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ANALYSIS OF GENETIC PARAMETERS FOR
GROWTH AND CARCASS TRAITS OF
CANADIAN CHAROLAIS CATTLE.

presented by

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has been accepted towards fulfillment
of the requirements for

M.S. degree in ANIMAL SCIENCE

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Date MAY 10, 1996

ANALYSIS OF GENETIC PARAMETERS FOR GROWTH AND CARCASS TRAITS OF CANADIAN CHAROLAIS CATTLE

By

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Animal Science

1996

ABSTRACT

Analysis of Genetic Parameters for Growth and Carcass Traits of Canadian Charolais Cattle.

By

Dwight A. Sexton

Growth and carcass records were received from the Canadian Charolais Association's Conception to Consumer Program which encompassed 5401 progeny of 172 sires, born from 1975 through 1993. Sires were randomly bred to mature commercial cows, and the offspring were placed in a commercial feedlot and a 112-day performance test. Progeny of sires were slaughtered when they visually reached the A1 or A2 Canadian carcass grade. Carcass weight, longissimus muscle area, 12th rib backfat, marbling score, carcass grade, and cutability were analyzed using slaughter age as a covariate. In a separate analysis, longissimus muscle area, 12th rib backfat, and marbling score were analyzed using carcass weight as a covariate. A five trait sire model that included sire relationships was employed using an average information REML (DMUAI) algorithm to estimate (co)variance components. Heritability estimates for the following traits included: birth weight, 0.22; adjusted 200 day weight, 0.11; adjusted 365 day weight, 0.19; post-weaning average daily gain, 0.21; end of test weight, 0.18; slaughter age adjusted carcass weight, 0.13; slaughter age adjusted marbling score, 0.27; carcass weight adjusted marbling score, 0.28; slaughter age adjusted longissimus muscle area, 0.29; carcass weight adjusted longissimus muscle area, 0.38; slaughter age adjusted 12th rib backfat thickness, 0.37; carcass weight adjusted 12th rib backfat thickness, 0.36; slaughter age adjusted carcass

carcass weight adjusted 12th rib backfat thickness, 0.36; slaughter age adjusted carcass grade, 0.23; slaughter age adjusted cutability, 0.32. Genetic (r_g) and phenotypic (r_p) correlations between the growth traits analyzed in most instances were moderate to high. With the exception of carcass weight, the (r_g) and (r_p) of growth by carcass traits were low to moderate. When adjusted to an age constant basis, the estimated genetic correlation (r_g) between carcass weight and longissimus muscle area was 0.18, while the estimate of (r_g) between carcass weight and 12th rib backfat thickness was 0.17. The (r_g) between marbling score (increased marbling had a lower numerical score) with longissimus muscle area and also to 12th rib backfat thickness was 0.16 and -0.32, respectively. The effect of selection on the females had little, if any, impact on the estimation of genetic parameters. These data indicate that successful selection for growth and carcass traits can occur, but antagonistic results may transpire.

DEDICATION

In loving memory of my father, Larry H. Sexton, whose greatest joy in life was the success of his four children. I'll keep trying to make you proud.

ACKNOWLEDGMENTS

The author is grateful to Dr. Dennis Banks for his guidance, insight and support throughout my program. Additionally, Dr. Al Booren, Dr. Dave Hawkins, and Dr. Harlan Ritchie have been great sources of inspiration to me. The support of everyone on my graduate committee has not only made me a better scientist, but also a better steward of the livestock industry.

Additionally, this project was only possible due to contribution of the Canadian Charolais Association for providing the data, and also to Dr. Ivan Mao and Dr. Just Jensen for making their computing resources available.

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1. INTRODUCTION

When the continental breeds of cattle were introduced into North America in the 1950's through the 1970's, a change in traits of economic importance under selection also occurred. Fat was no longer considered desirable, and leaner, faster growing cattle were desired. Additionally, through the inclusion of these later maturing breeds, commercial cattlemen were able to reap the rewards of selection, migration, and heterosis at a much faster pace. Furthermore, during this same time period, great strides were made in the field of animal breeding; and animal scientists were much better equipped to identify genetically superior animals through the use of mixed model methodology (Henderson, 1953).

In an effort to increase their market share in the beef industry, members of the Canadian Charolais Association designed an unbiased progeny test program that enabled bulls to be proven for growth and carcass traits. There was selection on the heifers used in the study, which may result in selection bias if it was not a random culling of the heifers. As a result of this program, data were available for the estimation of (co)variance components through the use of multiple trait mixed model methodology. Heritability values, in addition to genetic, environmental and phenotypic correlations, could be estimated. Heritability estimates enable producers to explain variation, or the lack of variation from parent to progeny, when designing selection programs. Genetic correlations give an indication of how traits not directly selected upon will change when producers use estimates of genetic merit when making their mating decisions. Environmental correlations are important to note in selection programs because they can either have antagonistic or desirable effects that will effect the phenotypic correlation. Phenotypic correlations are indicators of how traits will react together if they are not selected for with breeding values. With these statistics, members of the Canadian Charolais Association can measure the degree of potential progress possible through selection for the traits evaluated in the Conception to Consumer Program. In addition to what this information provides to individual breeders, these details are important to the Canadian Charolais Association as they continually update their sire summaries because they need prior values to use for their assessment of expected progeny differences.

The traits evaluated in this study include: birth weight, age adjusted 200 day weight, age adjusted 365 day weight, post-weaning average daily gain on test, and end of test weight. Additional carcass traits involved in this study include: hot carcass weight, longissimus muscle area, 12th rib backfat thickness, marbling score, carcass grade, and also cutability percentage.

The overall objective was to study progeny from 172 Charolais sires to provide heritability estimates on various traits. The specific objectives of this study were to:

1. Estimate the genetic and phenotypic parameters among growth and carcass traits.
2. Explore the potential selection bias from the selection on females in these data.

2. LITERATURE REVIEW

2.1 Introduction

Genetic estimates for growth and carcass traits in beef cattle provide an indication of the progress that can be made by selecting for certain traits and the resulting change in correlated traits. Falconer (1960) describes methods to show advances in the genetic makeup of livestock. The formula necessary to estimate genetic progress is as follows:

$$\Delta g = \frac{i\sqrt{h^2}\sigma_A}{G.I.}$$

where: Δg is genetic progress,

i is the notation for selection intensity, which is the "standardized" selection differential of normally distributed traits,

$\sqrt{h^2}$ is the square root of heritability (the accuracy of the breeding value based on individual phenotypic records),

σ_A is the additive genetic standard deviation for the trait, and

G.I. is the generation interval for the population.

Additionally, Falconer (1960) describes the measurement of the correlated response to selection, which is the response in a second trait that occurs after selection has occurred upon the initial trait. The formula for the correlated response to selection is:

$$C.R._Y = i\sqrt{h_X^2}\sqrt{h_Y^2}r_{g_{xy}}\sigma_Y$$

where: $C.R._Y$ is the correlated response of trait Y when trait X is selected for,

i is the notation for selection intensity, which is the "standardized" selection differential for the normal distribution,

$\sqrt{h_X^2}$ is the square root of heritability (the accuracy of the breeding value based on individual phenotypic records), for the selected trait X,

$\sqrt{h_Y^2}$ is the square root of heritability (the reliability of the phenotypic value as a guide to the breeding value) for the correlated trait Y,

$r_{g_{xy}}$ is the genetic correlation between traits X and Y,

σ_Y is the phenotypic standard deviation of trait Y, and

G.I. is the generation interval for the population.

Because of their importance to genetic evaluations, estimates of the genetic and phenotypic parameters are essential to the future of any and all populations undergoing selection.

2.2 Genetic Aspects Of Growth And Carcass Traits

2.2.1 Birth Weight

The birth weight of beef calves is of critical interest to beef cattle producers (B.I.F., 1990) as lighter weight calves tend to have lower mortality rates, are born easier, and result in less rebreeding difficulties for the dam. Koots et al. (1994a), in a paper which summarized published genetic parameters of 287 papers from North America and Europe analyzing 70 traits, reported 172 birth weight heritability values had a mean heritability of 0.35 with a 0.16 standard deviation. Koots et al. reported that the heritability values were affected by the mean and phenotypic standard deviation of the population, in addition to the effects of breed, sex, method of parameter estimation, feeding management, and data origin, although the magnitude and direction of the effects varied. Moreover, Koots et al. noted that traits with low heritability values tended to have the average heritability value overestimated. Johnston et al. (1992) used a two trait sire model without sire relationship information on 1444 Charolais sired progeny from the Canadian Charolais Association's Conception to Consumer Program to report a birth weight heritability estimate of 0.25. Koch et al. (1982) analyzed data from 2,453 steers at the Germ Plasm Evaluation project at the Meat Animal Research Center to estimate a birth weight heritability of 0.43. de Rose (1992) estimated 0.45 to be the birth weight heritability for Charolais in the Canadian Beef Sire Evaluation Program using a multiple trait animal model. Woodward et al. (1992) reported an estimate of birth weight heritability on 13,670 Simmental progeny to be 0.28 (Table 1). Heritability values of this magnitude suggest that genetic progress can be made when selecting for lower birth weights.

The genetic correlations reported in the literature of birth weight to other growth traits are represented in Table 2. The mean genetic correlations of birth weight and other growth traits (weaning weight, yearling weight, post-weaning average daily gain, and end of test weight) reported from a review of the literature cited were 0.45, 0.48, 0.43, and

0.41, respectively. Table 4 contains the average and range of literature genetic correlations for growth and carcass traits. The average genetic correlation between birth weight and carcass weight was 0.44, while the average correlation between birth weight and longissimus muscle area was 0.40. These growth and carcass trait correlations suggest that selection for lower birth weights would result in lighter weight cattle with smaller longissimus muscle areas. Additional genetic correlations of birth weight to 12th rib fat thickness, marbling score, and cutability included respective mean values of -0.27, 0.12, and 0.10. Therefore, when selecting for lighter birth weight calves, the correlated genetic response would yield carcasses with more fat, and lower cutability cattle with more marbling.

The mean phenotypic correlations for each of the trait combinations with birth weight possessed the same sign but had lower magnitudes than the respective genetic correlations (Table 2; Table 4; Table 5; Table 7). Koots et al. (1994b) analyzed 66 and 42 citings in the literature and determined the mean phenotypic correlations of birth weight to weaning weight and also birth weight to post-weaning average daily gain of 0.36 and 0.20, respectively. Koots et al. (1994b) conducted a weighted least squares analysis of literature estimates of each correlation and showed several factors significantly ($P<0.10$) affecting the estimates, including breed, country, sex, and decade in which data were collected. Other factors such as data origin (field data or experimental data), feeding regime (range or feedlot) and estimation method such as sire versus animal model and single versus multiple trait analysis generally did not significantly affect genetic and phenotypic correlations.

2.2.2 Weaning Weight

The weaning weight of a calf is the best measure of pre-weaning growth. Arnold et al. (1991) reported a weaning weight heritability of 0.09 from a study of 2411 Hereford steers from the American Hereford Association's sire evaluation program which used a two trait sire model in the analysis. de Rose (1992) used data from the Canadian Beef Sire Evaluation Program on Charolais and Charolais-sired cattle to estimate a heritability value of 0.25 for weaning weight with a multiple trait, animal model. Woodward et al. (1992), Núñez-Dominguez et al. (1993), and Veseth et al. (1993) reported heritability values of 0.18, 0.37, and 0.17, respectively, for weaning weight (Table 1). Johnston et al. (1992) also reported a weaning weight heritability value of 0.09 as did Arnold et al. (1991), but also cited Robertson (1977), noting that if selection of the parents is based on the trait on which heritability is being measured then the estimates may be biased due to reduced additive genetic variance of the parents. Koots et al. (1994a) summarized 239 weaning weight heritability estimates and found a mean of 0.27 with a standard deviation of 0.17. These results indicate that weaning weight is low to moderately heritable and moderately low genetic response to selection may be expected for this trait.

Weaning weight has been reported to have a medium to high genetic and phenotypic correlation with other growth traits. Koots et al. (1994b) determined a mean genetic correlation of 0.78 from 66 references and 0.72 for a mean phenotypic correlation from 77 sources for weaning weight correlated to yearling weight. Marshall (1994) also conducted a review of the recent scientific literature on breed characterization and genetic parameters for beef cattle carcass traits and after averaging correlations of weaning weight

Table 1. Mean and range of literature heritability estimates.

Trait	Range	Mean	Sources
Birth Weight	0.18 to 0.47	0.34	3, 5, 6, 8, 10, 11, 14
Weaning Weight [a]	0.09 to 0.37	0.20	4, 5, 6, 8, 10, 11, 14
Yearling Weight [b]	0.14 to 0.42	0.27	4, 5, 6, 10, 14
Post-weaning Average Daily Gain	0.13 to 0.57	0.36	2, 3, 4, 5, 11, 14
End Of Test Weight	0.37 to 0.52	0.44	2, 11, 14
Carcass Weight	0.24 to 0.56	0.40	1, 3, 4, 11, 12, 13, 14
Marbling Score [c]	0.23 to 0.47	0.36	1, 2, 3, 4, 7, 8, 9, 11, 12, 13, 14
Marbling Score [d]	0.28 to 0.73	0.41	1, 11, 14, 15
Longissimus Muscle Area [c]	0.32 to 0.60	0.45	1, 2, 3, 4, 7, 11, 12, 13, 14
Longissimus Muscle Area [d]	0.32 to 0.46	0.40	1, 14, 15
12th Rib Fat Thickness [c]	0.26 to 0.52	0.43	1, 2, 3, 4, 11, 12, 13, 14
12th Rib Fat Thickness [d]	0.43 to 0.53	0.47	1, 14, 15
Cutability [c]	0.18 to 0.49	0.35	1, 2, 8, 13, 14

[a] Age adjusted weaning weight.
[b] Age adjusted yearling weight.
[c] Slaughter age constant.
[d] Carcass weight constant.

<u>List of sources</u>:

1. Cundiff et al., 1971
2. Benyshek, 1981
3. Koch et al., 1982
4. Arnold et al., 1991
5. Johnston et al., 1992
6. de Rose, 1992
7. Van Vleck et al., 1992
8. Woodward et al., 1992
9. Barkhouse, 1993
10. Núñez-Dominguez et al., 1993
11. Veseth et al., 1993
12. Wilson et al., 1993
13. Marshall, 1994
14. Koots et al., 1994a
15. Brackelsberg et al., 1971

Table 2. Average and range of genetic correlations among growth traits.

	Genetic		
Variable	Range	Mean	Sources
Birth Weight * Weaning Weight	0.33 to 0.54	0.45	3, 4, 5
Birth Weight * Yearling Weight	—	0.48	5
Birth Weight * Post-weaning Average Daily Gain	0.32 to 0.61	0.43	1, 4, 5
Birth Weight * End Of Test Weight	0.28 to 0.53	0.41	4, 5
Weaning Weight * Yearling Weight	0.06 to 0.78	0.42	5
Weaning Weight * Post-weaning Average Daily Gain	-0.35 to 1.39	0.48	4, 5
Weaning Weight * End Of Test Weight	0.71 to 1.17	0.94	4 ,5
Yearling Weight * Post-weaning Average Daily Gain	0.17 to 0.81	0.49	2, 5
Yearling Weight * End Of Test Weight	—	0.63	5
Post-weaning Average Daily Gain * End Of Test Weight	0.76 to 1.04	0.90	4, 5

<u>List of sources</u>:

1. Koch et al., 1982
2. Arnold et al., 1991
3. Woodward et al., 1992
4. Veseth et al., 1993
5. Koots et al., 1994b

Table 3. Average and range of genetic correlations among carcass traits[a].

Variable	*Genetic*		
	Range	***Mean***	***Sources***
Carcass Weight * Marbling Score	-0.06 to 0.38	0.20	2, 3, 4, 7, 8, 9, 10
Carcass Weight * Longissimus Muscle Area	0.09 to 0.80	0.49	2, 3, 4, 7, 8, 9, 10
Carcass Weight * 12th Rib Fat Thickness	0.08 to 0.39	0.32	2, 3, 4, 8, 9, 10
Carcass Weight * Cutability	-0.33 to 0.12	-0.11	2, 9, 10
Marbling Score * Longissimus Muscle Area	-0.40 to 0.51	-0.07	1, 3, 4, 5, 7, 8, 9, 10
Marbling Score * 12th Rib Fat Thickness	-0.13 to 0.62	0.26	1, 3, 4, 8, 9, 10
Marbling Score * Cutability	-1.22 to -0.12	-0.53	2, 6, 9, 10
Longissimus Muscle Area * 12th Rib Fat Thickness	-0.44 to -0.06	-0.20	1, 3, 4, 8, 9, 10
Longissimus Muscle Area * Cutability	0.26 to 0.53	0.40	9, 10
12th Rib Fat Thickness * Cutability	-0.74 to -0.33	-0.54	2, 10

[a] All carcass traits are from a slaughter age constant analysis.

