

**GENETIC ANALYSIS OF ASSOCIATION AMONG JUVENILE GROWTH
AND FEMALE REPRODUCTIVE TRAITS IN CANADIAN ANGUS CATTLE**

A Thesis Presented to

The Faculty of Graduate Studies of
The University of Manitoba

By

Drona Prakash Rasali

In Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

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FACULTY OF GRADUATE STUDIES

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This work is dedicated to:

my parents,

Mr. Dhan Bahadur Rasali

and

Mrs. Sumitra Devi Rasali

GENETIC ANALYSIS OF ASSOCIATION AMONG JUVENILE GROWTH AND FEMALE REPRODUCTIVE TRAITS IN CANADIAN ANGUS CATTLE

ABSTRACT

The purpose of this research was to determine the genetic association between juvenile growth and female reproductive efficiency traits in beef cattle. Analyses of three data sets of calving records from 1984 to 2001 in five Angus herds were based on REML type mixed model methodology using a four trait model ($n=6,886$ animals in the pedigree, Study I) for birth weight (BW), weaning weight (WW), yearling weight (YW) and first calving date (CD1), a five trait model ($n=7,171$, Study II) for BW, WW, YW, calving date (CD) and calving interval (CI), and single trait models ($n=6,864$, Study III) for BW, WW and YW and stayability of cows to three years of age (Stay3, a binomial trait).

The results from four- and five trait animal models revealed that the estimates of direct heritability (h^2) for BW, WW and YW were ranged from 0.44 to 0.80 (Study I and II), and that for WW and YW in the Study III were relatively lower. The maternal heritability (m^2) estimates for BW, WW and YW in all three studies were between 0.10 and 0.25. The h^2 estimates of CD1 (Study I), CD and CI (Study II) were 0.16, 0.25 and 0.10, respectively. The estimates of genetic correlations, both direct (r_a) and maternal (r_m), among growth traits were positive and of a moderate to high magnitude (Study I and II). Direct-maternal genetic correlation (r_{am}) of each of the juvenile growth traits was negative indicating the antagonistic genetic relationship between animal's genetic potential for the trait and that for the mothering ability for the same trait (Study I and II). The r_a estimate

between CD1 and WW was 0.27, indicating their unfavorable genetic association, while the corresponding estimates between BW and CD1, and between YW and CD1 were negligible. The r_a estimates of BW, WW and YW with CD were -0.19, -0.31 and -0.21, respectively, and those with CI were -0.23, -0.38 and -0.65, respectively, indicating their favorable genetic relationships. The r_{am} estimates of trait CD with maternal genetic effects for BW, WW and YW were -0.02, -0.18 and -0.36, respectively. In contrast, the r_{am} estimates of CI with maternal genetic effects for BW and WW were zero and 0.07, respectively. Corresponding estimate between CI and maternal genetic effects for YW was 0.51, and possibly not consequential due to low heritabilities of both the traits. The results from the analyses of genetic trends (Study II) suggested that multiple traits played a role in the selection process. The culling rate of cows in their herds as indicated by their hazard function was highest at three years of age, and heritability for Stay3 was 0.38, demonstrating merit in genetic improvement. However, the EBVs for Stay3 were not significantly correlated with the direct or maternal EBVs for any of the three growth traits studied, except that maternal EBVs for WW and direct EBVs for Stay3 were positively correlated ($P < 0.10$).

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LIST OF ABBREVIATIONS

ΔG	Annual average genetic gain
%	Percent
σ^2_a	Direct additive genetic variance
σ_{am}	Direct-maternal covariance
σ^2_m	Maternal additive genetic variance
σ^2_p	Phenotypic variance
AMR	Animal, maternal and residual effects in the animal model
AMRC	Animal, maternal, residual and permanent environmental effects in the animal model
ANOVA	Analysis of Variance
AOD	Age of dam
BIF	Beef Improvement Federation
BLUP	Best Linear Unbiased Prediction
BW	Birth weight (BW_d for direct genetic effects; BW_m for maternal genetic effects)
c^2_p	Permanent environmental effects expressed as variance ratio
c^2_{pm}	Permanent maternal environmental effects expressed as variance ratio
CD	Calving date
CD1	First calving date
CI	Calving interval

CV	Coefficient of variation
CPUs	Central Processing Units
d	day
DFREML	Derivative Free Restricted Maximum Likelihood
e²	Residual permanent environmental effects expressed as variance ratio
EBV	Estimated breeding value
GLM	Generalized Linear Model
GS	Gibbs sampling
h²	Direct heritability
hr	Hour(s)
H-W	Heidelberger and Welch
HE	Hereford
HPC	High performance computing
kg	Kilogram(s)
lb	Pound
LSM	Least squares mean
m²	Maternal heritability
MCMC	Monte-Carlo Markov Chain
MHz	Megahertz
ML	Maximum likelihood
MTDFREML	Multiple-Trait Derivative Free Restricted Maximum Likelihood

MTGSAM	Multiple-Trait Gibbs Sampling to Animal Models
PDF	Probability density function
PEV	Prediction error of variance
PWG	Pre-weaning gain in body weight
r_{am}	Direct - maternal genetic correlation
r_e	Residual environmental correlation
r_{TI}	Correlation between the true and predicted breeding value (Accuracy of prediction)
REML	Restricted Maximum Likelihood
r_g, r_a	Direct or additive genetic correlation
r_m	Maternal genetic correlation
r_{pm}	Maternal environmental correlation
SAS	Statistical Analysis System
SD	Standard deviation
SDF	Survival density function
SE	Standard error
SEP	Standard error of prediction
Stay3	Stayability of cow to 3 year olds given the opportunity to calve two times
SY	A synthetic population
WG	Post-weaning gain in body weight
WW	Weaning weight (WW_d for direct genetic effects; WW_m for

maternal genetic effects)

YG Yearling gain in body weight

YW Yearling weight (YW_d for direct genetic effects; YW_m for maternal genetic effects)

1. GENERAL INTRODUCTION

Significantly large genetic progress has been achieved by the turn of the last century in beef cattle especially in terms of weight gain. A recent report of Canadian Angus Association (Wilson and Hassen 2003) showed that the breed's average genetic gain in weaning and yearling weights have been accelerated since 1980, possibly, as a result of the selection programs that focused mainly on growth performance from birth to slaughter (Meyer et al. 1991; Swalve 1993). In Canada for the last three decades, the selection programs have been based on predicted differences of beef bulls for weaning weight and yearling weight (Trus and Wilton 1988; Miller 2002).

There has been less emphasis placed on reproductive efficiency in the selection programs of beef cattle regardless of the economic importance of the traits that may be five times more than that of growth traits in breeding herds (Trenkle and Willham 1977; Bruns 1994), and at least twice as high as the latter in commercial cow-calf production systems (Moser 1995). The reproductive efficiency of cows is a critically important aspect of the beef industry (Bourdon and Brinks 1983; Rege 1985), due to the high cost of heifer replacement to be recovered from cows before their culling. An analysis of various factors contributing to production losses in the United States showed that cows not conceiving by the end of breeding season accounted for the greatest calf crop loss (14.6%), exceeding total calf crop loss (12.7%) from all other post-breeding factors combined (Bellows and Short 1994).

There exists a special circumstance in beef cattle production systems posed by the practice of a time-limited window of their breeding season. As a result, calving interval,

the usually recorded trait of female reproduction, turns out to be rather a bias measure of female reproduction. Calving date or its analogous trait days to calving may be a suitable indicator of reproductive efficiency in beef cows. A trait such as the stayability of cows to their certain critical age is directly related to their reproductive efficiency or fertility in the herds (Formigoni et al. 2002), and is considered an economically relevant trait (Golden et al. 2000) due to high cost of early replacement of culled cows with new heifers.

Various traits of juvenile growth and those of subsequent reproductive phases in the life of beef cattle are important components of their production. Both these components have direct bearing on the profitability of the cow-calf operation. Improvement of both the components simultaneously to their potential selecting for multiple traits is a desirable proposition for ensuring response in the aggregate genotype. The explanation for this constraint could be given as follows: Firstly, the growth traits are more heritable traits than the reproductive traits (Swalve 1993; Koots et al. 1994a). Secondly, an undesirable side effect of selection for high growth performance is that the genetic improvement in reproduction may be compromised because a high proportion of nutrients consumed by the fast-growing animal may be allocated to growth and not reproduction (Rauw et al. 1998).

