42 months
C— 42 to 72 months
D— 72 to 96 months
E— more than 96 months.

Marbling score is determined by visually evaluating the specks of intramuscular fat distributed in the longissimus muscle between the twelfth and thirteenth ribs. Marbling is associated with meat tenderness, juiciness, and flavor. There are 10 degrees of MS ranging from "devoid" to "abundant" (USDA, 1997). The relationships between MS, maturity, and QG are indicated in Table 1.

Table 1. Relationships between marbling score, maturity, and carcass quality grade[a]



[a] Assumes that firmness of lean is comparably developed with the degrees of marbling score and that the carcass is not a "dark cutter."
[b] Maturity increases from left to right (A through E).

Consumer acceptance factors

Ultimately, beef value is based on consumer acceptability. Although factors associated with consumer acceptability are difficult to quantify, they play a collective role in conveying overall impressions of palatability to consumers. Factors discussed in this review include MS, tenderness, juiciness, and flavor. Calpastatin activity and Warner-Bratzler shear force (**WBS**) are also evaluated. Factors such as amount of intermuscular fat (seam fat), color, aroma, texture, cooking loss, and perceived nutritive value can also be important characteristics in beef acceptance.

No consumer acceptance factor has received more consideration and research effort than tenderness. Unfortunately, there is substantial variation in tenderness that cannot be explained. Lack of tenderness can be attributed to several causes. Recent evidence has shown that one potential cause is calpastatin, a calpain inhibitor found in muscle fibers. Calpains are enzymes responsible for postmortem proteolysis in muscle, which determines the degree of postmortem tenderization (Hedrick et al.,1989). Other causes of decreased tenderness include amount of connective tissue, muscle fiber type, and intramuscular fat content. Researchers usually measure differences in tenderness by trained taste panels, or by using a WBS instrument. Higher values of shear force indicate increased toughness.

Juiciness imparts important flavor components to beef and assists in fragmenting and softening meat during chewing. Therefore, absence of juiciness severely limits beef's acceptability and destroys its unique palatability characteristics (Hedrick et al., 1989). For research purposes, a trained panel usually measures juiciness.

Flavor is also an influential part of overall satisfaction by consumers. It plays an important role in the psychological and physiological responses experienced when meat is eaten. In addition, flavor helps stimulate the flow of saliva and gastric juices, thus aiding in digestion (Hedrick et al., 1989). Flavor is also usually measured by a trained taste panel.

Associated growth traits

Although the focus of this review is centered around carcass traits, the importance of growth traits should not be overlooked. Most slaughter cattle are marketed with some consideration given to weight, and rapid growth is normally associated with improved feed efficiency and lower cost of gain. Yearling weight (**YW**) and postweaning rate-of-gain (**PWG**) are two common measures in cattle that will be regarded here. Birth weight (**BW**) and weaning weight (**WW**) are also reviewed. Birth weight is an indicator of calving difficulty and WW is useful in evaluating differences in mothering ability of cows and to measure growth potential of calves (BIF, 1996).

Slaughter end-points

Slaughter end-point simply refers to criterion which determines when animals are slaughtered. Animals are usually slaughtered when they reach a predetermined age, weight, or compositional end-point. This will vary for different research, production, and marketing systems.

Studies containing genetic parameter estimates reflect a wide range of slaughter end-points. This complicates summarizing estimates from several sources because end-points can alter the expression of genetic and environmental differences (Koch et al., 1995). For this reason, it is necessary to sort information into common slaughter end-point groups. Genetic parameter estimates in this review are separated into age or time-in-feedlot, slaughter weight, FT, and choice grade end-points. An age or time-in-feedlot end-point refers to when animals are slaughtered after they reach a particular age or after they have spent a certain amount of time in a feedlot. A predetermined live weight during the feeding period is utilized as criteria for a slaughter weight end-point. A FT end-point refers to when animals are slaughtered after they have been identified as having a designated amount of FT. Fat thickness on live animals can be identified visually or may be estimated by using an ultrasound machine. An ultrasound machine can also be utilized to predict when animals have reached a choice grade end-point.

Comparisons of carcass traits of different breeds of cattle are also complicated by the slaughter end-point at which the comparison is made. In this review, comparisons of Simmental and Simmental crosses to other breeds of cattle are divided into age or time-in-feedlot, slaughter weight, or 5% longissimus fat end-points. The 5% longissimus fat end-point corresponds to when animals reach a low choice grade.

Large differences exist in the carcass traits of beef cattle in North America. Importation of many new breeds and increased use of crossbreeding by producers is in part responsible for the diversity found in today's slaughter cattle population (Dolezal et al., 1993). In order to compensate for different genetic types of cattle and to fully exploit the value of carcass traits, cattle should be managed to an optimum slaughter end-point (Amer et al., 1994a,b). An optimum slaughter end-point can be defined as the ideal opportunity in the growth stage of a slaughter animal that will produce lean, high-quality beef. Differences in growth and maturation of cattle associated with mature size and fattening characteristics are largely responsible for the various optimum slaughter end-points present between breeds (Amer et al., 1994a).