List of sources:

1. Brackelsberg et al., 1971
2. Cundiff et al., 1971
3. Koch et al., 1982
4. Arnold et al., 1991
5. Van Vleck et al., 1992
6. Woodward et al., 1992
7. Veseth et al., 1993
8. Wilson et al., 1993
9. Marshall, 1994
10. Koots et al., 1994b

Table 4. Average and range of genetic correlations among growth and carcass traits[a].

	Genetic		
Variable	*Range*	*Mean*	*Sources*
Birth Weight * Carcass Weight	0.11 to 0.60	0.44	1, 4, 6
Birth Weight * Marbling Score	-0.18 to 0.31	0.12	1, 3, 4, 6
Birth Weight * Longissimus Muscle Area	0.31 to 0.57	0.40	1, 4, 6
Birth Weight * 12th Rib Fat Thickness	-0.27 to -0.27	-0.27	1, 6
Birth Weight * Cutability	0.05 to 0.14	0.10	3, 6
Weaning Weight * Carcass Weight	0.13 to 1.11	0.73	2, 4, 5, 6
Weaning Weight * Marbling Score	-0.17 to 0.81	0.24	2, 3, 4, 5, 6
Weaning Weight * Longissimus Muscle Area	0.33 to 0.72	0.49	2, 4, 5, 6
Weaning Weight * 12th Rib Fat Thickness	-0.28 to 0.37	0.05	2, 5, 6
Weaning Weight * Cutability	-0.20 to 0.42	0.04	3, 5, 6
Yearling Weight * Carcass Weight	-0.03 to 0.93	0.60	2, 5, 6
Yearling Weight * Marbling Score	-0.37 to 0.20	-0.04	2, 5, 6
Yearling Weight * Longissimus Muscle Area	-0.06 to 0.39	0.21	2, 5, 6
Yearling Weight * 12th Rib Fat Thickness	-0.13 to 0.32	0.11	2, 5, 6
Yearling Weight * Cutability	-0.13 to 0.87	0.37	5, 6
Post-weaning Average Daily Gain * Carcass Weight	0.00 to 1.11	0.69	1, 2, 4, 6
Post-weaning Average Daily Gain * Marbling Score	0.08 to 0.54	0.24	1, 2, 4, 6
Post-weaning Average Daily Gain * Longissimus Muscle Area	-0.18 to 0.82	0.31	1, 2, 4, 6
Post-weaning Average Daily Gain * 12th Rib Fat Thickness	0.05 to 0.22	0.15	1, 2, 6
Post-weaning Average Daily Gain * Cutability	—	0.25	6
End Of Test Weight * Carcass Weight	0.98 to 1.03	1.01	4,6
End Of Test Weight * Marbling Score	0.27 to 0.47	0.37	4, 6
End Of Test Weight * Longissimus Muscle Area	0.38 to 0.71	0.55	4, 6
End Of Test Weight * 12th Rib Fat Thickness	—	0.02	6
End Of Test Weight * Cutability	—	-0.20	6

[a] All carcass traits are from a slaughter age constant analysis.

<u>List of sources</u>:

1. Koch et al., 1982
2. Arnold et al., 1991
3. Woodward et al., 1992
4. Veseth et al., 1993
5. Marshall, 1994
6. Koots et al., 1994b

Table 5. Average and range of phenotypic correlations among growth traits.

	Phenotypic		
Variable	*Range*	*Mean*	*Sources*
Birth Weight * Weaning Weight	0.25 to 0.36	0.31	2, 3, 4
Birth Weight * Post-weaning Average Daily Gain	0.16 to 0.20	0.23	1, 3, 4
Birth Weight * End Of Test Weight	0.24 to 0.37	0.31	3, 4
Weaning Weight * Yearling Weight	—	0.72	4
Weaning Weight * Post-weaning Average Daily Gain	0.12 to 0.37	0.25	3, 4
Weaning Weight * End Of Test Weight	0.24 to 0.64	0.44	3, 4
Post-weaning Average Daily Gain * End Of Test Weight	0.73 to 0.80	0.77	3, 4

List of sources:

1. Koch et al., 1982
2. Woodward et al., 1992
3. Veseth et al., 1993
4. Koots et al., 1994b

Table 6. Average and range of phenotypic correlations among carcass traits[a].

	Phenotypic		
Variable	*Range*	*Mean*	*Sources*
Carcass Weight * Marbling Score	0.08 to 0.28	0.16	2, 3, 6, 7, 8, 9
Carcass Weight * Longissimus Muscle Area	0.43 to 0.58	0.48	2, 3, 6, 7, 8, 9
Carcass Weight * 12th Rib Fat Thickness	0.24 to 0.39	0.34	2, 3, 7, 8, 9
Carcass Weight * Cutability	-0.44 to 0.03	-0.24	2, 8, 9
Marbling Score * Longissimus Muscle Area	-0.07 to 0.16	0.03	1, 3, 4, 6, 7, 8, 9
Marbling Score * 12th Rib Fat Thickness	0.12 to 0.42	0.25	1, 3, 7, 8, 9
Marbling Score * Cutability	-0.33 to -0.15	-0.22	2,5, 8, 9
Longissimus Muscle Area * 12th Rib Fat Thickness	-0.25 to -0.07	-0.13	1, 3, 7, 8, 9
Longissimus Muscle Area * Cutability	—	0.45	8, 9
12th Rib Fat Thickness * Cutability	—	-0.36	2, 9

[a] All carcass traits are from a slaughter age constant analysis.

List of sources:

1. Brackelsberg et al., 1971
2. Cundiff et al., 1971
3. Koch et al., 1982
4. Van Vleck et al., 1992
5. Woodward et al., 1992
6. Veseth et al., 1993
7. Wilson et al., 1993
8. Marshall, 1994
9. Koots et al., 1994b

Table 7. Average and range of phenotypic correlations among growth and carcass traits[a].

	Phenotypic		
Variable	***Range***	***Mean***	***Sources***
Birth Weight * Carcass Weight	0.21 to 0.41	0.34	1, 3, 5
Birth Weight * Marbling Score	-0.04 to -0.02	-0.02	1, 2, 3, 5
Birth Weight * Longissimus Muscle Area	0.11 to 0.17	0.15	1, 3, 5
Birth Weight * 12th Rib Fat Thickness	-0.07 to -0.07	-0.07	1, 5
Birth Weight * Cutability	0.04 to 0.05	0.05	2, 5
Weaning Weight * Carcass Weight	0.57 to 0.68	0.63	3, 4, 5
Weaning Weight * Marbling Score	-0.04 to 0.16	0.06	2, 3, 4, 5
Weaning Weight * Longissimus Muscle Area	0.22 to 0.35	0.29	3, 4, 5
Weaning Weight * 12th Rib Fat Thickness	0.16 to 0.21	0.19	4, 5
Weaning Weight * Cutability	-0.19 to 0.34	0.02	2, 4, 5
Yearling Weight * Carcass Weight	—	0.72	4
Yearling Weight * Marbling Score	—	0.19	4
Yearling Weight * Longissimus Muscle Area	—	0.34	4
Yearling Weight * 12th Rib Fat Thickness	—	0.26	4
Yearling Weight * Cutability	—	-0.15	4
Post-weaning Average Daily Gain * Carcass Weight	0.60 to 0.79	0.70	1, 3, 5
Post-weaning Average Daily Gain * Marbling Score	0.07 to 0.24	0.15	1, 3, 5
Post-weaning Average Daily Gain * Longissimus Muscle Area	0.25 to 0.44	0.34	1, 3, 5
Post-weaning Average Daily Gain * 12th Rib Fat Thickness	0.17 to 0.19	0.18	1, 5
Post-weaning Average Daily Gain * Cutability	—	0.26	5
End Of Test Weight * Carcass Weight	0.90 to 0.94	0.92	3,5
End Of Test Weight * Marbling Score	0.14 to 0.24	0.19	3, 5
End Of Test Weight * Longissimus Muscle Area	0.30 to 0.49	0.40	3, 5
End Of Test Weight * 12th Rib Fat Thickness	—	0.19	5
End Of Test Weight * Cutability	—	-0.22	5

[a] All carcass traits are from a slaughter age constant analysis.

List of sources:

1. Koch et al., 1982
2. Woodward et al., 1992
3. Veseth et al., 1993
4. Marshall, 1994
5. Koots et al., 1994b

to 12th rib fat thickness and weaning weight to cutability, found mean genetic correlations of 0.37 and -0.11 and phenotypic correlations of 0.21 and -.019, respectively. These correlations indicate that genetic improvement should occur when producers use breeding values to make their selections, but there is an antagonistic phenotypic response on these traits from environmental influences. Woodward et al. (1992) analyzed 13,670 Simmental records from 1971-1988 with a multiple trait sire model and reported a genetic and phenotypic correlation of 0.16, and 0.02, respectively, between weaning weight and marbling. Seven hundred thirty-six Hereford bulls analyzed by Veseth et al. (1993) with Henderson's Method 3 (1953) produced genetic and phenotypic correlations for weaning weight to marbling of 0.81 and 0.16, respectively. Marshall (1994) reported respective genetic and phenotypic correlations for weaning weight to marbling of 0.39 and 0.08. Meanwhile, Arnold et al. (1991) estimated a genetic correlation of -0.01, while Koots et al. (1994b) reported a mean genetic correlation of -0.17 and a phenotypic correlation of -0.04 for weaning weight and marbling. These citings indicate that a medium to high response in carcass weight, longissimus muscle area, and other growth traits would occur when selecting for increased weaning weights. Nonetheless, only a moderate to low response in 12th rib fat thickness or marbling score would result when selecting for weaning weight.

2.2.3 Yearling Weight

Yearling weight of a calf is a primary estimate of a calf's post-weaning growth. Arnold et al. (1991), Johnston et al. (1992), and de Rose (1992) reported respective heritability estimates of 0.14, 0.16, and 0.30 (Table 1). Núñez-Dominguez et al. (1993) used a multiple trait sire model on the Charolais sired progeny on the U.S. Meat Animal Research Center's Germ Plasm Evaluation project to report a yearling weight heritability of 0.42. Koots et al. (1994a) reported a mean heritability value of 0.35 from 154 references that had a standard deviation of 0.22. The values indicate that moderate genetic gain can occur when selecting for increased yearling weights.

The average literature genetic correlation for each growth trait combination was 0.48, 0.42, 0.49, and 0.63, respectively, for yearling weight correlated to birth weight, weaning weight, post-weaning average daily gain, and end of test weight. Koots et al. (1994b) indicated a genetic correlation of -0.37 for yearling weight to marbling and a genetic correlation of 0.32 for yearling weight to 12th rib fat thickness. Again, the literature indicates with moderately high genetic correlations that selecting for increased growth should result in heavier carcasses with larger longissimus muscle areas and less marbling.

2.2.4 Post-weaning Average Daily Gain

Post-weaning average daily gain is measured from when the calf begins the post-weaning test until the end of test weight is taken. Benyshek (1981) analyzed 8474 Hereford steers that were raised from 1960-1977 for the American Hereford Association's sire evaluation program with a restricted maximum likelihood (REML) algorithm to report a post-weaning average daily gain heritability of 0.52. Koch et al. (1982) used data from the U.S. Meat Animal Research Center's Germ Plasm Evaluation project from 1970-1976 on 2453 steers of diverse biological types to report a post-weaning average daily gain heritability value of 0.57. Literature values of 0.13, 0.19, and 0.47, respectively, were reported by Arnold et al. (1991), Johnston et al. (1992), and Veseth et al. (1993) (Table 1). Koots et al. (1994a) averaged 24 heritability estimates for post-weaning average daily gain and reported a mean of 0.29 and a standard deviation of 0.20. This mean estimate indicates that medium genetic progress can be made for improving post-weaning average daily gains.

A genetic correlation of 0.89 and a phenotypic correlation of 0.72 was reported by Koch et al. (1982) between post-weaning average daily gain and carcass weight. Also, Koch et al. reported a genetic correlation of 0.05 for post-weaning average daily gain with 12th rib fat thickness and a phenotypic correlation of 0.17 for that trait combination. Additionally, they reported similar correlations between other growth traits with post-weaning average daily gain (Table 2; Table 5).

2.2.5 End of Test Weight

The end of test weight is taken at the conclusion of the post-weaning test period. A literature search for end of test weight heritability values yielded estimates of 0.52 (Benyshek, 1981) and 0.42 (Veseth et al., 1993). Koots et al. (1994a) analyzed 12 estimates which had a mean value of 0.37 with a standard deviation of 0.23 (Table 1). These estimates indicate medium to high genetic progress can be made when selecting to improve end of test weights.

Veseth et al. (1993) reported a genetic correlation of 0.28 between birth weight and end of test weight with a phenotypic correlation of 0.24. On the same data set of Hereford bulls, Veseth et al. determined a genetic correlation of 0.98 and a phenotypic correlation of 0.90 between end of test weight and carcass weight. Mean genetic and phenotypic correlations of 0.38 and 0.30, respectively, between end of test weight and longissimus muscle area were reported by Koots et al. (1994b) as well as -0.20 and -0.22 between end of test weight and cutability. The literature review indicates higher correlations exist between end of test weight and other growth traits that are measured as the age of the animal increases. These are to be expected as the traits are very similar in nature. Additionally, the mean cited genetic correlation values suggest that improvement in end of test weights should result in moderate to high response in longissimus muscle area but an antagonistic response in cutability.

2.2.6 Carcass Weight

A hot carcass weight is taken to assess carcass mass. Cundiff et al. (1971) used a regression adjustment for age at slaughter to adjust data on 503 Angus, Hereford, and Shorthorn steers that were born from 1961-1965 and reported a carcass weight heritability of 0.56. Koch et al. (1982) used Henderson's Method 3 (1953) to analyze 2453 steers of diverse biological types from the U.S. Meat Animal Research Center's Germ Plasm Evaluation project from 1970-1976 to report a carcass weight heritability of 0.43. Other age constant heritability values for carcass weight in the literature yielded estimates of 0.24, and 0.09 from Arnold et al. (1991), and Johnston et al. (1992), respectively.

Additionally, age constant carcass weight heritabilities included 0.38 and 0.41 (Núñez-Dominguez et al., 1993; Marshall, 1994) (Table 1). Wilson et al. (1993) utilized a multiple trait REML sire model that included an adjustment for slaughter age to analyze 9448 Angus records from the American Angus Association's carcass evaluation program and reported a carcass weight heritability of 0.31. Koots et al. (1994a) analyzed 19 age constant heritability estimates and reported a mean of 0.45 and a standard deviation of 0.22. These moderate and high heritability values suggest that progress can be made when selecting for carcass weight.

A review of the literature reveals high phenotypic and genetic correlations between carcass weight and growth traits. Marshall (1994), respectively, reported genetic and phenotypic correlations of 0.82 and 0.62 for carcass weight and weaning weight, along with 0.93 and 0.72 for carcass weight and yearling weight. Wilson et al. (1993), after analyzing 10,733 Angus field records, discovered a genetic correlation of 0.47 and a phenotypic correlation of 0.43 between carcass weight and longissimus muscle area (Table 3; Table 6). However, Wilson et al. (1993) found respective lower genetic correlations of 0.38 and -0.06, respectively, for carcass weight to 12th rib fat thickness and carcass weight to marbling. These references indicate that selection for increased carcass weight will result in faster growing, heavier muscled cattle that are fatter and have lower marbling scores.

Benyshek (1981) reported that carcass weight constant heritability values for carcass traits were lower than when both live weight and age were held constant. He additionally indicated that once carcass traits were adjusted for age, additional adjustment for carcass weight had little effect on heritability. Age, carcass weight, and finish adjustments remove the effects of size (scale), growth, and maturity, respectively. Therefore, traits adjusted for these different end points are biologically different (Koots et al., 1994a).