There have been comprehensive reviews describing direct and maternal genetic parameters for body weights at birth and subsequent ages (Woldehawariat et al. 1977; Mohiuddin 1993; Davis 1993; Koots et al. 1994a; Koots et al. 1994b; Rust et al. 1998). On the other hand, fewer studies on genetic parameters of female reproductive efficiency have been published (Smith et al. 1989b; Rege 1985). Information on the genetic

relationships between growth and female reproduction in beef cattle is negligible.

Possibly, simultaneous evaluation of the growth performance and reproductive efficiency may ensure favorable responses in reproductive traits from the selection programs that emphasize growth performance traits.

Genetic analyses of growth performance and reproductive efficiency, using either univariate or multiple trait models, require incorporation of several fixed and random effects rendering the computational aspects highly demanding. Estimation of genetic (co)variances based on mixed model for restricted maximum likelihood methodology (Henderson 1990) may require a major effort. Mostert et al. (1998) and Mwansa et al. (2002) have shown that genetic evaluation of multiple traits (up to five or six) is computationally feasible.

The present research was undertaken to evaluate juvenile growth performance and female reproductive efficiency simultaneously, utilizing the methodological and computational strategies that have been feasible more recently.

2. REVIEW OF LITERATURE

Growth and reproduction are fundamental attributes of an animal's life, necessary for its own perpetuation. There may exist an inherent competition between allocation of resources for these two types of traits. The 'Resource Allocation Theory' predicts that animals selected for one trait may compromise other attributes (Rauw et al. 1998). In beef cattle production, it is widely accepted that reproductive efficiency is a more important component than growth (Wiltbank, 1994), while producers are interested in growth of the animal as it can be easily appreciated and quantified (Lawrence and Fowler 1997). One of the challenges is in achieving a balance between the two characteristics for their genetic improvement. In order to achieve this balance, genetic evaluation procedures encompassing growth and reproduction are a prerequisite.

2.1. GROWTH TRAITS IN BEEF CATTLE

Animal growth, in its simplest definition, is an increase in body size either through hyperplasia or hypertrophy. For meat producing animals such as beef cattle, the primary interest lies in increasing the number of muscle and fat cells available for protein and fat accretion, respectively (Beitz 1985) to increase the body size. Body weights that result from protein and fat accretion are indicators of growth capacity in beef cattle (Golden et al. 2000), and measure the growth performance in beef cattle over different stages of their productive life from birth to maturity.

The knowledge of population parameters for these traits are prerequisites for their genetic improvement. Particularly, the phenotypic and genetic parameters of the juvenile

growth traits that are indicators of the cumulative body capacity of beef cattle from their pre-natal life to birth and subsequent life before maturity are extensively documented (Waldenhawariat et al. 1977; Rege 1985; Meyer 1992; Mohiuddin 1993; Koots et al. 1994a).

2.2. FEMALE REPRODUCTION TRAITS IN BEEF CATTLE

Female reproductive efficiency, which is dependent on the number of viable offspring produced during the lifetime of a female animal, is critical in determining profitability of beef cattle production (King 1993). The offspring produced over a cow's life are usually single calves born about a year apart following puberty. Reproduction in beef cows, though it appears straight forward, can be dissected into a number of components (Rege 1985). First of all, heifers must attain puberty, and be cycling estrus regularly by the time of the first breeding season at about 14 months of age. Following successful breeding, calving occurs for the first time at about two years of age. Clearly, the first calving is the cumulative result of a series of successful events in the reproductive life of heifers. The second component is a series of consecutive calving events in the life of beef cows leading to the total number of calvings. Economically important traits relating to these two components deserve consideration in genetic improvement programs. In addition to these component traits, the longevity or stayability of a cow in the herd is directly related to life-time fertility of cows in the herd (Golden et al. 2000). Therefore, achieving high reproductive efficiency of cows at both component and aggregate level (Rust and Groeneveld 2001) through maximizing the number of

calvings and optimizing the intervals between calving events are crucial for cow-calf producers.

Some of component traits of the female reproduction (Rege and Famula 1993) are calving date, calving interval, age at first calving, calving ease, conception rate and calving rate. Particularly when the breeding season begins at a fixed time of year, and lasts a fixed length of time, there are traits that indicate reproductive efficiency of a heifer or cow. Calving date, which refers to the numerical day of the year when a cow gives birth to a calf, is related to the day of breeding during the breeding season, and to the gestation length. As the gestation length of 282 days and its phenotypic standard deviation of 3 days in *Bos taurus* is low in variability, the performance of a heifer or cow in her expression of estrus and fertility during the breeding season is a major determinant of the calving date. Thus, as viewed by MacNeil and Newman (1994a, b), the biology of calving date is complex arising from the sources of calf, dam and sire. Calving date is less likely to be biased due to fixed season of beef cattle breeding than calving interval (Bourden and Brinks 1983), and appears to have potential merit for improvement of reproductive efficiency (Meacham and Notter 1987).

Calving interval, a usual measure of reproductive efficiency particularly in dairy cattle, is less likely to improve reproduction in beef cattle (Meacham and Notter 1987) because beef cows are not typically bred year-round like dairy cows, but during a time-limited season of breeding. Bourden and Brinks (1983) found that calving interval when adjusted for previous calving date was essentially the same as the raw measure of calving date. Marshall et al. (1990) also indicated that calving interval was likely to be a biased

measure of reproduction under the management conditions of a time-limited breeding season and culling of open cows. This was because, the cows' calving late either were rapidly rebred in the following season or remained open only to be culled soon after weaning of their existing calf.

Stayability and longevity traits are the aggregate traits of reproductive efficiency of cows that indicate how long cows remain in their herd. Stayability is defined as the probability of a cow surviving in the herd to a specific age, given the opportunity to reach that age (Hudson and Van Vleck 1981). The trait depends largely on cows being culled for reproductive failure following calving (Snelling and Golden 1994), and is associated with fertility contributing directly to beef herd productivity. Nunuz-Dominuez et al. (1991) reported that culling at the age of first calving could have significant impact on the subsequent herd productivity, as the economic efficiency of cows was maximized at nine years of age for those that calved first at two years.

The genetic studies on the reproductive efficiency traits in beef cattle are few. Some of the most studied traits are age at first calving, calving date, calving interval, calving ease, conception rate and calving rate in females and scrotal circumference in breeding males (Koots et al. 1994a; Moser 1995).

2.3. FIXED EFFECTS FACTORS INFLUENCING JUVENILE GROWTH AND REPRODUCTIVE TRAITS

According to Steel et al. (1997), fixed effects relate to a factor for which only the values of interest are in the experiment which could be repeated using the same levels of

the factor. The statistical models used in genetic studies of either growth or reproductive traits in farm animals often consist of fixed and random effects in a mixed model. The fixed effects are environmental effects. However, sex of the calf, a physiological difference between animals, is genetic in origin, but is usually considered as a fixed effect. Fixed effects in a mixed model are used to adjust animal performance for any influence the factor in question may have on it so that estimates of genetic merits of animals (the random effects in the mixed model) are more accurate. In genetic studies using field data, however, the knowledge of environmental effects is limited. These are herd, ages of animals, periodic accounts of major events in the life of animals, and other information available, and are generally limited to the level what the breeders can provide. Some of these factors as they relate to the present research are reviewed herein.

2.3.1. Herd, Year and Season Effects

The concept of contemporary group is used in models of animal genetic evaluation to account for environmental differences between groups of animals such that animals in each group are of similar effective age. This also allows us to observe that all animals receive the same environment in a macro sense. It is within these groups that differences in animal performance can be interpreted in terms of genetic effects and other effects of interest.

Animals expressing performance in the same herd and year are often considered as a contemporary group for field studies in that they receive the similar nutrition, management and climatic conditions. Such influences are important for beef cattle raised

extensively under the varying environmental local conditions.

The herd, year and season are major contributing factors constituting contemporary groupings of beef cattle used as discrete fixed effects in estimating the components of (co)variances (Rege and Famula 1993; Burrow 2001) for both the growth performance and reproductive efficiency traits. The herd effects within or between breeds of beef cattle have been reported as significant for various growth traits (Rutledge et al. 1971; Skrypzeck et al. 2000), and for calving interval and calving date (Morris 1984). The year of heifer's birth has been reported as a significant factor influencing her own birth, weaning and yearling weights, but not on her calf's birth weight (Nelsen et al. 1986). Significant effects of year and season of birth on calving date and calving interval have been also reported by Bourdon and Brinks (1983), Lopez de Torre and Brinks (1990) and MacGregor and Casey (1999). MacNeil and Newman (1994b) have shown that the environmental trend observed across years was continuous in the evaluation of calving date when the data were adjusted for the breeding season that began the year previous to calving. Rege (1985) suggested that significant year effects on variation in economic traits are the results of both systematic changes in the production environment and the genetic trend resulting from selection.