Genetic and phenotypic parameters

Heritabilities

Estimates of heritabilities are essential in implementing systematic multiple-trait breeding plans. Heritability is defined as the proportion of differences among parents, measured or observed, that is transmitted to the offspring. The higher the heritability of a trait, the more rapid should be the response to selection for that trait (BIF, 1996). Table 2 contains sources of carcass and growth trait heritability estimates found in the literature. Some of these sources were adapted from previous reviews by Woldehawariat et al. (1977), Koots et al. (1994a,b), and Marshall (1994). Heritability estimates are presented in Tables 3, 4, 5, 6, 7, and 8. The tables contain estimates for YG factors, QG factors, consumer acceptance factors, and associated growth traits. Ranges and simple (unweighted) averages are given for each table. Estimates that fell outside normal heritability bounds (0 to 1.0) were set to zero or one for calculation of ranges and averages.

Average heritability estimates for YG and QG factors were generally moderate to high at an age- or time-in-feedlot-, slaughter weight-, FT-, and choice grade-constant basis (Tables 3 and 4). Only three estimates of YG and five estimates of KPH were found in the literature. No estimates for QG were found. Yield grade and KPH heritabilities were not similar in the studies that reported estimates. Carcass weight heritabilities ranged from .18

to .48 across all end-points. The highest average was at a choice grade end-point, and the lowest average was found at a FT end-point. Average REA heritabilities remained essentially the same across all end-points. However, individual heritability estimates ranged from .01 to .73. The small REA heritability estimates reported by Dunn et al. (1970) and Reynolds et al. (1991) at an age or time-in-feedlot end-point might be explained by the low number of records contained in the studies.

Average FT heritabilities were considerably smaller at a FT end-point, but remained similar across all other end-points. Individual FT heritability estimates varied considerably at an age- or time-in-feedlot-constant basis. Marbling score had the greatest number of heritability estimates. Estimates ranged from -.15 to .93. The negative heritability estimate reported by Dunn et al. (1970) could once again be due to the small number of records contained in the study. The average MS heritability was surprisingly larger at a choice grade end-point. At an age- or time-in-feedlot-constant basis the average MS heritability was larger than for a slaughter weight- or FT-constant basis. Generally, the choice grade end-point contained the highest heritability averages for all traits, and all traits were extremely consistent from study to study at a slaughter weight end-point. Values were generally more variable at an age- or time-in-feedlot-constant basis, but this could be explained by the large number of sources found at this end-point.

Studies by Woodward et al. (1992) and Gregory et al. (1994c) contained Simmental data. Woodward et al. (1992) estimated heritability of MS to be .23, while Gregory et al. (1994c) estimated it to be .52. Gregory et al. (1994c) estimated heritability of FT to be .30.

Average heritability estimates for consumer acceptance factors were low to moderate at an age- or time-in-feedlot-, slaughter weight-, and FT-constant basis (Tables 5 and 6). Fewer estimates were found for consumer acceptance factors than YG and QG factors, and estimates tended to be from recent literature. The only heritability estimate found for consumer acceptance factors at a choice grade end-point was MS. Also, there were no heritability estimates for intermuscular fat (seam fat) found in the literature. Marbling score was included as a consumer acceptance factor in order that comparisons could be made between it and other traits. Average tenderness heritability estimates remained similar across all end-points. However, there was variation across end-points for WBS average heritabilities. The lowest average was reported at a slaughter weight end-point, and the largest average was found at a FT end-point. Also, WBS heritabilities were extremely consistent at a FT end-point. Three estimates for calpastatin activity were found in the literature. The average at a FT end-point was lower than the one reported for calpastatin activity at an age or time-in-feedlot end-point. Juiciness and flavor were both lowly heritable at an age or time-in-feedlot end-point. The single estimates reported for juiciness and flavor at a slaughter weight end-point, were similar to those reported at an age- or time-in-feedlot constant basis.

Heritability estimates for associated growth traits were generally moderate to high (Table 7). There were several sources of information available for these estimates which resulted in a wide range of heritabilities. However, heritability averages for both YW and PWG were .41. A review by Woldehawariat et al. (1977) reported the average heritability of BW and WW to be .39 and .31, respectively. A review by Koots et al. (1994a) reported the average heritability of BW and WW to be .35 and .27, respectively.

Table 8 contains heritability estimates of carcass and associated growth traits reported by several United States Breed Associations. Breed associations reported lower average heritabilities for YW, PWG, REA, and FT than those summarized in Tables 3 and 4. Marbling score and CW average heritabilities were essentially the same as averages reported in Tables 3 and 4. Average heritabilties for BW and WW were in agreement with averages reported by Woldehawariat (1977) and Koots et al. (1994). Red Angus and Limousin Breed Associations reported the largest number of carcass heritabilities. Red Angus was the only association to report a QG heritability, while Limousin was the only association to report a KPH heritability. The American Simmental Association reported a percent retail cut heritability, which was the same as the percent retail product heritability reported by the American Angus Association.