2.2.7 Longissimus Muscle Area

The longissimus muscle area is a measurement of the area of the longissimus dorsi muscle measured between the 12th and 13th rib. The longissimus muscle area is used as an indicator of total muscle because it is easy to measure and is one of the more valuable cuts of meat from the carcass. Previously reported heritability values on an age constant basis for longissimus muscle area include 0.41, 0.40, 0.56, and 0.46, from Cundiff et al. (1971), Benyshek (1981), Koch et al. (1982), and Arnold et al. (1991), respectively (Table 1). Van Vleck et al. (1992) utilized records on 1350 cattle from the U.S. Meat Animal Research Center's Germ Plasm Evaluation program and analyzed the data with a single trait animal model that accounted for slaughter age to report a longissimus muscle area heritability of 0.60. Additional age constant heritability values include 0.51, 0.32, 0.37 (Veseth et al., 1993; Wilson et al., 1993; Marshall, 1994). In 1994a, Koots et al. summarized 16 references and found a mean age constant heritability value of 0.43 with a standard deviation of 0.21. Additionally, Koots et al. (1994a) located 15 references which had a mean carcass weight constant heritability value of 0.41 with a standard deviation of 0.15. Other cited carcass weight constant heritability values for longissimus muscle area include 0.40 (Brackelsberg et al., 1971), and 0.32 (Cundiff et al., 1971). Brackelsberg et al. (1971) used a single trait sire model that adjusted for carcass weight on Angus and Hereford records that spanned a four year period to analyze their data.

Koots et al. (1994b) reported mean genetic correlations of 0.40 for longissimus muscle area to weaning weight and 0.38 for longissimus muscle area and end of test weight. Koch et al. (1982) published a genetic correlation of -0.14 for longissimus muscle area to marbling score, while also showing a genetic correlation for longissimus muscle area to 12th rib fat thickness of -0.44. Higher cutability, faster growing, lower marbled cattle should result when selection for improved longissimus muscle area occurs.

2.2.8 Marbling

Marbling scores indicate the relative amount of intramuscular fat located within the longissimus dorsi. The literature reviewed had marbling scores associated with numerical values, with the greatest amount of marbling corresponding to the highest numeric value. A review of the literature revealed heritability estimates on an age constant basis of 0.31, 0.47, 0.40, 0.35, and 0.45 (Cundiff et al., 1971; Benyshek, 1981; Koch et al., 1982; Arnold et al., 1991; and Van Vleck et al., 1992). Barkhouse (1993) obtained records on 1432 cattle of varying breed groups from the U.S. Meat Animal Research Center's Germ Plasm project and analyzed the data with a multiple trait sire model and restricted maximum likelihood with an age at slaughter covariate to yield a heritability estimate of 0.40. Additional age constant estimates include 0.23, 0.31, 0.26, and 0.35 from Woodward et al. (1992), Veseth et al. (1993), Wilson et al. (1993), and Marshall (1994), respectively (Table 1). A mean age constant heritability estimate of 0.37 was observed from 12 estimates from Koots et al. (1994a) that had a standard deviation of 0.18. Also, heritability estimates on a carcass weight constant basis include 0.73 (Brackelsberg et al., 1971), 0.33 (Cundiff et al., 1971), and 0.28 (Veseth et al., 1993). With a carcass weight constant, Koots et al. (1994a) detected four references which had a mean heritability value of 0.37 with a standard deviation of 0.03. These medium and high heritability estimates show improvement in marbling scores can be achieved through selection.

A review of the literature (Arnold et al., 1991; Woodward et al., 1992; and Marshall, 1994) exhibits relatively low genetic and phenotypic correlations between marbling and growth traits. Nevertheless, Marshall (1994) shows a mean genetic correlation of 0.37 between marbling score and 12th rib fat thickness from four estimates, while five papers reviewed by Koots et al. (1994b) indicated a mean genetic correlation between marbling score and cutability of -0.54. Therefore, selection for improved marbling will result in little change in growth traits, but correlated responses would indicate an increase in 12th rib fat thickness with decreasing longissimus muscle area and cutability.

2.2.9 Twelfth Rib Fat Thickness

Fat thickness measured between the 12th and 13th rib, ¾ of the lateral length of the longissimus muscle measured perpendicular from the split chine bone, gives an estimate of the amount of external fat that the carcass possesses. Due to the economic inefficiencies associated with fat accretion, its importance in selection programs is of concern. Cundiff et al. (1971), Benyshek (1981), Koch et al. (1982), and Arnold et al.

(1991), reported age constant heritability estimates of 0.50, 0.52, 0.41, and 0.49, respectively (Table 1). Likewise, age constant heritability estimates of 0.26 (Wilson et al., 1993), and 0.44 (Marshall, 1994) were determined, while Koots et al. (1994a) reported 26 estimates which had a mean of 0.43 and a standard deviation of 0.18 on an age constant basis. Other references in the literature on a carcass weight constant basis include 0.43 (Brackelsberg et al., 1971), and 0.53 (Cundiff et al., 1971). Fifteen references cited by Koots et al. (1994a) yielded a mean carcass weight constant heritability value for 12th rib fat thickness of 0.44 with a standard deviation of 0.15. These predominantly high heritability estimates suggest rapid changes in 12th rib fat thickness in beef cattle can be made.

Koots et al. (1994b) reported 10 genetic correlation estimates between 12th rib fat thickness and weaning weight that had a mean of 0.07, along with four genetic correlations between 12th rib fat thickness and end of test weight with a mean of 0.02. Additionally, Wilson et al. (1993) indicated a genetic correlation between 12th rib fat thickness and carcass weight of 0.38, while Koch et al. (1982) reported a genetic correlation of 0.16 between 12th rib fat thickness and marbling along with a genetic correlation of -0.44 between 12th rib fat thickness and longissimus muscle area. The genetic correlations reported in Table 2 indicate selection against 12th rib fat thickness will increase longissimus muscle area and cutability but decrease growth and marbling scores.

2.2.10 Carcass Grade

The Canadian Meat Council's carcass grades are composed of two factors, meat quality and carcass meat yield. Quality factors are composed of 12th rib fat thickness, marbling, fat and meat color, maturity, meat firmness, adequate muscle thickness, pizzle eye size, and crest development (an increase in the mass of various neck muscles). Carcass meat yield is predicted from 12th rib fat thickness and longissimus muscle area measurements (Jones, 1993). Young carcasses are broken down into two categories, A or B. If a carcass has at least Traces marbling, at least 4 mm of 12th rib fat thickness, good muscling, bright red meat color, and white fat, then it qualifies for the A grade. The A grade then is broken down due to different carcass yield percentages that follow: A1 ≥59% carcass yield (4-10 mm 12th rib fat thickness); A2 is from 54-58% carcass yield (10-15 mm 12th rib fat thickness); and A3 is ≤53% (>15 mm 12th rib fat thickness). A carcass that has less than 4 mm of 12th rib fat thickness or less than Traces marbling receives a B1 grade, while carcasses that have yellow fat, poor (light) muscling, or dark colored meat will receive a B2, B3, or B4 carcass grade, respectively. A review of the literature yielded no heritability estimates or correlation values for carcass grade under the Canadian grading system.

2.2.11 Cutability

Percent cutability is an estimate of the lean primal cuts from the carcass. Hot carcass weight, longissimus muscle area, and 12th rib fat thickness are the measurements which compromise cutability. The formula for percent cutability from the Lacombe Research Station is as follows:

percent cutability = 53 - 7 (12th rib fat thickness) + 0.7 (longissimus muscle area).

Cundiff et al. (1971), Benyshek (1981), Woodward et al. (1992), and Marshall (1994) reported respective age constant heritability estimates of 0.28, 0.49, 0.18, and 0.36 (Table 1). Koots et al. (1994a) summarized 12 age constant heritability estimates to have a mean and standard deviation of 0.41 and 0.14, respectively. These estimates indicate that moderate to high genetic progress can be made if selection is for cutability.

In the literature, there appears to be low genetic correlations between cutability and growth traits (Table 4) (Woodward et al., 1992; Marshall, 1994; Koots et al., 1994b). Koots et al. (1994b) reported a mean genetic correlation of 0.12 between cutability and carcass weight from three literature references, while Marshall (1994) averaged two literature references and indicated a negative genetic correlation for this same trait combination of -0.11. Additionally, Koots et al. (1994b) described a mean genetic correlation of 0.26 between longissimus muscle area and cutability, and -0.33 between 12th rib fat thickness and cutability. Incidentally, Koots et al. (1994b) reported a negative mean genetic correlation of -0.54 from five sources between cutability and marbling score.

2.3 Parameter Estimation

2.3.1 Model Specification

The evolution of sire evaluation yields a dependency upon certain criteria (Henderson, 1973, 1974):

1. The predictor has the same expectation as the unknown variable that is to be predicted.
2. Minimization of the variance of the error of prediction in the class of linear unbiased predictors.
3. Maximization of the correlation between the predictor and the predictand in the class of linear unbiased predictors.
4. When the distribution is multinomial normal:
    a. yields the maximum likelihood and the best linear unbiased estimator of the conditional mean of the predictand.
    b. in the class of linear, unbiased predictors, maximizes the probability of a correct pairwise ranking.

The Best Linear Unbiased Prediction (BLUP) developed by Henderson (1953) follows these criterion. However, Henderson (1975) recognized possible errors from model misspecification with BLUP. Ignoring relevant fixed effects yielded biased estimators. Also, the inclusion of irrelevant factors increased the sampling variance, while if random factors were excluded, even if relevant, the estimator and predictor would remain unbiased even though an increase in the sampling variance results.

Pollak and Quaas (1980) make several points comparing an “animal model” to a sire model. The equation for a record contains a term for the breeding value of the animal making the record. This allows for the possibility that sires and(or) dams may have records. It also means that evaluations will be obtained for animals that are not sires (or dams). A less desirable consequence is that the number of random elements to be predicted, at least one for each record, becomes exceedingly large. Other basic discussion of these two types of models include that in a sire model, the animal vector contains only the additive genetic effects from the male parents. One basic concept of a sire model is that the sires are randomly bred to dams and that the dams have only one progeny. The use of an animal model removes the potential bias from these assumptions as it models all animals in the population, including those without records, and connects the animals through the additive genetic relationship matrix.

The basic form of mixed linear models with one random factor is as follows:

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Zu} + \boldsymbol{e}$$

where: $\boldsymbol{y}$ is an N x1 vector of observations,

$\boldsymbol{b}$ is a p x 1 vector of fixed effects associated with $\boldsymbol{y}$,

$\boldsymbol{u}$ is a q x 1 vector of random effects associated with $\boldsymbol{y}$,

$\boldsymbol{X}$ is a known incidence matrix of order N x p that relates elements of $\boldsymbol{b}$ to elements of $\boldsymbol{y}$,

$\boldsymbol{Z}$ is a known incidence matrix of order N x q that relates elements of $\boldsymbol{u}$ to elements of $\boldsymbol{y}$, and

$\boldsymbol{e}$ is an N x 1 vector of residual effects.

Additional attributes of the general form of mixed linear models include the expectations of the random variable which include:

$$\mathrm{E}(y) = \boldsymbol{Xb},$$

$$\mathrm{E}(\boldsymbol{u}) = \boldsymbol{0}, \text{ and}$$

$$\mathrm{E}(\boldsymbol{e}) = \boldsymbol{0}.$$

The (co)variance structure is:

$$Var\begin{bmatrix} \boldsymbol{y} \\ \boldsymbol{u} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{ZGZ'+R} & \boldsymbol{ZG} & \boldsymbol{R} \\ \boldsymbol{GZ'} & \boldsymbol{G} & \boldsymbol{0} \\ \boldsymbol{R} & \boldsymbol{0} & \boldsymbol{R} \end{bmatrix}.$$

2.3.2 Single and Multiple Trait Mixed Model Methodology

The single trait mixed model equations described by Henderson's (1953) BLUP methodology assume that all correlations between traits are zero. An extension of Henderson's BLUP is accomplished through multiple trait analysis that improves the accuracy of genetic evaluation, especially of traits that have been selected upon or are lowly heritable. In animal breeding, most populations have been selected upon, and generally for more than one trait. An example of sequential selection occurs when observations for one trait are used to cull animals, and the selected group is then measured for subsequent traits. Single trait mixed model evaluations would therefore be potentially biased by selection for the first trait.

Multiple trait analysis eliminates the bias due to sequential selection and also selection on correlated traits (Pollak et al., 1984; Walter and Mao, 1983). Also, depending upon the genetic and error correlations used, a reduction in prediction error variance and therefore an increase in accuracy occurs through the use of multiple trait analysis (Schaeffer, 1984). Additionally, Schaeffer (1984) points out that multiple trait analysis allows all animals to be evaluated for every trait even without individual observations for each trait because of the non-zero genetic and residual covariances among the traits that are included in the analysis.

An advantage of single trait analysis is that there are less equations to be solved through the iteration process (Banks, 1986; Nwerume, 1994). Convergence can slow as the number of traits increases, and the complexity of multiple trait models increases rapidly past two traits.

2.3.3 (Co)variance Estimation

Due to the computational difficulty of fitting the expectations and reductions for large data sets, other techniques such as the method of maximum likelihood are preferred. Hartley and Rao (1967) present a maximum likelihood (ML) method that is applied to the general mixed model. Patterson and Thompson (1971) published a restricted maximum likelihood method (REML) of estimating intra-block and inter-block weights in the analysis of incomplete block designs with block sizes that are not necessarily equal. Another view of the problem is estimating constants and components of variance from data arranged in a general two-way classification when the effects of one classification are regarded as fixed and the effects of the second classification are regarded as random. The method they described takes the expectations over a conditional distribution with the treatment effects fixed at their estimated values. Their method consists of maximizing the likelihood, not of all the data, but of a set of selected error contrasts, using iterative techniques. Additionally, Harville (1977) describes techniques such for a given statistical model, when the estimating θ parameters, and with an assumed data distribution, the likelihood function $L(\theta)$ can be equated. In Harville's review of ML and REML, he notes Patterson and Thompson's computationally feasible REML method takes into account the loss of degrees of freedom resulting from the estimation of the fixed effects (Cunningham, 1989).

A derivative-free algorithm for use during the restricted maximum likelihood (DF-REML) variance component estimation was presented by Graser et al. (1987). This method avoids explicit evaluation of first derivatives and does not require matrix inversion. As a result, one round of the method involves computing the determinant of the coefficient matrix of the mixed model equations, which uses a one-dimensional search involving the variant part of the log likelihood to find the maximum of this function (Saama, 1992). The derivative-free multivariate REML algorithms are computationally expensive, especially if the likelihood function contains many parameters to be estimated. Due to this, other algorithms have been developed which utilize first and second derivatives of the likelihood function.

A REML algorithm which uses considerably less computer time, but gives almost identical parameter estimates as DF-REML, is named AI-REML (Madsen et al., 1994). AI-REML uses the average of the observed and expected information as the information matrix. The matrix of second derivatives is called the observed information matrix. Expectations of this matrix is the Fisher information matrix. REML algorithms which utilize observed or expected information will lead to either the Newton-Raphson or the Fisher-scoring algorithm, respectively. The terms that are involved in computing either respective information matrix are computationally difficult. Johnson and Thompson (1995) showed the average of the observed and expected information matrix was considerably easier to compute than either the observed or expected information matrix due to the cancellation of terms. Therefore, a compromise between the Newton-Raphson and the Fisher-scoring algorithms is AI-REML (Madsen et al., 1994).

2.3.4 Genetic Parameter Estimation

2.3.4.1 Heritability Estimators

Falconer (1960) indicates that the variation of a record can be reduced into three categories: additive variance, dominance variance, interaction (epistatic) variance. Additive variance is the variance of breeding values or the variance that can be passed on to offspring. Dominance variance is variation of a record that is due to dominant alleles, or genes that are more "robust" during segregation. Interaction variance is variance due to genes that interact during segregation and expression. An example of an interaction can be from additive by dominance effects. Generally, the effects of dominance variation and interaction variation are considered to be low and are not as readily assessed through observations made on the population, so in practice, the most important partition is due to additive variation. Falconer (1960) noted that the single most important function of the heritability in the genetic study of metric characters is its predictive role, expressing the reliability of the phenotypic value as a guide to the breeding value. Phenotypic values of individuals can be directly measured, but it is the breeding value that most often determines their influence on the next generation. Therefore if the breeder or experimenter chooses individuals to be parents according to their phenotypic values, his success in changing the characteristics of the population can be predicted only from a knowledge of the degree of correspondence between phenotypic values and breeding values. This degree of correspondence is measured by the heritability.