Several studies have included, in their statistical models, the significant effects of various combinations of interactions of the discrete and continuous factors including calving group x breed group (Marshall et al. 1990), herd x year x month (Johnston and Bunter 1996), and year x previous growth or calving traits (MacGregor and Casey 1999).

2.3.2. Effects of Age of Dam

Age of dam represents an important environmental effect on calf performance. This is because as cows age from puberty over their reproductive life, they increase in body size, cease to grow, are able to provide better environments to calves by producing more milk and/or have increased body capacity for holding a fetus. Inclusion of this factor in the models of genetic evaluation allows comparison of individuals based on their genetic potentials holding effective age of dam constant (Olthoff et al. 1990).

Genetic evaluation of growth and reproductive traits in beef cattle have included age of dam either as a fixed effect class with levels ranging from two to ten years (Fahmy and Lalande 1971; Bourdon and Brinks 1983; Morris 1984; Nelsen et al. 1986; Smith et al. 1989b; Rege and Famula 1993; MacGregor and Casey 1999; Burrow 2001) or as a continuous covariate (Rutledge et al. 1971; Skrypzeck et al. 2000; van der Westhuizen et al. 2001) in various models for estimating components of (co)variances.

The significant effects of dam's age on pre-weaning and post-weaning growth traits of their calves have been reported in several studies (Nelsen et al. 1986; Smith et al. 1989a; Rege and Famula 1993; MacGregor and Casey 2000). Fahmy and Lalande (1971) showed that birth weight of the calf increased to five years of dam's age, after which it remained unchanged or declined. This result is consistent with the BIF (1996) guidelines that suggested that there exists a curvilinear relationship between age of dam and early growth weights. Olthoff et al. (1990) suggested that the age-of- dam adjustment factors used for body weights from birth to one year of age might need periodical revision, as these factors changed with the change in performance within a selected line

or breed. However, Rutledge et al. (1971) did not find the direct contribution of age of dam as significant to the variation in weaning weight. Burfening (1988) also reported that the birth weight patterns were not significantly changed with the age of dam up to 48 months.

Some studies have reported the significant effect of cow's age on her calving interval (Morris 1984; MacGregor and Casey 1999), and calving date (Rege and Famula 1993; MacGregor and Casey 1999). However, a few other studies reported no significant effect of cow's age on days of first or second calving (Smith et al. 1989b), calving interval and calving date (Lopez de Torre and Brinks 1990).

2.3.3. Effects of Calf Sex and Type of Birth

Heterogametic male (XY) and homogametic female (XX) calves differ in their sex chromosome complement. Though males and female calves born to same parents in a breeder's herd may have similar genetic potential to grow under a given environment, the differences in effects of hormones between sexes could result in their genes being expressed differently.

Numerous studies (Rutledge et al. 1971; Lesmeister et al. 1973; Nelsen et al. 1986; Rege and Famula 1993; Rust et al. 1998; MacGregor and Casey 2000; Skrypzeck et al. 2000; Burrow 2001) have reported calf's sex as a significant fixed factor included in the genetic analyses of the body weights and weight gains from birth to subsequent productive life. Across these studies, the sex of calf has been included in a variety of combinations of fixed factors, usually with two categories of males and females. In

addition, a few authors have also included steers as a separate category of sex particularly for the post-weaning growth traits (Rege and Famula 1993; MacGregor and Casey 2000; Skrypzeck et al. 2000). Garcia Paloma et al. (1992) investigated the effect of calf's sex on juvenile growth traits across calving orders of the dams, and reported that its effect was highly significant in first two calvings. Marshall et al. (1990) had included calf's sex and the interactions of calving group x calf sex and breed group x calf sex in their full models for analyses of calf traits and weaning efficiency.

MacNeil and Newman (1994b) examining sex effects on calving date in a crossbred population of beef cattle reported that bull calves were born 1.58 ± 0.40 d later than heifer calves. However, a number of studies reported that sex of the previous calf was not significant for calving date and calving interval (Bourdon and Brinks 1983; MacGregor and Casey 1999) .

The published literature relating to the effect of type of birth or calving used as a fixed effects factor is scanty. It has been seldom included as a significant factor in the genetic analysis of growth or reproductive traits due to low proportion of the calves being born as twins or multiples (Fahmy and Lalande 1971). A study by Azzam and Nielsen (1987) included the calf type in the genetic analysis of gestation length, calving date and first breeding date, showing that these traits were slightly longer in the single births than the multiple births. Azzam and Nielsen (1987) combined fetal sex with twinning to include three categories of pregnancy type in an evaluation of birth date.

2.4. PERMANENT MATERNAL ENVIRONMENTAL EFFECTS ON GROWTH TRAITS

Permanent maternal environmental effects are provided by each dam commonly to all of their offspring born over space and time. These effects are the results of permanent environmental change occurring in dams' physiological characteristics, influencing the performance of each of their offspring repeatedly. Growth traits of calves are influenced by these common environmental effects provided by their dam along with the genes she transmits to her calves (Rege 1985). Mohiuddin (1993) reviewed a number of published estimates of these effects for some of the juvenile growth traits as expressed as the proportions of their variances. He reported that the proportions for calf's weight at birth (from 18 studies), at weaning (from 24 studies) and at one year of age (from 15 studies) averaged 0.03 (in the range from -0.38 to 0.18), 0.07 (in the range from -0.39 to 0.29) and 0.03 (in the range from 0.01 to 0.10), respectively. It may be noted that the negative values are not theoretically possible as reported for some of these ratios of variances, but they have been obtained by the computing procedure followed in the studies, especially when the values were low with high sampling errors. The corresponding estimates reported by Meyer (1995b) for birth and yearling weights in New Zealand and Australian Angus populations were between 0.05 and 0.07, while that for weaning weight in the two populations were 0.15 ± 0.007 and 0.16 ± 0.007 , respectively. Clearly, the permanent maternal environmental effects were not important factors influencing juvenile growth traits in the published studies.

2.5. GENETIC EFFECTS ON GROWTH AND REPRODUCTIVE TRAITS

Genetic effects on growth and reproduction are the results of many genes acting with their additive, dominance and epistasis effects. With present techniques, it is usually possible only to learn about additive genetic effects. In mixed models, these genetic effects on economic traits are random effects with their levels randomly drawn from a large population (Steel et al. 1997).

The genetic parameter estimates for traits are usually expressed as proportions of their genetic effects in corresponding total phenotypic (co)variances. Several authors (MacNeil et al. 1984; Meyer 1993; Meyer 1995a; Meyer 1995b) have reported the total phenotypic variances along with the genetic parameter estimates for a number of growth and reproductive traits. A few estimates of direct and maternal genetic variances and covariances for some of the selected growth and reproductive traits reported in the literature are summarized in Table 2.1. In particular, the direct-maternal genetic covariances between traits are very rarely found in the literature as reported by Swalve (1993).

2.6. DIRECT AND MATERNAL HERITABILITIES OF JUVENILE GROWTH TRAITS

Heritability, a key genetic parameter of economically important traits, is used to determine their selection criteria. Extensive reviews of heritability estimates of juvenile growth traits have been reported over the years (Woldenhawariat 1977; Mohiuddin 1993; Davis 1993; Koots et al. 1994a). These reviews have summarized numerous studies carried out in several beef cattle breeds across major beef producing countries, using

several methods of their estimation. These methods include correlations between paternal half-sibs, regression of offspring on dam, regression of offspring on mid-parent cumulative selection differential, correlation between full-sibs, regression of offspring on sire, restricted maximum likelihood (sire model), intra-sire regression of offspring on dam, regression of son on sire, restricted maximum likelihood (animal model) across numerous studies (Mohiuddin 1993). Studies using more recent methods, particularly those using maximum likelihood techniques and animal models, are relatively few (Rust et al. 1998).

The averages of direct and maternal heritability estimates for birth weight (BW), weaning weight (WW), pre-weaning gain (PWG), post-weaning yearling gain (WG), yearling weight (YW) and birth to yearling gain (YG) from numerous published studies are summarized in Table 2.2 showing the abundance of most of these estimates.