Overall YG and QG factors and associated growth traits tended to be more heritable than consumer acceptance factors. Lowest average heritability estimates for REA, tenderness, and juiciness were at an age- or time-in-feedlot-constant basis. Highest average heritability estimates for MS, KPH, FT, and CW were at a choice grade end-point. A slaughter weight end-point resulted in the least amount of variation between studies for all traits and estimates at a choice grade end-point were more consistent than age- or time-in-feedlot or FT end-points. Average heritabilities reported by United States Breed Associations were generally lower or the same as averages summarized in Tables 3 and 4.

Table 2. Sources of published genetic parameter estimates for carcass and associated growth traits[a]

Source	No. of records	No. of sires	Sex[b]	Sire breed[c]	Dam breed[c]	Mating system[d]
1. Shelby et al., 1960	542	116	B	H	H	S
2. Swiger, 1961	748	23	B, H	H	H	S
3. Swiger et al., 1961	351	48	B, H	H	H	S
4. Blackwell, 1962	841	43	H, S	H	H	S
5. Brinks et al., 1962	515	?	B	H	H	S
6. Koch et al., 1963	1,324	130	B, H	H, A, Sh	H, A, Sh	S
7. Shelby et al., 1963	616	87	S	H	H	S
8. Wilson et al., 1963	473	56	S	H	H	S
9. Brown and Gacula, 1964	201	20	B	H, A, Sh	H, A, Sh	S
10. Cundiff et al., 1964	265	47	S	H, A	H, A	S
11. Swiger et al., 1965	480	?	B, H, S	H, A, Sh	H, A, Sh	R, S
12. Dunn et al., 1970	191	49	H, S	H, A, Sh	H, A, Sh	R
13. Dunn et al., 1970	184	49	H, S	H, A, Sh	H, A, Sh	S
14. Brackelsberg et al., 1971	257	46	S	H, A	H, A	S
15. Cundiff et al., 1971	503	75	S	H, A, Sh	H, A, Sh	F, BC, S
16. Dinkel and Busch, 1973	679	70	S	H	H	S
17. Francoise et al., 1973	1,759	?	B, H	H, A	H, A	S
18. Koch et al., 1973	3,462	72	B	H	H	S
19. Andersen et al., 1974	327	64	B	Sh	Sh	S
20. Kennedy et al., 1975a,b	69,986	6,648	B, H, S	H, A	H, A	S
21. Wilson et al., 1976	646	46	H, S	H	A x Ho	F
22. Kalm et al., 1978	1,068	39	B, S, H	H, C	H, C	S
23. Koch, 1978	377	64	H	H	H	S
24. Mavrogenis et al., 1978	695	72	B	H	H	S
25. Nelsen and Kress, 1979	3,492	588	B, H	H, A	H, A	S
26. Benyshek, 1981	8,474	1,524	H, S	H	H	S
27. Massey and Benyshek, 1981	27,781	156	B, H	L	Lx	S

Table 2. Continued[a]

Source	No. of records	No. of sires	Sex[b]	Sire breed[c]	Dam breed[c]	Mating system[d]
28. Bourdon and Brinks, 1982	5,691	152	B, H	H, A, R	H, A, R	S
29. Koch et al.,1982	2,453	370	S	16[e]	H, A	F, S
30. Massey and Benyshek, 1982	28,942	144	B, H	L	Lx	S
31. Jensen and Andersen, 1984	2,217	296	B	4[f]	4[f]	S
32. Knights et al., 1984	717	80	B	A	A	S
33. MacNeil et al., 1984	1,683	187	H, S	7[g]	H, A	F, S
34. Frahm et al., 1985	3,762	?	B	H	H	S
35. Irgang et al., 1985	2,467	125	B	H	H	S
36. Aaron et al., 1986	2,746	?	B	H, A	H, A	S
37. Wilson et al., 1986	55,695	2,294	B, H	H, A	H, A	S
38. Alenda and Martin, 1987	2,576	71	B, H	A	A	S
39. DeNise and Ray, 1987	237	40	B	H	H	S
40. O'Ferrall et al., 1989	218	37	S	F	F	S
41. Lamb et al., 1990	824	95	B	H	H	S
42. Arnold et al., 1991	2,411	137	S	H	H	S
43. Kriese et al., 1991	24,465	2,151	B, H	4[h]	4[h]	S
44. MacNeil et al., 1991	527	124	B, S	6[i]	H, A	F, S
45. Reynolds et al., 1991	169	30	B	H	H	S
46. Van Vleck et al., 1992	682	111	S	5[j]	H, A	BC, F
47. Woodward et al., 1992	8,265	420	B, H, S	S	S	S
48. Bullock et al., 1993	131,740	10,346	B, H, S	H	H	S
49. Gilbert et al., 1993	318	59	B, H	H, A	H, A	S
50. Veseth et al., 1993	616	85	B	H	H	S
51. Veseth et al., 1993	401	75	B	H	H	S
52. Wilson et al., 1993	10,733	699	S, H	A	A	S
53. Gregory et al., 1994c	1,461	307	S	12[k]	12[k]	C, S
54. Koch et al., 1994	8,498	?	B, H	H	H	S