Falconer (1960) states that the half-sib correlation and the regression of offspring on father is a reliable heritability estimate for attempting to reduce sampling error and also environmental sources of covariance that cannot be statistically overcome. The formula for heritability estimates for trait *i* from paternal half-sibs is as follows:

$$\hat{h}_i^2 = \frac{4\hat{\sigma}^2_{s_i}}{\hat{\sigma}^2_{s_i} + \hat{\sigma}^2_{e_i}}$$

where: $\hat{h}_i^2$ is estimated heritability,

$\hat{\sigma}^2_{s_i}$ is the estimated sire variance component,

$\hat{\sigma}^2_{e_i}$ is the estimated error variance component.

The denominator is the phenotypic variance adjusted for fixed effects which were included in the model.

3.3.4.2 Correlation Estimators

Falconer (1960) described the pleiotropic action of genes, which is the property of a gene to affect two or more characters when segregating, to cause simultaneous variation in two or more traits. The correlation of breeding values is the genetic correlation, while the environmental correlation is the correlation of environmental deviations together with non-additive genetic deviations. A correlation is the ratio of the appropriate covariance to the product of the two standard deviations. The genetic correlation between two traits can be affected by selection if selection has been placed on the parents; and as the genetic correlation increases, the bias increases in a likewise direction of the estimated correlation with intense selection (Van Vleck, 1968).

3. MATERIALS AND METHODS

3.1 Description of the Data and Data Edits

Data for this project were provided by the Canadian Charolais Association's Conception to Consumer Program. The Conception to Consumer Program is a sire evaluation program which gives members of the Canadian Charolais Association an opportunity to sponsor bulls to be evaluated through a progeny test for growth and carcass characteristics. The program was initiated in 1968.

Annually, bulls are nominated by the producers for the program and are randomly bred to mature cows in cooperator herds located in Alberta, British Columbia, or Saskatchewan. The breed makeup of the cowherds consisted of varying breeds and breed combinations and were intended to be representative of 90% of the Canadian national beef herd. No virgin heifers were used as dams in the program. Birth weight records were collected by the cooperator herd operators, while the weaning weights were collected under the supervision of the Canadian Charolais Association.

In the fall (late October or early November), calves were weaned at an average age of 215 days and transported to the Cattleland Feedlot, Strathmore, Alberta. At the feedlot, cattle were managed under typical commercial practices and were under the supervision of the Canadian Charolais Association. Upon arrival at the feedlot, cattle were processed (given typical medication and induction treatments), sorted by sex and weight, and then were fed an adaptation ration for an average of 48 days. Following the adaptation period, the steers and heifers were placed on a bulk cereal-silage based diet for an average of 115 days until the end of test date. Following the end of test, cattle remained on the same ration until they were visually appraised to have reached the A1 or A2 carcass grade, at which time they were slaughtered. On average, the cattle were slaughtered 41 days after they came off test. The carcass grades are from the Canadian Meat Council and correspond to the respective twelfth rib backfat thickness of 4-10 and 10-15 mm for the A1 and A2 carcass grades.

After being delivered to the packing plant, all calves were slaughtered and "blue tagged," utilizing the program provided by Agriculture Canada. The meat graders collect the carcass information, which included hot carcass weight, 12th rib backfat thickness, longissimus muscle area, marbling score, and carcass grade. The backfat thickness was measured in tenths of inches, between the 12th and 13th rib, ¾ of the lateral length of the longissimus muscle measured from the split chine bone. The longissimus muscle area measurement was taken in square inches and measured to the nearest tenth. Marbling scores were also taken at the 12th and 13th rib section, and were classified using a nine point scale with a lower numeric number equating to more marbling. The numeric scores were: 1 = very abundant; 2 = abundant; 3 = moderately abundant; 4 = slightly abundant; 5 = moderate; 6 = modest; 7 = small; 8 = slight; and 9 = traces. The carcass meat quality and meat yield attributes were evaluated to place the carcass into one of seven carcass grades: A1, A2, A3, A4, B1, B2, and B3. These carcass grades were then associated with a numeric value to make the analysis possible. The association is: A1 = 1; A2 = 2; A3 = 3; A4 = 4; B1 = 5; B2 = 6; B3 = 7. Percent cutability was estimated as the percent of lean primal cuts. The lean primal cuts included closely trimmed boneless chuck, rib, loin, and round cuts. The formula for percent cutability from the Lacombe Research Station is as follows:

$$\text{Percent cutability} = 53 - 7\ (\text{12th rib backfat thickness}) + 0.7\ (\text{longissimus muscle area})$$

Contemporary groups were defined as animals in the same calving year, breeder herd, sex of calf, breed of dam group, and weaning group. The breed of dam was a visual appraisal given by the cooperating herd operator and is consistent only within herds.

The data set initially contained 5497 records from 1975 through 1993, but was edited to remove single record contemporary groups, gross recording errors, and all twin records (Table 8). There were 9 single record contemporary groups, 2 gross recording errors (>7 standard deviations away from the trait mean), and 85 twin records. No reference sires were used during the first 3 years of the program, but all 172 sires included in the program were connected through the use of pedigree additive relationship information on the sires (Henderson, 1974).

After edits, the resulting data set contained 5401 records which contained 368 contemporary groups, ranging in size from 2 to 141 calves. Fifty-three percent of the 5401 records were from steers. Forty-seven percent of the records were from heifers. Table 9 indicates the reduction in records by sex at different dates that traits were measured. Of the heifer records, there was a decrease in the number of records from

Table 8. Data editing criteria and number of records deleted.

Editing Criteria	Number of Records Deleted
Twin Records	85
Single Record Contemporary Groups	9
Gross Recording Errors	2
Total Records Edited	96

Table 9. Decrease of volume of records by sex.

Trait Date	Male	Female
Calving Year	2881	2520
Weaning Date	2660	2360
Start of Test Date	2383	1161
Slaughter Date	2162	1022

weaning (2360 records) to the start of the test period (1161 records). The loss of 1199 heifer records was a 50.8 percent decrease that indicates that selection occurred upon the heifer population from the date these two traits were measured.

The traits in the analysis include: birth weight (BW); 200 day age adjusted weaning weight (WW); 365 day age adjusted yearling weight (YW); post-weaning average daily gain on test (ADG); end of test period weight (EOTWT); hot carcass weight (CARCWT); marbling score (MARB); longissimus muscle area (LMA); 12th rib fat thickness (FAT); carcass grade (CARCGR); and cutability (CUT).

3.2 Estimation of Genetic Parameters

Following the edits for single record contemporary groups, gross recording errors, and all twin records, the number of records, means, and standard deviations were calculated and are presented in Table 10.

3.2.1 Model 1: Single Trait Mixed Model

Initial variance component estimates were estimated through the use of the PROC VARCOMP procedure from SAS Institute (1990). In the initial analysis, a simple model was used due to computational limitations. The model equated the dependent variable to contemporary group effect and a random sire effect. No sire relationship information was included. The model used included:

$$\boldsymbol{y}_i = \boldsymbol{X}_i\boldsymbol{b}_i + \boldsymbol{Z}_i\boldsymbol{u}_i + \boldsymbol{e}_i$$

where:

i = 1, 2, 3, . . ., 11 which corresponds to birth weight, adjusted weaning weight, adjusted yearling weight, post-weaning average daily gain, end of test weight, carcass weight, marbling score, longissimus muscle area, 12th rib fat thickness, carcass grade, and cutability,

y_i is an observation vector of the i^{th} trait,

b_i is vector of the fixed effect for contemporary group for the i^{th} trait,

u_i is a vector of random genetic sire effects for i^{th} trait,

X_i is an incidence vector associating fixed effects with the corresponding records in y,

Z_i is an incidence vector associating random sire genetic effects with the corresponding records in y, and

e_i is the random error effect for y.

The expectations for the model include:

$$E[y] = Xb$$

$$E[\sigma^2_S] = ¼\sigma^2_A$$

$$E[e] = 0.$$

where σ^2_A is defined as the additive genetic variation. The variance-covariance matrix

associated with the random effects in the model is:

$$Var\begin{bmatrix} \boldsymbol{u} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{G_o} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{R_o} \end{bmatrix}$$

where:

$$G_o = \left[\sigma^2_{G_i}\right]$$

$$R_o = \left[\sigma^2_{R_i}\right]$$

and where σ^2_G is the variance associated with the sire effect, and σ^2_R is the residual variance.

3.2.2 Model 2: Single Trait Mixed Model

Once the initial variance components were estimated using the simple model, a more complex single trait model was run using the multiple trait, average-information restricted maximum likelihood algorithm (AI-REML) of DMU (DMU-AI) (Jensen and Madsen, 1993) on a IBM RISC System 6000 computer. The prior variance estimates for Model 2 were taken from the VARCOMP procedure results. The models used included:

$$y_i = \boldsymbol{X_i \beta_i} + \boldsymbol{Z_i u_i} + \boldsymbol{e_i}$$

Table 10. Number of records after edits, means, and standard deviations.

Trait	Number of records	Mean	Standard Deviation
Birth Weight	5223	42.24 kg	6.44 kg
Adjusted Weaning Weight	4801	247.78 kg	35.24 kg
Adjusted Yearling Weight	3330	466.19 kg	56.24 kg
Post-weaning Average Daily Gain	3330	1.47 kg/day	0.025 kg/day
End Of Test Weight	3441	482.07 kg	53.03 kg
Carcass Weight	3176	308.16 kg	33.50 kg
Marbling Score	3184	6.93 units	0.75 units
Longissimus Muscle Area	3145	81.61 cm^2	9.81 cm^2
12th Rib Fat Thickness	3143	0.889 cm	0.305 cm
Carcass Grade	3166	1.32 units	0.57 units
Cutability	3143	58.94 %	1.48 %

where:

i = 1, 2, 3, . . ., 11 which corresponds to birth weight, weaning weight, yearling weight, post-weaning average daily gain, end of test weight, carcass weight, marbling score, longissimus muscle area, 12th rib fat thickness, carcass grade, and cutability,

$\mathbf{y}_i$ is an observation vector of the i^{th} trait,

β_i is matrix of the fixed effects for i^{th} trait,

$\mathbf{u}_i$ is a vector of random genetic sire effects for i^{th} trait,

X_i is an incidence matrix associating fixed effects with the corresponding records in y,

Z_i is an incidence matrix associating random sire genetic effects with the corresponding records in y, and

e_i is the random error effect for y.

The expectations for the model include:

$$E[y] = Xb$$

$$E[\sigma^2_S] = \frac{1}{4}\sigma^2_A$$

$$E[e] = 0.$$

where σ^2_A is defined as the additive genetic variation. The variance-covariance matrix

associated with the random effects in the model is:

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} \boldsymbol{G_o} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{R_o} \end{bmatrix}$$

where:

$$G_o = \left[\sigma^2_{G_l}\right]$$

$$R_o = \left[\sigma^2_{R_l}\right]$$

and where σ^2_G is the variance associated with the sire effect, and σ^2_R is the residual variance. Also, $\boldsymbol{G} = \boldsymbol{G_o} \otimes \boldsymbol{A}$, and $\boldsymbol{R} = \boldsymbol{R_o} \otimes \boldsymbol{I}$, as $\boldsymbol{A}$ is the numerator of the additive genetic relationship matrix among the 172 sires with $\otimes$ denoting the direct product operator.

With these results, the mixed-model equations are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}Z & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where: $\boldsymbol{G^{-1}} = \boldsymbol{G_o^{-1}} \otimes \boldsymbol{A^{-1}}$, and $\boldsymbol{R^{-1}} = \boldsymbol{R_o^{-1}} \otimes \boldsymbol{I}$. The A^{-1} elements were established using methods described by Henderson (1976) and Quaas (1976).

The fixed effects in the model included μ contemporary group and also one covariate, which was age at slaughter. Age at slaughter was included as a covariate in the model for carcass weight, marbling score, longissimus muscle area, 12th rib fat thickness, carcass grade, and cutability because the cattle were slaughtered at different ages to achieve a visual A1 or A2 carcass grade, and also to study differences in the carcass traits on a growth rate constant basis (Benyshek, 1981).

The algorithm used in the analysis is as follows (Johnson and Thompson, 1995; Madsen et al., 1994):

$$\boldsymbol{I}_A(\theta) = \boldsymbol{F'PF} = \boldsymbol{F'R}^{-1} - \left(\boldsymbol{C}^{-1}\boldsymbol{W'F}\right)' \boldsymbol{WR}^{-1}\boldsymbol{F}$$

where:

$\boldsymbol{I}_A(\theta)$ = average information matrix,

$\boldsymbol{F}$ = a matrix with the dimension of (number of observations by number of elements in θ), with the j^{th} column $\mathbf{f}_j$ equal to the vector $\frac{\partial \boldsymbol{V}}{\partial \theta_{\{j\}}} \boldsymbol{Py}$,

$\boldsymbol{P} = \boldsymbol{V}^{-1} - \boldsymbol{V}^{-1}\boldsymbol{X}\left(\boldsymbol{X'V}^{-1}\boldsymbol{X}\right)^{-1}\boldsymbol{X'V}^{-1}$,

$\boldsymbol{R}$ = residual (co)variance matrix,

$\boldsymbol{C}^{-1}$ = inverse of the coefficient matrix of the mixed model equations,

$\boldsymbol{W}$ = total (fixed and random effects) design matrix,

$\boldsymbol{V}$ = variance matrix of $\boldsymbol{y} = \boldsymbol{ZGZ'}+\boldsymbol{R}$,

$\boldsymbol{X}$ = design matrix corresponding to the fixed effects,

$\boldsymbol{y}$ = vector of observations,

$\boldsymbol{G}$ = variance of $\boldsymbol{u}$,

$\theta =$ scalar variance component,

$\boldsymbol{Z} =$ design matrix corresponding to the random effects.

Therefore, for a column in $\boldsymbol{F}$ corresponding to an element in $\boldsymbol{G}_{o_i}$, in such that $\boldsymbol{G}_{o_i}$ is a p_i x p_i (co)variance matrix of the traits in the i^{th} random effect, Madsen et al. (1994) indicate:

$$f\left(\theta_{i\{j,k\}}\right) = \left[\frac{\partial \boldsymbol{V}}{\partial \theta_{i\{j,k\}}}\right]\boldsymbol{Py} = \boldsymbol{Z}_i\left[\left(\boldsymbol{D}_{jk}\boldsymbol{G}_{o_i}^{-1}\right)\otimes \boldsymbol{I}\right]\hat{\boldsymbol{u}}_i$$

where: $\boldsymbol{D}_{jk}$ is a symmetric p_i x p_i indicator matrix containing ones in positions

corresponding to the $\boldsymbol{j,k}^{th}$ parameter in $\boldsymbol{G}_{o_i}$ and zeros elsewhere,

$\theta_{i\{j,k\}}$ is the corresponding element in $\boldsymbol{\theta}$, and

$\hat{\boldsymbol{u}}_i$ is the vector of all solutions for the i^{th} random effect.

To estimate the columns in $\boldsymbol{F}$ that correspond to the parameters in $\boldsymbol{R}_o$ the algorithm is:

$$f\left(\theta_{R\{j,k\}}\right) = \left[\frac{\partial \boldsymbol{V}}{\partial \theta_{R\{j,k\}}}\right]\boldsymbol{Py} = \boldsymbol{R}_{jk}\boldsymbol{R}^{-1}\left(\boldsymbol{y} - \boldsymbol{X}\hat{\boldsymbol{b}} - \boldsymbol{Z}\hat{\boldsymbol{u}}\right).$$

The convergence criterion used in all analyses was set at a level where the (co)variances changed less than 1×10^{-8} standard deviation units per round of iteration. After the initial run of the model reached convergence, the (co)variance components were used as starting values in a subsequent cold restart. After all restart runs were completed, the respective (co)variance results were averaged and the mean estimates and standard deviations were reported. Heritabilities and genetic, phenotypic, and environmental correlations were estimated from the paternal half-sib variances and covariances from the five trait analyses. Heritability (the proportion of the phenotypic variance which is explained by the additive genetic variance) was estimated from intraclass correlations of paternal half-sibs (Falconer, 1960):

$$h^2 = 4\sigma_s^2 / \sigma_p^2,$$

where $\sigma_p^2 = \sigma_s^2 + \sigma_e^2$. Dickerson (1958) noted that this estimate of heritability may be upwardly biased due to epistatic effects, such as any genotype by environment interactions.