Mohiuddin (1993) summarized the ranges of the heritability estimates reported in the literature, falling in the ranges, 0.14-0.61, 0.03-0.82, 0.07-0.66, 0.04-0.49, 0.12-0.50 and 0.02-0.20 for direct BW, maternal BW, direct WW, maternal WW, direct YW and maternal YW, respectively.

In addition to these major reviews, the estimates of heritabilities for growth traits have been continually reported in a number of recent studies (Meyer 1995a,b; Johnston and Bunter 1996; Rust et al. 1998; Mostert et al. 1998; Burrow 2001). These studies have reported the direct heritability estimate for BW in the range from 0.29 to 0.57, whereas Skrypzeck et al. (2000) reported the estimate as high as 0.72. The maternal heritability estimates for BW in all these studies were within the range from 0.06 to 0.18.

The direct heritability estimate for WW was moderate within the range from 0.17 to 0.33 in a number of studies (Meyer 1992; Meyer 1993; Rust et al. 1998; Mostert et al. 1998; Burrow 2001), whereas a relatively higher estimate of 0.53 was also reported by Skrypzeck et al. (2000). The maternal heritability estimates for WW reported in these published studies were in agreement with the range of estimates from 0.08 to 0.19 reported by Mostert et al. (1998).

Most of the recent estimates of direct heritability for YW have been reported within the range from 0.13 to 0.49 (Meyer 1995a; Johnston and Bunter 1996; Mostert et al. 1998; Rust et al. 1998), and were consistent with the weighted average of the large number of corresponding estimates (Table 2.2). Similarly, the maternal heritability estimates for yearling weight reported by Rust et al. (1998), Mostert et al. (1998) and Burrow (2001) within the range from 0.05 to 0.12 were consistent with the several estimates reported in the past.

Davis (1993) and Burrow (2001) reported that the direct heritability estimates for pre-weaning gain ranged between 0.14 and 0.22 which varied across methods of analyses. These were relatively lower than the weighted averages of published estimates, 0.33 and 0.31, reported by Woldenhawariat et al. (1977) and Koots et al. (1994a), respectively (Table 2.2).

2.7. HERITABILITIES OF CALVING TRAITS OF COWS

There are rather a few heritability estimates in the literature for calving traits of cows. A major review of literature published until 1991 (Koots et al. 1994a) on estimates

of heritabilities for these reproductive traits included only 10 studies for calving date (CD) with its average heritability estimate, 0.07. They also reviewed four and seven studies in cows and heifers, respectively for calving interval (CI), with their average heritability estimates being 0.10 and 0.09, respectively. Low average estimates have also been shown in published individual studies for calving date (Meacham and Notter 1987; Smith et al. 1989b; Meyer et al. 1990; Brown et al. 1990; Davis 1993; Burrow 2001) and calving interval (Meacham and Notter 1987; Lopez de Torre and Brinks 1990) both in the range of 0.01 - 0.10. However, Rege (1985) estimated the heritability for calving date as a dams' trait in Hereford cattle to be 0.19 ± 0.06 , and the estimate for the calving date as a calf's trait reported by MacNeil and Newman (1994b) was 0.15. The heritability estimates of birth date as the calf's trait reported by Azzam and Nielsen (1987) were 0.09 ± 0.03 , 0.17 ± 0.03 and 0.24 ± 0.06 in the first, second and last parity of dams, respectively. Similarly, Smith et al. (1989b) reported that the heritability estimates for the day of first and second calving as dam traits were 0.09 ± 0.13 and 0.36 ± 0.18 , respectively. On the other hand, Meacham and Notter (1987) found the heritability estimate for first calving date (0.17) to be relatively higher than that for second calving date (0.07 ± 0.06) from pooled data from nine herds. Other moderate estimates of heritabilities for calving date, excluding open cows at first parity and including them, reported by Buddenberg et al. (1990) were 0.20 ± 0.16 and 0.39 ± 0.21 , respectively. All these low to moderate estimates of direct heritability for calving date across studies tended to indicate that the trait may be genetically variable, and useful as a selection criterion to improve the reproductive efficiency in beef cows.

2.8. DIRECT GENETIC CORRELATIONS AMONG GROWTH TRAITS

Direct genetic correlations, which relate to the relationship between the breeding values for direct genetic effects of two economic traits, have been well documented for juvenile growth traits in beef cattle. A large number of published studies from early 1940s to early 1990s that have been reviewed by Waldenhawariat (1977), Mohiuddin (1993), Davis (1993) and Koots et al. (1994b) showed that the direct correlation estimates among BW, WW and YW were moderate to high and positive. In particular, the ranges of estimates summarized by Mohiuddin (1993) were from 0.25 to 0.99 for BW-WW, from 0.41 to 0.61 for BW-YW and from 0.18 to 0.90 for WW-YW, while the corresponding weighted averages of the estimates summarized by Koots et al. (1994b) were 0.50, 0.55 and 0.81, respectively.

These reviews were in agreement with, or closely comparable, to the results from several recent studies (Meyer 1995b; Robinson 1996; Mostert et al. 1998, Burrow 2001) in which the estimates of moderate to high direct genetic correlations of BW with WW and YW indicated that many genes influencing BW were shared by subsequent body weights. The corresponding estimates between WW and YW was close to unity in most of these studies indicating that most genes responsible for expressing both these two traits are same.

2.9. MATERNAL GENETIC CORRELATIONS AMONG JUVENILE GROWTH TRAITS

Maternal genetic effects were assumed to influence mainly the juvenile growth traits, and several estimates of maternal genetic correlations (r_m) among BW, WW and

YW, have been reported in the literature (Swalve 1993; Meyer 1993; Meyer et al. 1993; Meyer 1994; Meyer 1995a; Mostert et al. 1998; Rust et al. 1998). Although these published estimates ranged from 0.10 to 1.0, the average r_m estimates for BW-WW, BW-YW and WW-YW pairs of traits were 0.50 ± 0.18 , 0.58 ± 0.23 and 0.93 ± 0.10 , respectively, indicating a consistent tendency across these studies that the estimate between WW and YW, in particular, was approaching unity. This would be expected given the part-and-whole relationship existing between the two traits which are controlled by the same set of genes expressing maternal genetic effects mainly through the dam's milk. On the contrary, an estimate of maternal genetic correlation between BW and YW reported by Meyer (1994) was -0.13, which was attributed to an artifact of sampling errors, while the r_m estimates between BW and WW, and between WW and YW reported in the study were 0.30 and 1.00, respectively, in Angus cattle.

2.10. GENETIC CORRELATIONS AMONG CALVING TRAITS

The genetic correlation (r_g) estimates among the female reproductive traits found in the literature were relatively few, and most of them related to calving traits.

The literature estimates of direct genetic correlation between age at first calving and calving interval averaged 0.06 (Koots et al. 1994b). This was contrary to a recent finding of Frazier et al. (1999) who examined the genetic association among reproductive traits in a large sample of Angus beef cattle across the United States, and reported that the genetic correlations of age at first calving with first calving interval and mature calving interval ranged from -0.93 to -0.60. More recently, van der Westhuizen et al. (2001) and

Gutierrez et al. (2002) reported a very low negative estimates, -0.03 and -0.08, respectively, between the two traits.

Lopez de Torre and Brinks (1990) reported an estimate of genetic correlation of 0.06 between CD and CI, but when CI was adjusted for the time that bulls were not available to the cow, the corresponding estimate was 0.22. They also reported that the corresponding estimate between CI with the time from the beginning of the breeding season to calving was much higher ($r_g = 0.89$). These results were comparable to a high and positive genetic correlation between calving date and calving interval ($r_g = 0.75$) reported by van der Westhuizen et al. (2001). On the contrary, a negative estimate of -0.28 ± 0.05 was reported by Gutierrez et al. (2002) in agreement with the same sign of the estimate as reported by Meacham and Notter (1987). The discrepancies across these estimates could be mainly due to large environmental bias affecting CI that was inseparable from the genetic effects of the trait. Furthermore, the usefulness of these estimates is low due to low genetic variation particularly in CI.

The literature estimates of genetic correlations between the traits relating to calving ease were reviewed by Koots et al. (1994b) summarizing that the mean direct genetic correlation between calving ease of cows and heifers was 0.81 based on four published studies, and similarly, their corresponding maternal genetic correlation was 0.75. On the other hand, the estimates of direct-maternal genetic correlations among calving ease traits of cows and heifers ranged from -0.50 to -0.32 indicating their antagonistic relationships (Koots et al. 1994b).

2.11. DIRECT GENETIC CORRELATIONS AMONG TRAITS MEASURED IN DIFFERING SEXES

Sex-limited traits are compromised in the scope of mass selection of animals for genetic improvement of the traits due to availability of performance records only in one sex. However, the records measured in close relatives have been utilized in the genetic evaluation of animals of the opposite sex. The knowledge of genetic correlation between the traits measured in differing sexes provides an opportunity to realize correlated response in one trait through selection of another trait even if they are measurable only in animals of a particular sex. On the other hand, selection for certain traits in one sex may have adverse effects on traits in the opposite sex (Splan 1997).

There are only a few studies in the literature (MacNeil et al. 1984; Toelle and Robison 1985; Meyer et al. 1991; Frazier et al. 1999) in which the genetic correlations between the traits measured in male and female beef cattle have been reported. MacNeil et al. (1984) used an adaptation of the method of Wright's path coefficients to estimate genetic correlations of weight gain and carcass traits expressed by males with reproductive traits expressed by females. They showed that selection for post weaning daily gain would result in increased age and weight at puberty, increased mature weight, improved fertility, reduced maternal gestation length, reduced maternal calving difficulty, increased maternal birth weight and reduced maternal pre-weaning gain.

Using a path coefficient method, Toelle and Robison (1985) estimated genetic correlations of testicular measurements in males with female reproductive traits from half-sib and sire-daughter analyses. They reported favorable genetic correlations of

scrotal circumference with age at first breeding in females (-0.55) and age at first calving (-0.66) for Hereford cattle. Smith et al. (1989a) also found a favorable relationship between scrotal circumference of sires and earlier age at first calving of female relatives. The results of bivariate analyses by DFREML on animal models (Meyer et al. 1991) showed that there were moderate but consistently favorable genetic correlation estimates (from -0.41 to -0.25) between scrotal circumference and days to calving. Koots et al. (1994b) reported that the mean genetic correlation of scrotal circumference with calving interval was low but with favorable tendency (-0.11), while that of yearling height with calving interval was 0.35.

Reviewing the literature estimates, Koots et al. (1994b) summarized that birth weight, post weaning gain, weaning weight and yearling weight had negative genetic correlation with calving ease, while weaning gain and calving ease had a low but positive genetic correlation estimate.

Johnston and Graser (1998) estimated the genetic correlation between scanned P8 fat depth and days to calving to be -0.24, using the bivariate analysis of data from the Angus breed in Australia. Using multivariate analyses, Frazier et al. (1999) found that EPDs of sires for birth weight, weaning weight, yearling weight, mature weight and scrotal circumference were predictors of age at first calving ($P < 0.001$), but the model including all these EPDs explained less than 7% of the variation in age at first calving.

Thus, the present state of knowledge on the genetic correlations among the sex-limited traits in males and females is limited hindering the effective choice of selection objectives.

2.12. GENETIC CORRELATIONS BETWEEN JUVENILE GROWTH AND CALVING TRAITS

There are a relatively greater number of studies involving estimation of genetic parameters for growth traits than for reproductive traits (Koots et al. 1994b), despite the higher economic importance of the latter. The number of studies which have considered both of these types of traits together is even more limited (MacNeil et al. 1984; Toelle and Robison 1985; Smith et al. 1989b; Meyer et al. 1991). Consequently, there is a paucity of knowledge of genetic correlations between reproductive and growth performance traits. There are also limited estimates of direct-maternal genetic correlations involving growth and calving traits (Bennett and Gregory 2001). Overall, the studies on genetic relationships among growth and reproductive traits so far reported are very few, and some of the important traits have not even been considered in any of the published studies.

2.12.1 Direct Genetic Correlations

Direct genetic correlations between juvenile growth traits and reproductive traits have an implication of selecting for the former on the latter as correlated traits or vice versa. Among the juvenile growth traits and the calving traits studied together, calving ease is the one most well documented for its genetic correlation estimates with weights at birth, weaning and one year of age, which averaged -0.71, -0.16 and -0.29 from 27, 24 and 14 studies, respectively (Koots et al. 1994b).

Bourdon and Brinks (1982) reported that the estimates of genetic correlation of gestation length with all growth traits ranged from -0.41 ± 0.32 to -0.18 ± 0.27 indicating a

favorable relationship between growth and early parturition.

Smith et al. (1989b) reported the genetic correlations estimates (r_g) of calving date with post weaning gain, weaning weight and yearling weight to be negative with their low to moderately high estimates, -0.16, -0.53 and -0.13, respectively. Reviewing few studies in Northern Australian beef cattle, Davis (1993) reported average estimates of genetic correlations of days to calving with body weights at 400 days and 500 days of their age to be -0.36 and -0.66, respectively. Similarly, Rege and Famula (1993) reported that the estimates of genetic correlations of calving date with birth weight, post-weaning average daily gain and yearling weight for large populations of Hereford cattle across the United States were -0.30 ± 0.10 , -0.64 ± 0.19 and -0.60 ± 0.11 , respectively, indicating their favorable relationships. However, the corresponding estimates of calving date with pre-weaning average daily gain and weaning weight were very low, -0.03 ± 0.08 and -0.05 ± 0.03 , respectively. On the other hand, Johnston and Bunter (1996) reported positive but relatively very low genetic correlations of days to first calving with weaning weight ($r_g = 0.10 \pm 0.20$) and yearling weight ($r_g = 0.08 \pm 0.18$). Nelsen et al. (1986) reported that the estimates of genetic correlations of the day of calf's birth with its 18th and 23rd month weights were contrasting values of -0.37 ± 2.74 and 0.13 ± 2.76 , respectively. They reported an estimate for the day of calf's birth with yearling weight was low (-0.03 ± 2.22), while that with birth and weaning weights exceeded unity resulting from sampling errors that have no logical biological interpretation to derive from.

Bivariate analyses carried out on animal models (Meyer et al. 1991) showed a little, if any, favorable genetic correlations of days to calving with yearling and final

weights in a temperate breed Angus, but the corresponding estimates in Zebu crosses were markedly larger and favorable, -0.36 and -0.66, respectively, when the traits were not adjusted for weight at mating.

More recently, Burrow (2001) reported that there was an unfavorable genetic correlation estimate of days to calving with birth weight ($r_g = 0.22$), while the corresponding estimates with weaning, yearling and final slaughter weight, and pre-weaning and post-weaning gains were favorable, -0.18, -0.34, -0.43, -0.27 and -0.48, respectively.

2.12.2. Direct- Maternal Genetic Correlations

All mammalian mothers have the ability to nurture their young during their pre-natal and post-natal periods. The direct-maternal genetic correlation of a trait is the correlation between the breeding value of an animal for its capability to perform in that trait and the corresponding breeding value for its ability to contribute as a mother to its offspring's performance in that trait if it were a dam. Several studies on direct-maternal genetic correlation (r_{am}) estimates for growth traits have been reported in the literature (Meyer 1992; Mohiuddin 1993; Swalve 1993; Rust et al. 1998). Most of these studies have been reported for pre-weaning growth traits, while few estimates are reported for post- weaning growth traits.

The r_{am} for birth weight is the correlation between newborn calves' own genetic potential for the trait and their genetic potential to contribute pre-natal (uterine) environment for the performance of their offspring's birth weight if they were to become

dams later in their life. Reviewing from published studies, Meyer (1992) listed 13 estimates of r_{am} for this trait ranging from -0.51 to -0.12, although there was also an out-of-bound estimate of -1.05. Other three estimates reviewed by Meyer (1992) were low to moderate values of 0.01, 0.07 and 0.55. Meyer's (1992) own r_{am} estimates for the trait in Hereford and Angus cattle ranged from 0.04 to 0.28. Mohiuddin (1993) reviewed 27 estimates for the trait ranging from -1.05 to 0.55 averaging -0.35, which was also the weighted mean of 24 estimates summarized by Koots et al. (1994b). Similarly, the estimates reviewed by Swalve (1993) and Rust et al. (1998) ranged from -0.38 to -0.04. Further to these reviews, a few additional estimates from more recent studies published in 1993 onwards are presented in Table 2.3.