3.2.3 Model 3: Five Trait Mixed Model

A third analysis was conducted using the results from the second analysis with single trait procedures as prior variance component values. In the third analysis, a five trait mixed model was employed in which adjusted weaning weight (WW) was included in each 5 trait combination. This model was used to explore the hypothesis of selection bias in estimation of genetic parameters due to the relative increase in the loss of female post-weaning records (Henderson and Quaas, 1976; Pollak and Quaas, 1980). The model used in this analysis is as follows:

$$\begin{bmatrix} \boldsymbol{y}_{ww} \\ \boldsymbol{y}_{i} \\ \boldsymbol{y}_{i'} \\ \boldsymbol{y}_{i''} \\ \boldsymbol{y}_{i'''} \end{bmatrix} = \begin{bmatrix} \boldsymbol{X}_{ww} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{X}_{i} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{X}_{i'} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{X}_{i''} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{X}_{i'''} \end{bmatrix} \begin{bmatrix} \boldsymbol{b}_{ww} \\ \boldsymbol{b}_{i} \\ \boldsymbol{b}_{i'} \\ \boldsymbol{b}_{i''} \\ \boldsymbol{b}_{i'''} \end{bmatrix}$$

$$+ \begin{bmatrix} \boldsymbol{Z}_{ww} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{Z}_{i} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z}_{i'} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z}_{i''} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{Z}_{i'''} \end{bmatrix} \begin{bmatrix} \boldsymbol{u}_{ww} \\ \boldsymbol{u}_{i} \\ \boldsymbol{u}_{i'} \\ \boldsymbol{u}_{i''} \\ \boldsymbol{u}_{i'''} \end{bmatrix} + \begin{bmatrix} \boldsymbol{e}_{ww} \\ \boldsymbol{e}_{i} \\ \boldsymbol{e}_{i'} \\ \boldsymbol{e}_{i''} \\ \boldsymbol{e}_{i'''} \end{bmatrix}$$

where:

i = trait 2, 3, 4, or 5, in addition to $i \neq i' \neq i'' \neq i''' \neq$ weaning weight, all trait combinations were computed so as to fill a correlation matrix, while still having weaning weight remain in every multivariate model,

y is an observation vector of ***i***, and weaning weight,

b is a vector of the fixed effects for ***i***, and weaning weight, the fixed effects in the model included μ contemporary group and also one covariate, which was age at slaughter. Age at slaughter was included as a covariate in the model for carcass weight, marbling score, longissimus muscle area, 12th rib fat thickness, carcass grade, and cutability

u is a vector of random genetic sire effects for $\boldsymbol{i}$, and weaning weight,

$\boldsymbol{X}$ is an incidence matrix associating fixed effects with the corresponding records in $\boldsymbol{y}$,

$\boldsymbol{Z}$ is an incidence matrix associating random sire genetic effects with the corresponding records in $\boldsymbol{y}$, and,

$\boldsymbol{e}$ is the random error effect for $\boldsymbol{i}$, and weaning weight.

The expectations for the model include:

$$\mathrm{E}[\boldsymbol{y}] = \boldsymbol{Xb}$$

$$\mathrm{E}[\sigma^2_{\mathrm{S}}] = \tfrac{1}{4}\sigma^2_{\mathrm{A}}$$

$$\mathrm{E}[\boldsymbol{e}] = \boldsymbol{0}$$

where σ^2_{A} is defined as the additive genetic variation. The variance-covariance matrix associated with the random effects in the model is:

$$Var\begin{bmatrix} \boldsymbol{u} \\ \boldsymbol{e} \end{bmatrix} = \begin{bmatrix} \boldsymbol{G}_o & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{R}_o \end{bmatrix}$$

where:

$$G_o = \begin{bmatrix} \sigma^2_{G_{ww}} & \sigma_{WWG_l} & \sigma_{WW_lG_{l'}} & \sigma_{WW_lG_{l''}} & \sigma_{WW_lG_{l'''}} \\ & \sigma^2_{G_l} & \sigma_{G_lG_{r'}} & \sigma_{G_lG_{l''}} & \sigma_{G_lG_{l'''}} \\ & & \sigma^2_{G_{l'}} & \sigma_{G_lG_{ll''}} & \sigma_{G_lG_{l'''}} \\ & & & \sigma^2_{G_{l''}} & \sigma_{G_lG_{l'''}} \\ \text{Symetric} & & & & \sigma^2_{G_{r''}} \end{bmatrix}$$

$$R_o = \begin{bmatrix} \sigma^2_{R_{ww}} & \sigma_{R_{ww}R_i} & \sigma_{R_{ww}R_{l'}} & \sigma_{R_{ww}R_{l''}} & \sigma_{R_{ww}R_{r'''}} \\ & \sigma^2_{R_l} & \sigma_{R_lR_{l'}} & \sigma_{R_{l'}R_{l''}} & \sigma_{R_lR_{l'''}} \\ & & \sigma^2_{R_{l'}} & \sigma_{R_l.R_{l''}} & \sigma_{R_rR_{r''}} \\ & & & \sigma^2_{R_{l''}} & \sigma_{R_{r''}R_{l'''}} \\ \text{Symetric} & & & & \sigma^2_{R_{r''}} \end{bmatrix}$$

and where σ^2_G are variances associated with the sire effects, and σ^2_R are residual variances. In addition, $\sigma_{G_lG_{l'}}$ are covariances associated with sire effects, and $\sigma_{R_lR_{l'}}$ are covariances analogous to the dependent traits analyzed. Also, $\boldsymbol{G} = \boldsymbol{G_o} \otimes \boldsymbol{A}$, and $\boldsymbol{R} = \boldsymbol{R_o} \otimes \boldsymbol{I}$, as $\boldsymbol{A}$ is the numerator of the additive genetic relationship matrix among the 172 sires with $\otimes$ denoting the direct product operator.

With these results, the mixed-model equations are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}Z & Z'R^{-1}Z + G^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where: $\boldsymbol{G^{-1}} = \boldsymbol{G_o^{-1}} \otimes \boldsymbol{A^{-1}}$, and $\boldsymbol{R^{-1}} = \boldsymbol{R_o^{-1}} \otimes \boldsymbol{I}$.

The A^{-1} elements were established using methods described by Henderson (1976) and Quaas (1976). The (co)variance components were estimated using AI-REML (Newton-Fisher REML Estimation) utilizing the multivariate mixed model package DMU (Jensen and Madsen, 1993). The algorithm used in the analysis is as follows (Johnson and Thompson, 1995; Madsen et al., 1994):

$$I_A(\theta) = F'PF = F'R^{-1} - \left(C^{-1}W'F\right)' WR^{-1}F$$

where:

$I_A(\theta)$ = average information matrix,

F = a matrix with the dimension of (number of observations by number of elements in θ), with the jth column $\mathbf{f}_j$ equal to the vector $\frac{\partial V}{\partial \theta_{\{j\}}} Py$,

$P = V^{-1} - V^{-1}X\left(X'V^{-1}X\right)^{-1}X'V^{-1}$,

R = residual (co)variance matrix,

C^{1} = inverse of the coefficient matrix of the mixed model equations,

W = total (fixed and random effects) design matrix,

V = variance matrix of $y = ZGZ' + R$,

X = design matrix corresponding to the fixed effects,

y = vector of observations,

G = variance of u,

θ = scalar variance component,

$\boldsymbol{Z}$ = design matrix corresponding to the random effects.

Therefore, for a column in $\boldsymbol{F}$ corresponding to an element in $\boldsymbol{G}_{o_i}$, in such that $\boldsymbol{G}_{o_i}$ is a p_i x p_i (co)variance matrix of the traits in the i^{th} random effect, Madsen et al. (1994) indicate:

$$f\left(\theta_{i\{j,k\}}\right) = \left[\frac{\partial V}{\partial \theta_{i\{j,k\}}}\right] \boldsymbol{P}\boldsymbol{y} = \boldsymbol{Z}_i\left[\left(\boldsymbol{D}_{jk}\boldsymbol{G}_{o_i}^{-1}\right) \otimes \boldsymbol{I}\right]\hat{\boldsymbol{u}}_i$$

where: $\boldsymbol{D}_{jk}$ is a symmetric p_i x p_i indicator matrix containing ones in positions

corresponding to the j,k^{th} parameter in $\boldsymbol{G}_{o_i}$ and zeros elsewhere,

$\theta_{i\{j,k\}}$ is the corresponding element in $\boldsymbol{\theta}$, and

$\hat{\boldsymbol{u}}_i$ is the vector of all solutions for the i^{th} random effect.

To estimate the columns in $\boldsymbol{F}$ that correspond to the parameters in $\boldsymbol{R}_o$ the algorithm is:

$$f\left(\theta_{R\{j,k\}}\right) = \left[\frac{\partial V}{\partial \theta_{R\{j,k\}}}\right] \boldsymbol{P}\boldsymbol{y} = \boldsymbol{R}_{jk}\boldsymbol{R}^{-1}\left(\boldsymbol{y} - \boldsymbol{X}\hat{\boldsymbol{b}} - \boldsymbol{Z}\hat{\boldsymbol{u}}\right).$$

The convergence criterion used in all analyses was set at a level where the (co)variances changed less than 1×10^{-8} standard deviation units per round of iteration. After the initial run of the model reached convergence, the (co)variance components were used as starting values in a subsequent cold restart. After all restart runs were completed, the respective (co)variance results were averaged and the mean estimates and standard deviations were reported. Heritabilities and genetic, phenotypic, and environmental correlations were estimated from the paternal half-sib variances and covariances from the five trait analyses.

Heritability (the proportion of the phenotypic variance which is explained by the additive genetic variance) was estimated from intraclass correlations of paternal half-sibs (Falconer, 1960):

$$h^2 = 4\sigma_s^2 / \sigma_p^2,$$

where $\sigma_p^2 = \sigma_s^2 + \sigma_e^2$. Dickerson (1958) noted that this estimate of heritability may be upwardly biased due to epistatic effects, such as any genotype by environment interactions.

The formula used for genetic correlation of trait i and i' is (Falconer, 1960):

$$r_g = \sigma_{G_i G_{i'}} / \sqrt{\sigma_{G_i}^2 \sigma_{G_{i'}}^2} .$$

The formula for environmental correlation of trait i and i' is defined as (Falconer, 1960):

$$r_e = \sigma_{E_i E_{i'}} / \sqrt{\sigma_{E_i}^2 \sigma_{E_{i'}}^2} .$$

The phenotypic correlation formula for trait i and i' is (Falconer, 1960):

$$r_p = \sigma_{P_i P_{i'}} / \sqrt{\sigma_{P_i}^2 \sigma_{P_{i'}}^2} = \sigma_{G_i G_{i'}} + \sigma_{E_i E_{i'}} / \sqrt{\left(\sigma_{G_i}^2 + \sigma_{E_i}^2\right)\left(\sigma_{G_{i'}}^2 + \sigma_{E_{i'}}^2\right)} .$$

An approximate method to estimate the variance of the intraclass correlation (t) from half sibs was used (Swiger et al., 1964). The paternal half-sib correlation is $t = \sigma_s^2 / \sigma_p^2$. The variance of t for a simple one-way classification model is:

$$V(t) \cong \{2(n.-1)(1-t)^2[1+(k-1)t]^2\} / [k^2(n.-B)(B-1)]$$

where:

n. = total number of animals,

B = number of sires,

k = $[n.-(\Sigma n_i^2)/n.]/(B-1)$ and,

n_i = number of progeny of sire i.

Therefore, the variance of heritability is:

$V(h^2) = V(t)/a_{ii}^2 = 16V(t)$

where, a_{ii} = 1/4, the additive relationship of paternal half sibs.

The subsequent approximate standard errors are expected to underestimate the actual standard errors (Swiger et al., 1964).

3.2.4 Model 4: Four Trait Mixed Model

A fourth analysis was run to investigate the variation in marbling score, longissimus muscle area, and 12th rib fat thickness while holding carcass weight constant to observe differences in marbling score, longissimus muscle area and 12th rib fat thickness proportions of the carcass (Cundiff et al., 1971). In the fourth analysis, a four trait mixed model was used in which weaning weight was included. This model was used to explore the hypothesis of selection bias in estimation of genetic parameters due to the relative increase in the loss of female post-weaning records (Henderson and Quaas, 1976; Pollak and Quaas, 1980). The model used in this analysis is as follows:

$$\begin{bmatrix} y_{WW} \\ y_{CMARB} \\ y_{CLMA} \\ y_{CFAT} \end{bmatrix} = \begin{bmatrix} X_{WW} & 0 & 0 & 0 \\ 0 & X_{MARB} & 0 & 0 \\ 0 & 0 & X_{LMA} & 0 \\ 0 & 0 & 0 & X_{FAT} \end{bmatrix} \begin{bmatrix} b_{WW} \\ b_{MARB} \\ b_{LMA} \\ b_{FAT} \end{bmatrix}$$

$$+ \begin{bmatrix} Z_{WW} & 0 & 0 & 0 \\ 0 & Z_{MARB} & 0 & 0 \\ 0 & 0 & Z_{LMA} & 0 \\ 0 & 0 & 0 & Z_{FAT} \end{bmatrix} \begin{bmatrix} u_{WW} \\ u_{MARB} \\ u_{LMA} \\ u_{FAT} \end{bmatrix}$$

$$+ \begin{bmatrix} e_{WW} \\ e_{MARB} \\ e_{LMA} \\ e_{FAT} \end{bmatrix}$$

where:

y is an observation vector of adjusted weaning weight (WW), marbling score (CMARB), longissimus muscle area (CLMA), and 12th rib fat thickness (CFAT),

b is a vector of the fixed effects for weaning weight, marbling score, longissimus muscle area, and 12th rib fat thickness, the fixed effects in the model included μ contemporary group and also one covariate, which was carcass weight,

u is a vector of random genetic sire effects for weaning weight, marbling score, longissimus muscle area, and 12th rib fat thickness,

X is an incidence matrix associating the fixed effects μ contemporary group and the carcass weight covariate with the corresponding records in ***y***,

Z is an incidence matrix associating random sire genetic effects with the corresponding records in **y**, and,

e is the random error effect for weaning weight, marbling score, longissimus muscle area, and 12th rib fat thickness.

The expectations for the model include:

$$E[\boldsymbol{y}] = \boldsymbol{Xb}$$

$$E[\sigma^2_S] = \tfrac{1}{4}\sigma^2_A$$

$$E[\boldsymbol{e}] = \boldsymbol{0}$$

where σ^2_A is defined as the additive genetic variation. The variance-covariance matrix

associated with the random effects in the model is:

$$Var\begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} G_o & 0 \\ 0 & R_o \end{bmatrix}$$

where:

$$G_o = \begin{bmatrix} \sigma^2_{G_{ww}} & \sigma_{WWG_l} & \sigma_{WW_lG_{l'}} & \sigma_{WW_lG_{l''}} & \sigma_{WW_lG_{l'''}} \\ & \sigma^2_{G_l} & \sigma_{G_lG_{l'}} & \sigma_{G_lG_{l''}} & \sigma_{G_lG_{l'''}} \\ & & \sigma^2_{G_{l'}} & \sigma_{G_lG_{ll''}} & \sigma_{G_lG_{l'''}} \\ & & & \sigma^2_{G_{l''}} & \sigma_{G_lG_{l'''}} \\ \text{Symetric} & & & & \sigma^2_{G_{l'''}} \end{bmatrix}$$

$$R_o = \begin{bmatrix} \sigma^2_{R_{ww}} & \sigma_{R_{ww}R_i} & \sigma_{R_{ww}R_{l'}} & \sigma_{R_{ww}R_{l''}} & \sigma_{R_{ww}R_{l'''}} \\ & \sigma^2_{R_l} & \sigma_{R_lR_{l'}} & \sigma_{R_{l'}R_{l''}} & \sigma_{R_lR_{l'''}} \\ & & \sigma^2_{R_{l'}} & \sigma_{R_l.R_{l''}} & \sigma_{R_{l'}R_{l'''}} \\ & & & \sigma^2_{R_{l''}} & \sigma_{R_{l''}R_{l'''}} \\ \text{Symetric} & & & & \sigma^2_{R_{l'''}} \end{bmatrix}$$

and where σ^2_G are variances associated with the sire effects, and σ^2_R are residual variances. In addition, $\sigma_{G_lG_{l'}}$ are covariances associated with the sire effects, and $\sigma_{R_lR_{l'}}$ are the covariances analogous to the dependent traits analyzed. Also, $G = G_o \otimes A$, and $R = R_o \otimes I$, as A is the numerator of the additive genetic relationship matrix among the 172 sires with $\otimes$ denoting the direct product operator.

With these results, the mixed-model equations are:

$$\begin{bmatrix} X'R^{-1}X & X'R^{-1}Z \\ Z'R^{-1}Z & Z'R^{-1}Z+G^{-1} \end{bmatrix} \begin{bmatrix} \beta \\ u \end{bmatrix} = \begin{bmatrix} X'R^{-1}y \\ Z'R^{-1}y \end{bmatrix}$$

where: $G^{-1} = G_o^{-1} \otimes A^{-1}$, and $R^{-1} = R_o^{-1} \otimes I$.

The A^{-1} elements were established using methods described by Henderson (1976) and Quaas (1976). The (co)variance components were estimated using AI-REML (Newton-Fisher REML Estimation) utilizing the multivariate mixed model package DMU (Jensen and Madsen, 1993). The algorithm used in the analysis is as follows (Johnson and Thompson, 1995; Madsen et al., 1994):

$$I_A(\theta) = F'PF = F'R^{-1} - \left(C^{-1}W'F\right)' WR^{-1}F$$

where:

$I_A(\theta)$ = average information matrix,

F = a matrix with the dimension of (number of observations by number of elements in θ), with the j^th^ column f_j equal to the vector $\frac{\partial V}{\partial \theta_{\{j\}}} Py$,

$P = V^{-1} - V^{-1}X\left(X'V^{-1}X\right)^{-1}X'V^{-1}$,

R = residual (co)variance matrix,

C^{1} = inverse of the coefficient matrix of the mixed model equations,

$\boldsymbol{W}$ = total (fixed and random effects) design matrix,

$\boldsymbol{V}$ = variance matrix of $\boldsymbol{y} = \boldsymbol{ZGZ'}+\boldsymbol{R}$,

$\boldsymbol{X}$ = design matrix corresponding to the fixed effects,

$\boldsymbol{y}$ = vector of observations,

$\boldsymbol{G}$ = variance of $\boldsymbol{u}$,

θ = scalar variance component,

$\boldsymbol{Z}$ = design matrix corresponding to the random effects.

Therefore, for a column in $\boldsymbol{F}$ corresponding to an element in $\boldsymbol{G}_{o_i}$, in such that $\boldsymbol{G}_{o_i}$ is a p_i x p_i (co)variance matrix of the traits in the i^{th} random effect, Madsen et al. (1994) indicate:

$$f\left(\theta_{i\{j,k\}}\right) = \left[\frac{\partial V}{\partial \theta_{i\{j,k\}}}\right] Py = Z_i\left[\left(D_{jk} G_{o_i}^{-1}\right) \otimes I\right] \hat{u}_i$$

where: $\boldsymbol{D}_{jk}$ is a symmetric p_i x p_i indicator matrix containing ones in positions corresponding to the $\boldsymbol{j,k}^{th}$ parameter in $\boldsymbol{G}_{o_i}$ and zeros elsewhere,

$\theta_{i\{j,k\}}$ is the corresponding element in θ, and

$\hat{\boldsymbol{u}}_i$ is the vector of all solutions for the i^{th} random effect.

To estimate the columns in $\boldsymbol{F}$ that correspond to the parameters in $\boldsymbol{R}_o$ the algorithm is:

$$f\left(\theta_{R\{j,k\}}\right) = \left[\frac{\partial V}{\partial \theta_{R\{j,k\}}}\right] Py = R_{jk} R^{-1}\left(y - X\hat{b} - Z\hat{u}\right).$$

The convergence criterion used in all analyses was set at a level where the (co)variances changed less than 1×10^{-8} standard deviation units per round of iteration. After the initial run of the model reached convergence, the (co)variance components were used as starting values in a subsequent cold restart. Heritabilities and genetic, phenotypic and environmental correlations were estimated from the paternal half-sib variances and covariances from the four trait analyses. Heritability (the proportion of the phenotypic variance which is explained by the additive genetic variance). was estimated from intraclass correlations of paternal half-sibs (Falconer, 1960):

$$h^2 = 4\sigma_s^2 / \sigma_p^2,$$

where $\sigma_p^2 = \sigma_s^2 + \sigma_e^2$. Dickerson (1958) noted that this estimate of heritability may be upwardly biased due to epistatic effects, such as any genotype by environment interactions.

The formula used for genetic correlation of trait i and i' is (Falconer, 1960):

$$r_g = \sigma_{G_i G_{i'}} / \sqrt{\sigma_{G_i}^2 \sigma_{G_{i'}}^2} \ .$$

The formula for environmental correlation of trait i and i' is defined as (Falconer, 1960):

$$r_e = \sigma_{E_i E_{i'}} / \sqrt{\sigma_{E_i}^2 \sigma_{E_{i'}}^2} \ .$$

The phenotypic correlation formula for trait i and i' is (Falconer, 1960):

$$r_p = \sigma_{P_iP_{i'}} / \sqrt{\sigma^2_{P_i}\sigma^2_{P_{i'}}} = \sigma_{G_iG_{i'}} + \sigma_{E_iE_{i'}} / \sqrt{\left(\sigma^2_{G_i} + \sigma^2_{E_i}\right)\left(\sigma^2_{G_{i'}} + \sigma^2_{E_{i'}}\right)}.$$

An approximate method to estimate the variance of the intraclass correlation (t) from half sibs was used (Swiger et al., 1964). The paternal half-sib correlation is $t = \sigma^2_s / \sigma^2_p$. The variance of t for a simple one-way classification model is:

$$V(t) \cong \{2(n.-1)(1-t)^2[1+(k-1)t]^2\} / [k^2(n.-B)(B-1)]$$

where:

n. = total number of animals,

B = number of sires,

k = $[n.-(\Sigma n_i^2)/n.]/(B-1)$ and,

n_i = number of progeny of sire i.

Therefore the variance of heritability is:

$$V(h^2) = V(t) / a^2_{ii} = 16V(t)$$

where, a_{ii} = 1/4, the additive relationship of paternal half sibs.

The subsequent approximate standard errors are expected to underestimate the actual standard errors (Swiger et al., 1964).

4. RESULTS AND DISCUSSION

4.1 Model 1 Genetic Parameters

The estimates of sire variance, environmental variance, and heritability for birth weight (BW), adjusted weaning weight (WW), adjusted yearling weight (YW), post-weaning average daily gain (ADG), end of test weight (EOTWT), carcass weight (CARCWT), marbling score (MARB), longissimus muscle area (LMA), 12th rib fat thickness (FAT), carcass grade (CARCGR), and cutability (CUT) from Model 1 are reported in Table 11. This procedure is not capable of modeling continuous variables, so covariates were not included in the model. Additionally, no sire relationship information was included in the Model 1 analysis. With the exception of adjusted yearling weight heritability, all other traits are below the mean of heritability values listed in Table 1. It was expected that the estimates of sire variance would be initially low from this single trait model due to the limitation of the effects modeled, in addition to the biases that occur from selection on correlated traits to the single trait in the model. However, initial variance components were obtained.

4.2 Model 2 Genetic Parameters

The results of Model 2 are included in Table 12. Estimates achieved from Model 2 are from single trait mixed models, and therefore could be subject to bias from sequential

Table 11. Model 1 estimates of sire variance, residual variance, and heritability.

Trait	Sire Variance	Environmental Variance	Heritability
Birth Weight	2.049	25.507	0.30
Adjusted Weaning Weight	17.647	597.320	0.11
Adjusted Yearling Weight	142.564	1682.450	0.31
Post-weaning Average Daily Gain	0.003	0.044	0.28
End of Test Weight	132.868	1788.687	0.28
Carcass Weight	28.758	693.077	0.16
Marbling Score	0.011	0.417	0.11
Longissimus Muscle Area	4.112	71.134	0.22
12th Rib Fat Thickness	0.007	0.076	0.34
Carcass Grade	0.018	0.277	0.24
Cutability	0.156	1.720	0.33

Table 12. Model 2 estimates of heritability and sire, residual, and phenotypic variance.

Trait	Sire Variance	Environmental Variance	Phenotypic Variance	Heritability
Birth Weight	1.512	25.690	27.206	0.22
Adjusted Weaning Weight	16.289	581.562	597.855	0.11
Adjusted Yearling Weight	83.380	1643.093	1726.473	0.19
Post-weaning Average Daily Gain	0.002	0.044	0.047	0.21
End of Test Weight	89.842	1811.569	1901.411	0.19
Carcass Weight	17.323	686.893	704.216	0.10
Marbling Score	0.030	0.403	0.433	0.28
Longissimus Muscle Area	5.536	70.884	76.420	0.29
12th Rib Fat Thickness	0.007	0.075	0.082	0.36
Carcass Grade	0.018	0.277	0.295	0.24
Cutability	0.152	1.758	1.910	0.32

selection and also bias from selection on correlated traits (Pollak et al., 1984; Walter and Mao, 1983). The heritability values reported in Table 12 are lower than the mean literature cited estimates listed in Table 1. This model attempted to remove the biases from omitting genetic relationship information through the additive relationship matrix, in addition to the effects of slaughtering the cattle at different ages. A comparison of Model 1 and Model 2 indicate that there was an increase in the sire variance and heritabilities of carcass traits estimated from Model 2. Although there was a decrease in the heritability estimates for the growth traits, a review of Henderson (1975) suggests that Model 1 could be biased due to the omission of relevant factors of the model. Additionally, Model 2 showed greater differences in the heritability values for both adjusted yearling weight and marbling score. Adjusted yearling weight heritability from Model 2 could be lower due to modeling the covariance associated with the sire additive genetic relationship matrix. Marbling score might be higher in Model 2 for this same reason, in addition to effects associated with possible removal of environmental variation from slaughtering cattle at different ages.

4.3 Model 3 Genetic Parameters

Table 13, Table 14, and Table 15 contain the genetic, environmental, and phenotypic variance estimates, respectively, from each five trait combination for Model 3. Table 16 contains the heritability estimates from each five trait combination of Model 3. Tables 17, 18, and 19 contain the mean, standard deviation, and range of the genetic, environmental, and phenotypic variances obtained from each five trait analysis of Model 3.

Table 13. Model 3 genetic variances of five trait combination subsets.

Trait	Analysis 1	Analysis 2	Analysis 3	Analysis 4	Analysis 5	Analysis 6	Analysis 7	Analysis 8	Analysis 9	Analysis 10
Birth Weight	1.466		1.528	1.517			1.517			
Adjusted Weaning Weight	12.756	16.566	15.753	15.613	16.012	16.357	15.521	16.312	16.600	16.549
Adjusted Yearling Weight	69.444				82.593	84.301		84.349		
Post-weaning Average Daily Gain	0.003				0.002	0.002		0.002		
End of Test Weight	70.189		88.233	89.634			89.346			
Carcass Weight [a]		22.829	25.014		29.490				23.084	
Marbling Score [a]		0.031	0.029		0.029				0.030	
Longissimus Muscle Area [a]		5.661		5.644		5.627				5.428
12th Rib Fat Thickness [a]		0.008		0.008		0.008				0.008
Carcass Grade [a]							0.017	0.017	0.017	0.016
Cutability [a]							0.158	0.155	0.160	0.154

[a] Analyzed with an age at slaughter covariate.

Table 14. Model 3 environmental variances of five trait combination subsets.

Trait	Analysis 1	Analysis 2	Analysis 3	Analysis 4	Analysis 5	Analysis 6	Analysis 7	Analysis 8	Analysis 9	Analysis 10
Birth Weight	25.569		25.698	25.674			26.293			
Adjusted Weaning Weight	571.627	581.482	587.515	587.538	591.976	581.561	587.558	581.569	581.470	581.464
Adjusted Yearling Weight	1523.992				1660.849	1660.540		1660.110		
Post-weaning Average Daily Gain	0.044				0.044	0.044		0.044		
End of Test Weight	1727.823		1849.748	1848.635			1848.386			
Carcass Weight [a]		715.296	774.182		800.250				715.136	
Marbling Score [a]		0.403	0.404		0.403				0.403	
Longissimus Muscle Area [a]		71.800		72.965		73.400				71.842
12th Rib Fat Thickness [a]		0.075		0.075		0.075				0.075
Carcass Grade [a]							0.278	0.278	0.278	0.278
Cutability [a]							1.783	1.779	1.766	1.167

[a] Analyzed with an age at slaughter covariate.

Table 16. Model 3 heritability estimates of five trait combination subsets.

Trait	Analysis 1	Analysis 2	Analysis 3	Analysis 4	Analysis 5	Analysis 6	Analysis 7	Analysis 8	Analysis 9	Analysis 10
Birth Weight	0.22		0.22	0.22			0.22			
Adjusted Weaning Weight	0.09	0.11	0.10	0.10	0.11	0.11	0.10	0.11	0.11	0.11
Adjusted Yearling Weight	0.17				0.19	0.19		0.19		
Post-weaning Average Daily Gain	0.24				0.20	0.21		0.21		
End of Test Weight	0.16		0.19	0.19			0.18			
Carcass Weight [a]		0.12	0.13		0.14				0.13	
Marbling Score [a]		0.28	0.27		0.27				0.28	
Longissimus Muscle Area [a]		0.29		0.29		0.29				0.28
12th Rib Fat Thickness [a]		0.37		0.37		0.36				0.37
Carcass Grade [a]							0.23	0.23	0.22	0.22
Cutability [a]							0.33	0.32	0.33	0.32

[a] Analyzed with an age at slaughter covariate.

Table 17. Model 3 mean, standard deviation, and range of genetic variance estimates.

Trait	Mean	Standard Deviation	Minimum	Maximum	Range
Birth Weight	1.507	0.0278	1.466	1.528	0.062
Adjusted Weaning Weight	15.804	1.144	12.758	16.597	3.839
Adjusted Yearling Weight	80.182	7.198	69.444	84.350	14.906
Post-weaning Average Daily Gain	0.002	0.00018	0.0024	0.0028	0.0004
End of Test Weight	84.350	9.461	70.189	89.634	19.445
Carcass Weight [a]	25.129	3.058	22.929	29.490	6.561
Marbling Score [a]	0.030	0.00115	0.0288	0.0313	0.0025
Longissimus Muscle Area [a]	5.590	0.109	5.428	5.661	0.233
12th Rib Fat Thickness [a]	0.008	0.00003	0.0075	0.0076	0.0001
Carcass Grade [a]	0.017	0.00059	0.0158	0.0171	0.0013
Cutability [a]	0.157	0.00268	0.154	0.160	0.006

[a] Analyzed with an age at slaughter covariate.

Table 18. Model 3 mean, standard deviation, and range of environmental variance estimates.

Trait	Mean	Standard Deviation	Minimum	Maximum	Range
Birth Weight	25.809	0.328	25.670	26.293	0.623
Adjusted Weaning Weight	583.376	5.591	571.627	591.976	20.349
Adjusted Yearling Weight	1626.374	68.255	1523.992	1660.849	136.857
Post-weaning Average Daily Gain	0.044	0.0003	0.0437	0.0443	0.0006
End of Test Weight	1816.628	60.540	1727.823	1849.748	121.925
Carcass Weight [a]	751.216	42.910	715.136	800.250	85.114
Marbling Score [a]	0.403	0.0003	0.403	0.404	0.001
Longissimus Muscle Area [a]	72.487	0.784	71.800	73.340	1.54
12th Rib Fat Thickness [a]	0.075	0.0001	0.0746	0.0748	0.0002
Carcass Grade [a]	0.278	0.0003	0.278	0.278	0.000
Cutability [a]	1.774	0.0085	1.766	1.783	0.017

[a] Analyzed with an age at slaughter covariate.

Table 19. Model 3 mean, standard deviation, and range of phenotypic variance estimates.

Trait	Mean	Standard Deviation	Minimum	Maximum	Range
Birth Weight	27.169	0.0793	27.054	27.236	0.182
Adjusted Weaning Weight	598.150	5.430	584.384	603.267	18.883
Adjusted Yearling Weight	1714.130	67.471	1593.437	1744.840	151.403
Post-weaning Average Daily Gain	0.047	0.0001	0.0465	0.0467	0.0002
End of Test Weight	1902.515	69.674	1798.012	1938.268	140.256
Carcass Weight [a]	776.344	45.752	738.219	829.738	91.519
Marbling Score [a]	0.433	0.0005	0.432	0.433	0.001
Longissimus Muscle Area [a]	78.064	0.836	77.253	78.960	1.707
12th Rib Fat Thickness [a]	0.082	0.0003	0.0819	0.0826	0.0007
Carcass Grade [a]	0.295	0.0002	0.294	0.295	0.001
Cutability [a]	1.930	0.0086	1.921	1.941	0.02

[a] Analyzed with an age at slaughter covariate.

Table 20. Model 3 mean, standard deviation, and range of heritability estimates.