The direct-maternal genetic correlation for WW indicates the relationship between the weaned calves' own genetic potential for the trait and their genetic potential to contribute to their offspring's performance in WW through their uterine nurturing and pre-weaning mothering ability if they were to become dams. Reviewing a number of published studies, Meyer (1992) listed nine estimates of r_{am} for weaning weight that ranged from -0.72 to -0.04, while she also reported two null values and three positive values, 0.04, 0.16 and 0.16 reviewed. Meyer's (1992) own r_{am} estimates for the trait ranged from -0.78 to -0.59 in Hereford cattle and Zebu crosses, but the corresponding estimates in Angus cattle ranged from 0.20 to 0.22 on which the models used could also have some influence. Mohiuddin (1993) reviewed 26 estimates for the trait ranging from -0.91 to 0.26 with an average of -0.15 in agreement with the weighted mean, -0.16 of 23 corresponding estimates reviewed by Koots et al. (1994b). Swalve (1993), reviewing

from three published studies, listed the estimates for the trait also falling within similar range. Further to these reviews, a few additional estimates from more recent studies published in 1993 onwards are given in Table 2.3.

The existence of direct-maternal genetic covariance of the growth traits later after weaning is likely due to a carry-over effects of pre-weaning traits via their part-and-whole relationships (Meyer 1993). Thus, the direct-maternal genetic correlation of YW indicate the relationship between the yearlings' own genetic potential for this trait and their genetic potential to contribute to their offspring's YW through their carry-over mothering ability (both uterine and pre-weaning nurturing) until one year of age, if they were to become dams. Meyer (1992) reported that r_{am} estimates for YW ranged from -0.48 to -0.38 in Hereford cattle and Zebu crosses, respectively, while the corresponding estimates in Angus cattle were in the contrasting range from 0.45 to 0.49; these inconsistencies could have been at least partly due to their differences in selection history and the sampling errors in their analyses. Mohiuddin (1993) averaged 10 published estimates of r_{am} for YW to be -0.26 that ranged from -0.91 to 0.49. Further to this review, a few additional estimates for the trait from more recent studies published in 1993 onwards are given in Table 2.3.

Thus, numerous studies that reported negative r_{am} estimates of the three juvenile growth traits, irrespective of breeds of beef cattle, country and data sets or the methods of genetic analyses, indicated an antagonistic relationship between individual's genetic contribution to the trait and its capability as a mother to contribute to the offspring's corresponding trait. This relationship is thought to be logical from evolutionary

standpoint of maintaining checks and balances between the growth and milk yield, and is attributed to both genetic and environmental effects (Cundiff 1972). Another explanation for this antagonistic result is that there is a negative environmental covariance between dam and offspring where daughters of dams with superior maternal capability may provide an inferior maternal environment for their offspring (Meyer 1992). This could introduce a bias into the estimate of the direct-maternal genetic correlation due to confounding of direct and maternal effects (Meyer 1992; Robinson 1996).

Only a few studies have documented direct-maternal genetic correlations between any two of birth, weaning and yearling weights (Swalve 1993; Meyer 1992; Meyer 1993; Meyer 1994; Mostert et al. 1998; Rust et al. 1998). Most of these studies reported the negative r_{am} estimates between the direct genetic effects of one juvenile growth trait and maternal genetic effects of another juvenile growth trait falling within the range from -0.75 to -0.02, but with a few exceptions. Swalve (1993) reported an estimate of 0.06 between direct effects of birth weight and maternal effects of yearling weight, while the estimate of 0.06 was also reported between maternal genetic effects of birth weight and direct genetic effects of yearling weight by Mostert et al.(1998). Meyer (1994) reported the r_{am} estimates between either effects of weaning weight and the other effects of yearling weight in Angus cattle ranging from 0.27 to 0.34. Rust et al. (1998) also reported the positive correlation estimates of 0.14 and 0.13 for the direct genetic effects paired with maternal genetic effects of weaning and yearling weights, respectively. Hence, the consistency among the between-trait r_{am} estimates was not evident across studies probably as a result of sampling errors.

There have been no reports of estimation of direct-maternal genetic correlations between any of the growth and calving traits published to date.

2.13. HERITABILITIES OF STAYABILITY TRAITS

It is economically important that the cows and heifers which are selected as breeding stock for their higher genetic potential are kept in the herd long enough to produce a number of calves at least to cover the investment of time and resources involved in replacing them (Doyle et al. 2000). As the stayability of cows involves selection by its definition (Van Vleck, 1980), it is also important that their selection for continuing rebreeding performance is not detrimental to the growth performance of their calves. Genetic analysis of stayability has been well documented in dairy cattle (Everett et al. 1976a,b; Hudson and Van Vleck 1981; Van Doormaal et al. 1984).

The published heritability estimates for longevity and stayability of cows are numerous for dairy cattle. Robertson and Barker (1966) reported the h^2 estimates for cows' survival to 2nd lactation in three dairy breeds to range from 0.008 to 0.072, while relatively higher estimates particularly in Ayrshire cows (from 0.126 to 0.203) were reported for survival to two or more lactations. Generally low estimates (<0.10) have been reported for cows' survival rates to different lactations (Schaeffer and Burnside 1974), for stayability to survival ages from 36 to 84 months (Hudson and Van Vleck 1981), for culling age, productive life and lactation number (Hoque and Hodges 1980), for various months of total and productive life (Van Doormaal et al. 1984), and for various herd life traits including percent survival to 48, 54 and 84 months (Dentine et al.

1987). More recent h^2 estimates for cows' herd life to 84 months and months in milk (productive life) to 84 months (Weigel et al. 1995), and for herd life, length of productive life and stayability to 36, 48, 60 and 72 months (Vollema and Groen 1996) were also all in the range from 0.01 to 0.10. In agreement with these studies in dairy cattle, a study on stayability of Large White and Landrace sows from first to second litter and first to third litter revealed their h^2 estimates between 0.08 and 0.11, respectively (Lopez-Serrano et al. 2000).

The published h^2 estimates for beef cows' stayability traits are very limited. Snelling and Golden (1994) and Snelling et al. (1995) reported the h^2 estimates for two Red Angus herds varying from 0.019 to 0.680 using various methods of analyses. They found that the estimates were higher when using animal models in regression based method (Method R), and also that stayability traits for longer life had higher h^2 estimates. Doyle et al. (2000) reported h^2 estimate for stayability in Angus females from the same herds to be 0.15. The results from Snelling et al. (1995) and Doyle et al. (2000) indicate that stayability of beef cows is a heritable trait with potential usefulness in selection programs. However, other recently published estimates (van der Westhuizen et al. 2001) for various measures of cows' stayability and longevity in beef cattle were less optimistic. They found heritabilities for calving success, stayability at 36, 48, 60, 72 and 84 months of age ranging from 0.03 to 0.11. Another study (Vega-Murillo et al. 1999) had estimates as low as 0.0 to 0.02 for stayability traits in beef cattle.

2.14. GENETIC CORRELATIONS BETWEEN STAYABILITY AND PRODUCTION TRAITS

Stayability and longevity traits appear to have positive genetic correlations to one another (Everett et al. 1976a; Hoque and Hodges 1980; Hudson and Van Vleck 1981; Van Doormaal et al. 1984; Vollema and Groen 1996). Cows that have the genetic potential to remain in the herd to a given time in their lives tend to have the genetic capability to survive longer to a later time-point in their lives. Published estimates of genetic correlations of stayability and productive herd life traits with production traits in dairy cows such as milk yield and milk fat traits have been reported in the range from 0.20 to 0.78 (Everett et al. 1976a; Hoque and Hodges 1980; Hudson and Van Vleck 1981). Weigel et al. (1995) reported that the genetic correlation between days of productive life and months in milk was 0.99. Other studies of this genetic relationship have relied on correlation between sire proofs, which is an estimate of its genetic merit based on records from self and relatives. Technically, these should give results similar to genetic correlations. The correlations among sire proofs for daughters' survival to 48, 54 and 84 months of herd life reported by Dentine et al. (1987) ranged from 0.42 to 0.84. The correlations between sire proofs of milk and fat traits and stayability traits ranged from 0.24 to 0.46 (Everett et al. 1976a). The correlations of sire proofs for milk and fat yields with those of stayability to 17 and 30 months of productive life in dairy cows were positive and favorable as reported by Van Doormaal et al. (1986).