Trait	Mean[a]	Standard Deviation of the Estimate	Minimum	Maximum	Range
Birth Weight	0.22 ± 0.078	0.0023	0.219	0.224	0.005
Adjusted Weaning Weight	0.11 ± 0.079	0.0075	0.087	0.112	0.025
Adjusted Yearling Weight	0.19 ± 0.081	0.0092	0.174	0.193	0.019
Post-weaning Average Daily Gain	0.21 ± 0.081	0.0167	0.202	0.238	0.036
End of Test Weight	0.18 ± 0.081	0.0140	0.156	0.185	0.029
Carcass Weight[b]	0.13 ± 0.082	0.0088	0.124	0.142	0.018
Marbling Score[b]	0.27 ± 0.081	0.0065	0.266	0.279	0.013
Longissimus Muscle Area[b]	0.29 ± 0.081	0.0050	0.280	0.292	0.018
12th Rib Fat Thickness[b]	0.37 ± 0.080	0.0017	0.364	0.368	0.004
Carcass Grade[b]	0.23 ± 0.081	0.0074	0.216	0.232	0.016
Cutability[b]	0.32 ± 0.081	0.0059	0.320	0.333	0.013

[a] Column contains the mean of the heritability estimate and the mean of the heritability estimate's approximate standard error. There were four heritability estimates for every trait except adjusted weaning weight which had 11 estimates.

[b] Analyzed with an age at slaughter covariate.

Table 20 contains the mean of the heritability estimate and the mean of the heritability estimate's approximate standard error, in addition to the standard deviation of the heritability and range for each trait. Inspection of the standard deviations and ranges in Tables 17, 18, and 19, respectively, indicate the largest deviation of the variance estimates occurred for adjusted yearling weight and end of test weight. A reason for this is there is more genetic variation for this trait within the Canadian Charolais population. Also, greater environmental variation was estimated to exist in these two traits, possibly due to environmental influences which had more time to oppose existing genetic factors. Although there was deviation in the variance estimates, no range of the heritability estimates exceeded the approximate standard errors, which are expected to be underestimated (Swiger et al., 1964).

4.3.1 Heritability Estimates

Average heritability estimates for the traits analyzed are presented in Table 20. The heritability for birth weight from this study was 0.22 ± 0.078. Other studies have reported birth weight heritability to be moderate to highly heritable. This value is lower than the average of 172 estimates by Koots et al. (1994a) of 0.35 for birth weight heritability. However, it is in close agreement with the value reported by Johnston et al. (1992) of 0.25 that was attained from the Canadian Charolais Association's Conception to Consumer program data, and is higher than the estimate of 0.18 found by Veseth et al. et al. (1993) on 736 Hereford bulls.

The average heritability estimate for WW was 0.11 ± 0.079. Previous estimates cited from the literature indicate that WW is a low to moderately heritable trait. Koots et al. (1994a) reported an average heritability value of 0.27 from 239 literature sources. The present study's heritability value is in agreement with other investigations that have shown WW heritability values of 0.09, 0.09, and 0.18, respectively (Arnold et al., 1991; Johnston et al., 1992; Woodward et al., 1992), but is in the low range reported in Table 1.

The heritability value discovered in this analysis for YW was 0.19 ± 0.081. Koots et al. (1994a) after reviewing 154 papers detected YW heritability to be moderately heritable with a mean value of 0.35. This study's results, however, are in agreement with other published results of 0.14, and 0.16, respectively (Arnold et al., 1991; Johnston et al., 1992) and also the 0.25 estimate reported by de Rose (1992) from Charolais data obtained from the Canadian Beef Sire Evaluation Program.

Koots et al. (1994a) analyzed 24 heritability estimates for ADG and reported a mean value of 0.24. Other heritability estimates in the literature indicate that ADG is moderate to highly heritable, with values of 0.13, 0.19, 0.47, and 0.52 (Arnold et al., 1991; Johnston et al., 1992; Veseth et al., 1993; Benyshek, 1981). The results of this analysis indicate a heritability value for ADG of 0.21 ± 0.081, which is within the range of estimates throughout the literature.

The heritability estimate for EOTWT was 0.18 ± 0.081. Other cited heritability estimates for EOTWT in the literature include 0.42, and 0.52 from Veseth et al. (1993) and Benyshek (1981), respectively. Koots et al. (1994a) analyzed twelve EOTWT heritability estimates that had a mean value of 0.37. The EOTWT heritability estimates in the literature suggest that EOTWT is moderate to highly heritable. Therefore, this study yielded a heritability value that was low for this trait, which could be due to reduced variation in the reduced population of sires that possibly were selected for growth traits.

Koots et al. (1994a) reported a mean heritability value of 0.45 from 19 literature sources for hot carcass weight that were estimated at an age constant slaughter basis. Additional references for age constant carcass weight include 0.31, 0.38, 0.41, and 0.43 from Wilson et al. (1993), Veseth et al. (1993), Marshall (1994), and Koch et al. (1982), respectively. This study's heritability of 0.13 ± 0.082, which is below the moderate and high heritability values indicated throughout the literature. The apparent low heritability values for the various growth traits, including age constant carcass weight, may be due to the selected sample of sires used in the Conception to Consumer program, which had a tendency to be growth bulls. Robertson (1977) reported that if selection on the parents is based on the trait on which heritability is being measured then the estimates may be biased downward due to reduced additive genetic variance of the parents.

Heritability values of 0.27 ± 0.081 for MARB were estimated from these data. Koots et al. (1994a) estimated heritability values of 0.37 for age constant marbling score, with the estimate being the mean of 12 estimates. Other heritability values cited throughout the literature for MARB include 0.23, 0.26, 0.31, 0.31, and 0.35 (Woodward et al., 1992; Wilson et al., 1993; Cundiff et al., 1971; Veseth et al., 1993; Marshall, 1994), respectively. The referenced heritability estimates for MARB indicate that the trait is moderate to highly heritable, and these data show a similar conclusion.

This study estimated a heritability value of 0.29 ± 0.081 for LMA. Other heritability values for LMA in the literature include 0.32, 0.37, 0.40, and 0.41 from Wilson et al. (1993), Marshall (1994), Benyshek (1981), and Cundiff et al. (1971), respectively. Koots et al. (1994a) found 16 LMA estimates to average 0.43. The literature values suggest that LMA is a moderate to highly heritable trait, which would indicate that the present study's LMA estimate is at the low range of cited estimates.

Heritability values reported in the literature for FAT include 0.26, 0.41, 0.44, 0.49, and 0.52 (Veseth et al., 1993; Koch et al., 1982; Marshall, 1994; Arnold et al., 1991; and Benyshek, 1981), respectively. Koots et al. (1994a) reported 26 literature references for FAT that had a mean heritability value of 0.43. The current study's FAT heritability value of 0.37 ± 0.080 indicates that the FAT heritability value fits into the low range of reported heritability values. The age constant 12th rib fat thickness indicates differences in the rate of fat deposition, which is affected by the age that an animal reaches physiological maturity. Carcass weight constant 12th rib fat thickness predicts differences in the volume of fat thickness, thereby indicating at what size physiological maturity is reached.

The present study yielded a heritability estimate for CARCGR of 0.23 ± 0.081. There were no references detected in the literature for carcass grade under the Canadian grading system, in part because the carcass grading standards were revamped in 1987, and also because many of the major component traits for carcass grade have been previously analyzed.

Koots et al. (1994a) reported 12 heritability estimates for CUT to have a mean value of 0.41. Additional literature estimates include 0.18, 0.28, 0.36, and 0.49 from

Woodward et al. (1992), Cundiff et al. (1971), Marshall (1994) and Benyshek (1981), respectively. These literature estimates indicate a considerable range for heritability estimates, although they indicate for the most part that CUT is moderate to highly heritable. The present research resulted in a heritability value of 0.32 ± 0.081 for CUT. This result appears to be well within the range of reported values for CUT.

The deviations associated with the variance estimates, in addition to relatively low heritability estimates compared to literature values, certainly have positive implications. The Charolais bulls used in this study were a group selected for high growth, which the current data indicate variability exists within these growth traits. In a breeding program, Charolais breeders certainly have more opportunity to select breeding stock at the extremes of their given traits of interest which will allow for more rapid improvement. If no variation existed within the population, no progress can be made, as breeding stock would produce offspring that exhibit the same performance as the parents.

These data suggest that the growth and performance traits of birth weight, adjusted weaning weight, adjusted yearling weight, post-weaning average daily gain, end of test weight, and even carcass weight, are low to moderately heritable. Carcass traits analyzed including marbling score, longissimus muscle area, 12th rib fat thickness, carcass grade, and cutability were moderately heritable. Higher heritability values allow breeders to make more accurate decisions when selection occurs using estimates of genetic merit of livestock. Lower heritability values indicate more progress might be made for a trait through changes in the animal's environment.

Table 21.

Model 3 average genetic and environmental correlations for growth traits [a, b].

	BW	WW	YW	ADG	EOTWT
Birth Weight	**0.22**	0.40	0.32	0.18	0.24
Adjusted Weaning Weight	0.34	**0.11**	0.73	0.34	0.76
Adjusted Yearling Weight	0.22	0.67	**0.19**	0.83	0.83
Post-weaning Average Daily Gain	0.14	0.19	0.61	**0.21**	0.94
End Of Test Weight	0.34	0.64	0.58	0.39	**0.18**

[a] Average genetic correlations above the diagonal, average environmental correlations below the diagonal, heritabilities on the diagonal.

[b] BW = Birth Weight; WW = Adjusted Weaning Weight; YW = Adjusted Yearling Weight; ADG = Post-weaning Average Daily Gain; EOTWT = End of Test Weight.

Table 22.
Model 3 average genetic and environmental correlations for carcass traits [a, b,c].

	CARCWT	MARB	LMA	FAT	CARCGR	CUT
Carcass Weight	**0.13**	-0.19	0.18	0.17	0.17	0.01
Marbling Score	0.05	**0.27**	0.16	-0.32	-0.07	0.34
Longissimus Muscle Area	0.53	0.11	**0.29**	-0.24	-0.19	0.85
12th Rib Fat Thickness	0.06	-0.16	-0.18	**0.37**	0.87	-0.67
Carcass Grade	-0.04	-0.07	-0.17	0.63	**0.23**	-0.60
Cutability	0.34	0.16	0.82	-0.62	-0.45	**0.32**

[a] Average genetic correlations above the diagonal, average environmental correlations below the diagonal, heritabilities on the diagonal.

[b] CARCWT = Carcass Weight; MARB = Marbling Score; LMA = Longissimus Muscle Area; FAT = 12th Rib Fat Thickness; CARCGR = Carcass Grade; CUT = Cutability.

[c] Carcass traits were analyzed with an age at slaughter covariate.

Table 23. Model 3 average genetic and environmental correlations between growth and carcass traits [a, b, c].

	BW	WW	YW	ADG	EOTWT	CARCWT	MARB	LMA	FAT	CARCGR	CUT
Birth Weight	**0.22**					0.27	0.17	0.22	-0.04	-0.03	0.21
Adjusted Weaning Weight		**0.11**				0.65	-0.11	0.09	0.31	0.31	-0.09
Adjusted Yearling Weight			**0.19**			0.90	-0.16	0.10	0.26	0.23	-0.08
Post-weaning Average Daily Gain				**0.21**		0.83	-0.08	0.09	0.15	0.15	-0.06
End Of Test Weight					**0.18**	0.85	-0.26	0.11	0.28	0.24	-0.09
Carcass Weight	0.44	0.69	0.90	0.58	0.86	**0.13**					
Marbling Score	0.08	0.05	0.04	0.03	0.04		**0.27**				
Longissimus Muscle Area	0.24	0.39	0.44	0.24	0.42			**0.29**			
12th Rib Fat Thickness	-0.13	0.01	0.08	0.07	0.08				**0.37**		
Carcass Grade	-0.10	-0.04	-0.01	0.01	-0.01					**0.23**	
Cutability	0.26	0.26	0.27	0.14	0.25						**0.32**

[a] Average genetic correlations above the diagonal, average environmental correlations below the diagonal, heritabilities on the diagonal.

[b] BW = Birth Weight; WW = Adjusted Weaning Weight; YW = Adjusted Yearling Weight; ADG = Post-weaning Average Daily Gain; EOTWT = End of Test Weight; CARCWT = Carcass Weight; MARB = Marbling Score; LMA = Longissimus Muscle Area; FAT = 12th Rib Fat Thickness; CARCGR = Carcass Grade; CUT = Cutability.

[c] Carcass traits were analyzed with an age at slaughter covariate.

4.3.2 Genetic Correlations

With highly positive genetic correlations between any given traits X and Y, bulls that excel in trait X are also expected to produce progeny that excel in trait Y. Likewise, if the genetic correlation is highly negative between traits X and Y, bulls that excel in trait X are expected to sire offspring that are inferior for trait Y, respectively. Therefore, genetic correlations provide an indication of response due to selection to producers when heritability values are similar and selection intensity is held constant. The average genetic correlations among growth traits, among carcass traits, and among growth and carcass traits are included in Tables 21, 22, and 23, respectively.

This study's genetic correlations between BW and WW and BW and YW were 0.40 and 0.32, respectively. Woodward et al. (1992) analyzed data from the American Simmental Association, in addition to other studies in the literature from Veseth et al. (1993); and Koots et al. (1994b) reported genetic correlations between BW and WW of 0.33, 0.54, and 0.47, respectively. Koots et al. (1994b) provided a similar mean genetic correlation from 37 sources between BW and YW of 0.48. The current study is in agreement with the published results, with only a minor decrease in magnitude for genetic correlation between these trait combinations.

Koots et al. (1994b) reported 66 genetic correlation estimates between WW and YW, in addition to WW and ADG to have a mean value of 0.78, and 0.39, respectively. This study detected a genetic correlation between WW and YW of 0.73, along with a genetic correlation between WW and ADG of 0.34, respectively. This study agrees with results published in that selection for increased WW will result in a highly correlated response in YW, while still achieving a moderate increase in ADG. The genetic correlations between the post-weaning growth traits of YW, ADG, and EOTWT are all high (≥ 0.83) and in agreement with the magnitudes from results published by Koch et al. (1982), Veseth et al. (1993), and Koots et al. (1994b).

A genetic correlation between MARB and LMA of 0.16 was discovered from these data. Selection for improved marbling should yield lighter muscled cattle. These results, which have the highest marbling score numerically the lowest, are in agreement with the respective reported values of -0.12, -0.14, -0.14, and -0.23 (Brackelsberg et al., 1971; Koch et al., 1982; Marshall, 1994; Koots et al., 1994b), but yet do differ from the results of Van Vleck et al. (1992) and also Veseth et al. (1993) who reported genetic correlations of -0.40 and 0. 51 between MARB and LMA.

This study additionally found the genetic correlations between MARB in combination with FAT and also CUT respectively of -0.32 and 0.34. Marshall (1994) and Koots et al. (1994b) report similar genetic correlations between MARB and FAT of 0.37 and 0.36, respectively. Additionally, these same published results indicated a genetic correlation between MARB and CUT of -0.24 and -0.54, respectively. This suggests that selection for improved marbling scores will result in a moderately correlated increase in FAT and a decrease in CUT.

A genetic correlation of -0.60 was found between CARCGR and CUT. As is expected in the Canadian meat grading system, an improvement in carcass grade will result in a highly correlated increase in cutability. Furthermore, a genetic correlation between LMA and FAT along with LMA and CARCGR was -0.24 and -0.19, respectively. The genetic correlation between LMA and FAT is intermediate to the published results of -0.06, -0.08, -0.09, -0.37, and -0.44, respectively (Wilson et al., 1993; Koots et al., 1994b; Brackelsberg et al., 1971; Arnold et al., 1991; Koch et al., 1982). These results indicate that selection for heavier muscled cattle should result in a low to moderate improvement in fat thickness and also carcass grade. Furthermore, this study's genetic correlation between LMA and CUT is 0.85. Marshall (1994) reported a correlation of 0.53, and Koots et al. (1994b) found three papers that had a mean genetic correlation for LMA and CUT of 0.26. Moreover, the genetic correlation between FAT and CUT was -0.67. This high correlation is intermediate to the genetic correlations reported by Cundiff et al. (1971) and Koots et al. (1994b) of -0.74 and -0.33, respectively. In addition, the genetic correlation between FAT and CARCGR was discovered to be 0.87. These high genetic correlations between CUT and LMA along with FAT, in addition to CARCGR and FAT can be expected, as they are component traits of CARCGR.