There is still very little published information available on genetic relationships between production traits and stayability in meat animals. Lopez-Serrano et al. (2000) recently reported negative and unfavorable genetic correlation estimates in the range from

-0.32 to -0.06, between daily gain and stayability traits in two breeds of sows, and positive but unfavorable genetic correlations, from 0.11 to 0.27, between backfat thickness and stayability. In beef cattle, Snelling et al. (1995) have suggested the need of additional studies to quantify the genetic relationships of stayability measures with other economically important traits, while it was only recently that the estimates of correlations between genetic merits for growth traits and stayability (Rasali et al. 2002), and the genetic correlations between these traits (Mwansa et al. 2002) have been reported. Rasali et al. (2002) reported the preliminary results from an analysis of a subset of the present population comprising a large herd of Angus cattle. The results indicated that the correlations of direct EBVs for BW, and maternal EBVs for BW and WW with EBVs for cows' stayability to three years of age were favorable, falling in the range from 0.11 to 0.23. On the contrary, Mwansa et al. (2002) reported negative correlations of direct BW, and direct and maternal of WW with cows' survival to 3rd calving and up. Possibly, the discrepancy is simply due to the difference in definitions of the stayability traits and methods of analysis, and differences in selection history in the herds analysed. Mwansa et al. (2002) used survival to a given number of calvings for scoring a calving success, while in the study reported by Rasali (2001) both the age and number of calvings were used as criteria of scoring a calving success.

2.15. DIRECT AND CORRELATED GENETIC TRENDS

Planned comparisons among specific breeding groups were commonly adopted to measure their genetic progress under selection (Smith 1962). A number of modern

techniques were developed to measure genetic change in populations under selection in dairy cattle (Van Vleck and Henderson 1961; Henderson 1973), and in farm livestock using field records (Smith 1962). Henderson (1973) described a number of models that can be used to estimate genetic trends, and suggested that mixed model methodology involving best linear unbiased prediction (BLUP) is particularly a powerful and advantageous tool.

In beef cattle, a number of studies on genetic progress in growth have originated from selection experiments (Bailey et al. 1971; Koch et al. 1974; Barlow 1978; Irgang et al. 1985; Aaron et al. 1986; Nwakalor et al. 1986; Mrode 1988; Archer et al. 1998; Mercadante et al. 2003). These studies have shown that when growth performance was emphasized as primary traits for selection, the result was generally positive genetic progress in these traits. Furthermore, it is not unusual to find genetic progress in a selected line as great as, or greater than the expected (Bailey et al. 1971). Barlow (1978) reviewed a number of published studies on pre-weaning growth traits, and reported that their annual genetic responses ranged from 0.18 to 1.80 kg for BW and from 0.56 to 2.07 kg for WW, while only one negative estimate was reported. Similarly, Mrode (1988) summarized several literature estimates of annual genetic change to be positive. In most of the selection experiments reviewed by Mrode (1988), the genetic progress in terms of mid-parent selection differentials, converted to standard deviation (SD) units, amounted to about 0.20 SD per year for single-trait selection. This constituted about 2% of the mean for the traits with coefficient of variation (CV) of 10%. The actual annual genetic change in WW and YW realized from the selection experiments reviewed were in the ranges,

from 0.56 to 2.10 and from 1.03 to 4.06 kg year⁻¹, respectively.

In a comparative study in purebred Hereford (HE) and a synthetic population in (SY) in Canada, Sharma et al. (1985) reported the annual genetic changes estimated by control population and BLUP methods for BW (0.06 ± 0.21 and 0.08 ± 0.06 kg, respectively), WW (1.80 ± 0.03 and 1.10 ± 0.21 kg, respectively), and YW (5.81 ± 9.39 and 8.21 ± 6.00 kg, respectively) in HE, and those for BW (0.29 ± 0.22 and 0.07 ± 0.06 kg, respectively), WW (1.64 ± 0.92 and 0.86 ± 0.43 kg, respectively), and YW (11.31 ± 12.17 and 6.78 ± 2.15 kg, respectively) in SY. Similarly, Olthoff et al. (1989) reported that average directed and correlated genetic change in BW, WW and YW in Shorthorn cattle selected for yearling weight were 0.21 ± 0.06 , 1.50 ± 0.05 and 4.6 ± 0.90 kg yr⁻¹, respectively.

Correlated responses in other growth traits from direct selection for WW or YW are invariably positive, while that for the latter have been reported to be generally larger than that for the former (Mrode 1988). On the other hand, there has been a serious concern that selection for growth performance might have negative effects on fertility of cows (Barlow 1978; Archer et al. 1998). However, Meyer et al. (1991), Archer et al. (1998) and Mercadante et al. (2003) reported positive genetic trends for growth without significantly compromising the reproductive performance traits of cows, especially the days to calving and calving success.

2.16. METHODS AVAILABLE FOR GENETIC ANALYSES OF FIELD RECORDS

Field records of performance are the major source of data for genetic analyses in beef cattle, as only a limited number of planned selection experiments have been carried

out in Canada and world over. These records accumulated by breeders over a number of years require development of variety of models for analysis across studies depending upon the country, breed, prevailing production-marketing situations, methods and computational resources available.

Estimation of genetic (co)variances between traits is the intermediate step in genetic analyses for estimation of the population parameters such as heritabilities and genetic correlations among traits from the ratios of sums of squares and products of the estimated (co)variances (Rege 1985). In the past half century, various methods have evolved for estimation of variances and covariances among the traits of interest in animal breeding (Henderson 1990). These methods include the early method of equating mean squares from analysis of variance (ANOVA) to their expectations (Henderson's Methods 1, 2 and 3). More recent methods included mixed models and their use in the maximum likelihood (ML) method and the restricted maximum likelihood (REML) method (Henderson 1990). As the computing power has increased in the latter part of 20th century, the REML method has been the method of choice for estimating the (co)variance components in animal breeding (Meyer 1989). Several approaches have been developed to allow application of the REML type analyses to large data sets with more complicated models. These include the derivative-free REML (DFREML) method (Graser et al. 1987) and the Bayesian approach (Gianola and Fernando 1986; Gianola et al. 1986).

The DFREML method is an iterative procedure that searches for the maximum likelihood estimate of variances (Meyer 1994). Very simply, this method looks for the estimates of genetic and other (co)variances that are most likely to represent the given

data set. This is done by maximizing the log likelihood function for the animal model (Boldman et al. 1995). The method has also been extended to handle a wide range of mixed models with one or more fixed and random effects. The analyses can be univariate (Meyer 1989) or multivariate (Meyer 1991; Boldman et al. 1995), and are designed to utilize pedigree information (i.e. additive genetic relationships) of all animals with or without records. Genetic groups are also accommodated to account for the lack of records of some parents in the base population by fixing their effects by the year of their birth (Westell et al. 1988).

Another approach, which is based on Bayesian inference, was introduced in animal breeding by Gianola and Foulley (1982), and was further extended (Gianola and Fernando 1986; Gianola et al. 1986). The Bayesian estimators of variance components are derived from the marginal posterior distributions of variance components which are generated by an iterative sampling procedure. This method gives results similar to the REML estimates, and has the advantages of yielding the measures of uncertainty associated with the estimates of other parameters (Blasco 2001). What is produced by this procedure is not a single point estimate of a parameter (Blasco 2001), but a posterior distribution that can be summarized in terms of its descriptive statistics including mean and confidence interval, and the parameter so estimated is regarded as a random variable (Pretorius and van der Merwe 2000). The technique often uses Monte-Carlo Markov Chain (MCMC) methods such as Gibbs sampling, to make the approach computationally feasible (Blasco 2001). Although this approach uses variance component information as priors to start the Gibbs sampling process, given enough data, the prior information has

little influence on the posterior distributions (Blasco 2001).

The theoretical background of Gibbs sampling has been summarized by Brooks (1998) in more general terms, reviewed by Blasco (2001) as it is applied to animal breeding, and described by Van Tassell and Van Vleck (1995; 1996) as it is applied to broad range of mixed animal models. Van Tassell and Van Vleck (1996) implemented their multivariate Gibbs sampler for Animal Models (MTGSAM) programs for generation of Gibbs samples for (co)variances, correlations, heritabilities, fixed effects and other random effects in their linear combinations. These authors found that averages of posterior means of variance components estimated using MTGSAM programs with informative and flat priors were empirically unbiased, and their correlations with the estimates from another method, MTDFREML, were close to unity.