Genetic correlations between BW and CARCWT, and BW and LMA of 0.27 and 0.22, respectively. When analyzing the genetic correlation between BW and CARCWT, Koch et al. (1982) and Veseth et al. (1993) detail correlations of 0.60 and 0.11, respectively. The same authors also reported genetic correlations between BW and LMA of 0.31 and 0.57, respectively. The results of this paper are in agreement with these cited estimates that the genetic correlations between BW and CARCWT, and BW and LMA are positive and moderately correlated, although this study's results are slightly lower in magnitude. A high correlation of 0.76 was detected between WW and CARCWT. Other genetic correlations found in the literature between WW and CARCWT include 0.13, 0.82, and 0.84, respectively (Arnold et al., 1991; Marshall, 1994; Koots et al., 1994b). This study agrees with results published in such that selection for increased WW will result in a highly correlated response in CARCWT.

The genetic correlation between BW and MARB was found to be 0.17, while a genetic correlation of -0.04 was found between BW and FAT. Koch et al. (1982) reported a genetic correlation between BW and marbling score of 0.31, while Woodward et al. (1992) and Veseth et al. (1993) reported correlations of the same trait combination of 0.05, and -0.18, respectively. As the marbling score scale is reversed in the present study, these results are extremely close to the correlation found by Veseth et al. (1993), such that selection for lower birth weights will result in increased marbling. The genetic correlation between BW and FAT found in this study of -0.04, although it has the same sign as the -0.27 correlation found by Koch et al. (1982), is lower in magnitude, and would indicate that selection for reduced birth weights will yield only a low correlated increase in FAT.

The genetic correlations between the post-weaning growth traits of YW, ADG, EOTWT, and also CARCWT are all high (≥ 0.83) and in agreement with the magnitudes from results published by Koch et al. (1982), Veseth et al. (1993), and Koots et al. (1994b). These traits (YW, ADG, EOTWT, CARCWT) also have very similar genetic correlations with the carcass traits MARB (range = -0.08 to -0.26), LMA (range = 0.09 to 0.18), FAT (range = 0.15 to 0.28), CARCGR (range = 0.15 to 0.24), and CUT (range = -0.09 to 0.01). Koch et al. (1992) was in agreement with these ranges where applicable, but reported higher correlations for the combinations with LMA (range = 0.34

to 0.44). Arnold et al. (1991) had mutual results with the exception of ADG x MARB (0.54), CARCWT x MARB (0.33), and CARCWT x FAT (0.36). Additionally, Arnold et al. (1991) also found negative genetic correlations for YW and ADG in combination with LMA, -0.06, -0.18, respectively. The results of Marshall (1994) and also Koots et al. (1994b) support these ranges in most instances, with the exception of the combinations with LMA and CUT, which had more extreme genetic correlations.

4.3.3 Environmental Correlations

Environmental correlation estimates are presented with the genetic correlation estimates between growth traits analyzed in Model 3 in Table 20. Birth weight yielded a low environmental correlation to post-weaning average daily gain (0.14), but was moderately correlated to the other growth traits with a correlation of 0.34 to adjusted weaning weight and also end of test weight. Adjusted weaning weight possessed a low environmental correlation to post-weaning average daily gain of 0.19. However, adjusted weaning weight, adjusted yearling weight, and also end of test weight all had high environmental correlations of 0.67, 0.64, and 0.58. This suggests that environmental influences, which include feedlot conditions and diet, tends to impact these traits so that cattle that had high adjusted weaning weights tended to also have high adjusted yearling weights and end of test weights.

Environmental correlations between carcass traits are included in Table 22. Carcass weight had a high environmental correlation to longissimus muscle area, but a low environmental correlation to other carcass traits. The -0.04 environmental correlation between carcass weight and carcass grade is desirable, which due to the carcass grade scale indicates that cattle that had heavier carcass weights also possessed advantageous carcass grades. Marbling score had only low environmental correlations to other carcass traits; but yet as marbling score goes down numerically, environmental influence yields a correlated increase in 12th rib fat thickness (-0.16 environmental correlation). There was a high environmental correlation between longissimus muscle area and cutability (0.82). Moreover, carcass grade had a medium environmental correlation to cutability as well as a high positive environmental correlation to 12th rib fat thickness.

Environmental correlations between the growth and carcass traits are included in Table 24. Carcass grade, 12th rib fat thickness, and marbling score all had low environmental correlations to every growth trait modeled. Cutability and also longissimus muscle area were moderately environmentally correlated to growth traits, but carcass weight had high environmental correlations to growth traits.

4.3.4 Phenotypic Correlations

Phenotypic correlations are the result of the combination of effects from environmental variation and also the genetic variation. The phenotypic correlation formula can be shown as (Searle, 1951):

$$r_p = r_g(h_1h_2)^{.5} + r_e[(1-h_1)(1-h_2)]^{.5}$$

where:

r_p is the phenotypic correlation,

r_g is the genetic correlation,

r_e is the environmental correlation,

h_1 is the heritability of trait one, and

h_2 is the heritability of trait two.

If the ratio of the environmental correlation to the genetic correlation exceeds the ratio $[1-(h_1h_2)^{.5}]/\ [(1-h_1)(1-h_2)]^{.5}$, then the phenotypic correlation exceeds the genetic correlation. When this occurs, the phenotypic correlation will then follow the sign of the environmental correlation. This discussion serves to show the magnitude that lowly heritable traits have on influencing phenotypic correlations. If the discussed traits one and two possess high heritabilities, then the effect of environmental correlation is reduced, as the denominator of this ratio is reduced. But when trait one and trait two heritabilities are low, the denominator of the ratio is increased, and the environmental correlation is multiplied by a larger value in the phenotypic correlation equation.

Phenotypic correlations between the growth traits analyzed in Model 3 are presented in Table 24. Birth weight had only low to moderate phenotypic correlations to other growth traits. Adjusted weaning weight, adjusted yearling weight, and also end of test weight had high phenotypic correlations amongst each trait. This suggests that cattle that have high adjusted weaning weights also tended to have high adjusted yearling and end of test weights. These results are in general agreement with the estimates cited in the literature. Post-weaning average daily gain had a high phenotypic correlation of 0.67 to adjusted yearling weight, but had a low phenotypic correlation to both birth weight and also adjusted weaning weight.

Phenotypic correlations between carcass traits are included in Table 25. Carcass weight had minimal phenotypic correlations to other carcass traits, with the exception of cutability, and also longissimus muscle area, which are moderate and highly phenotypically correlated, respectively. Cundiff et al. (1971) reported a phenotypic correlation between carcass weight and cutability of -0.44 on British breed steers, while Koots et al. (1994b) found three phenotypic correlations to have a mean of -0.03. These literature values differ from the 0.34 phenotypic correlation found in this study.

Carcass weight expressed a genetic correlation to marbling score of -0.19, but only a correlation of 0.05 and 0.04 for environmental and phenotypic correlations, respectively. This would indicate that selection for carcass weight using breeding values would result in more marbling, but the environmental effects that cause carcass weight to increase also cause less marbling. Marbling score possessed a moderately negative genetic correlation to 12th rib fat thickness (-0.32), yet only expressed a phenotypic correlation of -0.17. Similar results occurred between marbling score and cutability, indicating more desirable results should be achieved through selection using breeding values. This study analyzed a phenotypic correlation between cutability and longissimus muscle area in addition to cutability and 12th rib fat thickness of 0.82 and -0.62, respectively. These values are higher than the cited estimates of 0.45 and -0.36 reported by Marshall (1994), and Cundiff et al. (1971), respectively.

Phenotypic correlations between the growth and carcass traits are included in Table 26. Carcass weight had high phenotypic correlations to all growth traits, in addition to the results of this study being greater in magnitude than the average correlations of carcass weight to growth traits listed in Table 7. Nevertheless, marbling score, 12th rib fat thickness, and carcass grade all had low phenotypic correlations to growth traits. If producers use breeding values to select for improved marbling, they should achieve desirable results in correlated growth traits with the exception of birth weight. However, the importance of using breeding values in selection is apparent as the phenotypic correlations between marbling score and growth traits causes antagonistic responses. These same results were concluded by Koots et al. (1994b) in their mass review of published estimates. Longissimus muscle area possessed moderate correlations to all growth traits, as was expected by the literature phenotypic correlations.

When producers place no genetic selection either on carcass grade or cutability, they will achieve desirable responses in correlated growth traits due to favorable environmental influences. However, if breeders select for either carcass grade or cutability on genetic merit, they should observe antagonistic results in correlated growth traits. These correlations of antagonistic traits are important for breeders to note, so they can identify genetic sources that do not follow these results, therefore making simultaneous improvement in both traits.

4.4 Model 4 Genetic Parameters

A fourth analysis was run to look at the variation in marbling score, longissimus muscle area, and 12th rib fat thickness whole holding carcass weight constant to observe differences in marbling score, longissimus muscle area, and 12th rib fat thickness as proportions of the carcass (Cundiff et al., 1971).

4.4.1 Heritability Estimates

Model 4 heritability estimates are presented in Table 27, in addition to the Model 4 variance components. Koots et al. (1994a) estimated heritability values of 0.37 for carcass weight constant marbling score, with the estimate being the mean of four estimates. Heritability values of 0.28 ± 0.081 for carcass weight constant marbling score (CMARB) were estimated from these data. Literature estimates for carcass weight constant marbling score heritability values include 0.28, 0.33, and 0.73, respectively, from Veseth et al. (1993), Cundiff et al. (1971), and Brackelsberg et al. (1971). The referenced heritability estimates for CMARB indicate that the trait is moderate to highly heritable, and this study's results show a likewise conclusion.

This study estimated a heritability value of 0.38 ± 0.080 for carcass weight constant longissimus muscle area (CLMA). Heritability estimates from the literature for CLMA heritability values include 0.32 and 0.40. Koots et al. (1994a) found 15 heritability values for CLMA to average 0.41. The literature values suggest that CLMA is a

Table 24. Model 3 average phenotypic correlations for growth traits [a].

Trait	BW	WW	YW	ADG	EOTWT
Birth Weight					
Adjusted Weaning Weight	0.34				
Adjusted Yearling Weight	0.22	0.67			
Post-weaning Average Daily Gain	0.14	0.20	0.62		
End Of Test Weight	0.33	0.64	0.59	0.41	

[a] BW = Birth Weight; WW = Adjusted Weaning Weight; YW = Adjusted Yearling Weight; ADG = Post-weaning Average Daily Gain; EOTWT = End of Test Weight.

Table 25. Model 3 average phenotypic correlations for carcass traits [a,b].

Trait	CARCWT	MARB	LMA	FAT	CARCGR	CUT
Carcass Weight						
Marbling Score	0.04					
Longissimus Muscle Area	0.51	0.11				
12th Rib Fat Thickness	0.07	-0.17	-0.19			
Carcass Grade	-0.03	-0.07	-0.17	0.64		
Cutability	0.32	0.17	0.82	-0.62	-0.46	

[a] CARCWT = Carcass Weight; MARB = Marbling Score; LMA = Longissimus Muscle Area; FAT = 12th Rib Fat Thickness; CARCGR = Carcass Grade; CUT = Cutability.

[b] Carcass traits were analyzed with an age at slaughter covariate.

Table 26.

Model 3 average phenotypic correlations between growth and carcass traits [a,b].

Trait	BW	WW	YW	ADG	EOTWT
Carcass Weight	0.43	0.69	0.90	0.59	0.86
Marbling Score	0.08	0.04	0.03	0.02	0.03
Longissimus Muscle Area	0.24	0.38	0.42	0.23	0.40
12th Rib Fat Thickness	-0.12	0.03	0.09	0.07	0.09
Carcass Grade	-0.10	-0.02	0.00	0.01	0.00
Cutability	0.25	0.25	0.25	0.13	0.23

[a] BW = Birth Weight; WW = Adjusted Weaning Weight; YW = Adjusted Yearling Weight; ADG = Post-weaning Average Daily Gain; EOTWT = End of Test Weight.

[b] Carcass traits were analyzed with an age at slaughter covariate.

Table 27. Model 4 heritability, genetic variance, environmental variance, and phenotypic variance estimates [a].

Trait	Heritability and Approximate Standard Errors	Genetic Variance	Environmental Variance	Phenotypic Variance
Adjusted Weaning Weight	0.11 ± 0.079	16.571	581.478	598.049
Marbling Score	0.28 ± 0.081	0.030	0.405	0.435
Longissimus Muscle Area	0.38 ± 0.081	5.519	51.885	57.404
12th Rib Fat Thickness	0.36 ± 0.080	0.007	0.074	0.082

[a] Carcass traits had a carcass weight covariate.

Table 28. Model 4 genetic, environmental, and phenotypic correlations [a, b].

Trait	WW	MARB	LMA	FAT
Adjusted Weaning Weight	**0.11**	-0.11	-0.11	0.28
Marbling Score	0.07	**0.28**	0.22	-0.29
	0.07			
Longissimus Muscle Area	0.08	0.01	**0.38**	-0.29
	0.08	0.10		
12th Rib Fat Thickness	-0.04	-0.16	-0.26	**0.36**
	-0.04	-0.16	-0.26	

[a] Genetic correlations above diagonal, environmental correlations above the phenotypic correlations below diagonal, heritability on diagonal.

[b] WW = Adjusted Weaning Weight; MARB = Marbling Score; LMA = Longissimus Muscle Area; FAT = 12th Rib Fat Thickness.

moderate to highly heritable trait, and this study's CLMA heritability estimate is supported by literature estimates.

Koots et al. (1994a) analyzed 15 heritability estimates for carcass weight constant 12th rib fat thickness (CFAT) and reported a mean value of 0.44. A review of the literature revealed CFAT heritability of 0.43 and 0.53 from Brackelsberg et al. (1971), and Cundiff et al. (1971), respectively. The current study's CFAT heritability value of 0.36 ± 0.080 indicates the CFAT heritability estimate is below the literature CFAT estimates.

4.4.2 Correlation Estimates

Genetic, environmental, and phenotypic correlations for Model 4 that used a carcass weight covariate are included in Table 28. As was expected from the results of Benyshek (1981), the genetic and phenotypic correlations between the trait combinations that had either slaughter age or carcass weight modeled as a covariate did yield quite similar results. The lone exception was the genetic and phenotypic correlation between WW and LMA. The genetic correlation between WW and age constant longissimus muscle area versus WW and carcass weight constant longissimus muscle area is 0.09 and -0.11, respectively. Additionally, the phenotypic correlation between WW and age constant longissimus muscle area versus WW and carcass weight constant longissimus muscle area is 0.38 and 0.08, respectively. Moreover, the heritability values for age constant longissimus muscle area and carcass weight constant longissimus muscle area was 0.29 and 0.38, respectively. The differences can be explained due to the residual variance being larger in these data when slaughter age is held constant versus a carcass weight constant.

5. CONCLUSIONS

The results of this study indicate that there was no detectable selection bias in these data, as the multiple trait heritability values for both growth and carcass traits closely correspond to those achieved from the single trait analysis. Additionally, this study concluded that heritability values for such growth traits such as weaning weight, yearling weight, post-weaning average daily gain, and end of test weight are low to moderately heritable. When selection pressure is placed upon these traits, some improvement will result from the selection. The data indicated moderate heritability values for such carcass traits as marbling score, longissimus muscle area, 12th rib fat thickness, carcass grade, and cutability. These results suggest that a moderate response to selection can be achieved when selecting for these carcass traits, and also that more response to selection can be achieved from selecting for these carcass traits than for selecting for the growth traits analyzed in this study.

Additionally, this study indicates that selection for faster growing, heavier muscled cattle can be accomplished but not without antagonistic results. Yearling weight had both high genetic and phenotypic correlations to other growth traits such as weaning weight, post-weaning average daily gain, and end of test weight. Moreover, yearling weight was highly correlated to carcass weight and had a -0.16 correlation to marbling score, but unfortunately the current data indicated a genetic correlation of 0.26 between yearling weight and fat thickness in addition to a negative genetic correlation of yearling weight to cutability. Marbling score had a numerically inverse genetic correlation to end of test weight, however, phenotypically was positively correlated to end of test weight. An additional antagonistic environmental correlation was concluded from the correlation of cutability and yearling weight, which had a positive phenotypic correlation of 0.25 but a negative genetic correlation of -0.08. Nevertheless, selection for faster growing cattle will result in heavier birth weights, along with lower cutability cattle with more fat. When Canadian Charolais breeders select for heavier muscled, higher cutability cattle, they will again see a moderate increase in birth weights in addition to a low to moderate decrease in marbling. Therefore, producers must identify seedstock which do not follow these genetic antagonisms to be able to produce beef that is profitable and fits into the industry's specifications to achieve consumer acceptance.

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