The diagnostic methods for analyzing the Gibbs samples for assessment of their convergence or “stationarity” have been reviewed in terms of their practical implementation (Cowles and Carlin 1996) and their mathematical background (Brooks and Roberts 1998).

Table 2.1. A sample of estimates of genetic (co)variances and phenotypic variances reported in the literature for growth and calving traits.

Trait	Literature estimates of (co)variances or their ranges				References
	σ_a^2 ^z	σ_m^2	σ_{am}	σ_p^2	
Birth weight	3.0 to 4.9	-6.5 to -3.3	3.32 to 11.69	18.4 to 17.86	Cantet et al. (1988)
	21.87	1.6			Swalve (1993)
	3.1 to 5.3	0.4 to 2.15.3	-0.99 to -3.4	7.8 to 9.7	Tawah et al. (1993)
	11.8	3.8	-1.7	20.9	Burrow et al. (2001)
	5.3	2.1	-1.45	16.4	Maiwashe et al. (2002)
Weaning weight	171.8 to 158.4	-143.7 to -83.5	136.9 to 367.84	497.8 to 546.1	Cantet et al. (1988)
	832.5	149.0			Swalve (1993)
	199.7 to 242.5	145.2 to 220.5	-116.6 to -89.7	727.8 to 832.6	Tawah et al. (1993)
	72.0	139.0	-19.2	411.8	Burrow et al. (2001)
	117.9	88.1	-54.9	481.9	Maiwashe et al. (2002)
Yearling weight	1464.9	167.0			Swalve (1993)
	148.0	55.0 ⁴	11.7	477.9	Burrow et al. (2001)
Calving date	23.0	5.8	-5.7		MacNeil and Newman (1984)
Days to calving	108.5			1578.0	Burrow et al. (2001)
Birth date	13.2 to 30.7	3.8 to -14.3	-2.7 to 8.9	127.9 to 153.7	Azzam and Nielsen (1987)

^z σ_a^2 , σ_m^2 , σ_{am} and σ_p^2 are direct genetic variance, maternal genetic variance, direct-maternal covariance and phenotypic variance, respectively.

Table 2.2. Summary of the averages of published heritability estimates for juvenile growth traits across large number of studies reviewed until 1994.

Growth trait	N ^z	Average h ² estimate	Authors of the review
Birth weight	43	0.27	Mohiuddin (1993)
Birth weight	8	0.30 ^y	Davis (1993)
Birth weight - Direct	167	0.31 ^x	Koots et al. (1994a)
Birth weight - Direct	43	0.30	Mohiuddin (1993)
Birth weight - Direct	75	0.45 ^x	Woldehawariat et al. (1977)
Birth weight - Maternal	34	0.14 ^x	Koots et al. (1994a)
Birth weight - Maternal	38	0.10	Mohiuddin (1993)
Pre-weaning gain	7	0.31	Davis (1993)
Pre-weaning gain - Direct	104	0.29 ^x	Koots et al. (1994a)
Pre-weaning gain - Direct	62	0.30	Woldehawariat et al. (1977)
Pre-weaning gain - Maternal	15	0.24 ^x	Koots et al. (1994a)
Weaning weight	53	0.23	Mohiuddin (1993)
Weaning weight - Direct	53	0.22	Mohiuddin (1993)
Weaning weight - Direct	234	0.24 ^x	Koots et al. (1994a)
Weaning weight - Direct	83	0.24	Woldehawariat et al. (1977)
Weaning weight - Direct	14	0.36 ^y	Davis (1993)
Weaning weight - Maternal	41	0.13	Mohiuddin (1993)
Weaning weight - Maternal	38	0.13 ^x	Koots et al. (1994a)
Weaning weight - Maternal	7	0.09 ^y	Davis (1993)
Post-weaning gain	177	0.31 ^x	Koots et al. (1994a)
Post-weaning gain	8	0.16	Davis (1993)
Post-weaning gain	57	0.33	Woldehawariat et al. (1977)
Yearling gain - Direct	23	0.34 ^x	Koots et al. (1994a)
Yearling weight	35	0.31	Mohiuddin (1993)
Yearling weight	7	0.32 ^y	Davis (1993)
Yearling - Direct	55	0.45	Woldehawariat et al. (1977)
Yearling - Direct	35	0.31	Mohiuddin (1993)
Yearling - Direct	147	0.33 ^y	Koots et al. (1994a)
Yearling weight - Maternal	6	0.11	Koots et al. (1994a)
Yearling weight - Maternal	23	0.11	Mohiuddin (1993)

^z N = Number of published estimates reviewed by the author(s).

^y The estimate averaged from the published estimates reviewed in beef cattle of North Australia by Davis (1993).

^x The average estimate weighted by standard error (Koots et al. 1994a).

Table 2.3. Recent estimates of the direct-maternal genetic correlation (r_{am}) of three juvenile growth traits reported in studies published from 1993 to 2001.

Published studies	r_{am}		
	BW	WW	YW
Swalve (1993):			
Univariate analyses	-0.16 to 0.46 ^z	-0.32 to -0.05	-0.38 to 0.00
Multivariate analyses	-0.36 to -0.11	-0.60 to -0.21	-0.09 to -0.02
Robinson (1996):			
in Australian Angus cattle			
Univariate models with:			
AMR ^y	-0.54	-0.41	-0.56
AMRC ^x	-0.61	-0.52	-0.73
Multivariate model with AMRC	-0.52	-0.45	-0.37
Rust et al. (1998):			
in Simentaler cattle	-0.45	-0.61	-0.59
Meyer (1993):			
in Australian Polled Hereford			
Univariate models	-0.57	-0.67	-0.58
Bivariate models	-0.64 to -0.57	-0.39 to -0.34	-0.43 to -0.65
Mostert et al. (1998):			
in five breeds	-0.60 to -0.35	-0.81 to -0.49	-0.73 to -0.49
Skrypzeck et al. (2000):			
in a South African composite	-0.40	-0.65	-
Burrow (2001):			
in a tropical composite breed	-0.25	-0.19	0.13
Univariate analysis for sexes:			
male	-0.57	-0.24	-0.52
female	-0.46	-0.38	-0.12
Bivariate analysis for sexes:			
male	-0.45	-0.19	-0.36
female	-0.40	-0.24	-0.06

^z the ranges of literature estimates varied with breeds, data sets or methods used in the analyses;

^y AMR = animal, maternal and environmental effects in the animal model of analyses;

^x AMRC = animal, maternal, environmental and permanent environmental effects in the animal models.

3. HYPOTHESIS AND OBJECTIVES OF THE RESEARCH

A general hypothesis conceptualized, in statistical term, for the present research was that the genetic parameters of traits associated with juvenile growth and reproductive efficiency in a given population of five herds of Angus cattle are significantly different from zero. In practical terms, the present study was envisaged for investigating whether the selection for a juvenile growth trait would result in significant correlated response in traits associated with reproductive efficiency in Angus cattle.

Based on the premises of the general hypothesis conceptualized, the overall objectives of the research are set out as follows:

1. To quantify the parameters providing insights into genetic association between three juvenile growth traits and first calving date of Angus heifers;
2. To quantify the parameters providing insights into genetic association between juvenile growth traits and two calving traits, calving date and calving interval in Angus cows; and
3. To quantify the parameters providing insights into genetic association between juvenile growth traits and stayability in Angus cattle herds.

4. STUDY - I:

MULTIPLE-TRAIT ANALYSIS OF GENETIC PARAMETERS WITH THEIR CONFIDENCE MEASURES FOR JUVENILE GROWTH TRAITS AND FIRST CALVING DATE IN CANADIAN ANGUS CATTLE

4.1. ABSTRACT

The purpose of this study is to determine genetic relationships between the juvenile growth traits and the first calving date (CD1) in herds of Canadian Angus cattle. Records of birth, weaning and yearling weights (BW, WW and YW, respectively), and CD1 were pooled from a large herd (A) and other four relatively smaller herds (B, C, D and E) involving 6,886 animals in the pedigree. The data were analysed using multiple-trait derivative free restricted maximum likelihood (MTDFREML) and multiple-trait Gibbs sampling animal models (MTGSAM) procedures. The results revealed that the estimates of direct heritability (h^2) for BW, WW, YW and CD1 were 0.51 ± 0.015 , 0.70 ± 0.019 , 0.52 ± 0.016 and 0.18 ± 0.008 , respectively, and those of maternal heritability (m^2) for BW, WW and YW were 0.10 ± 0.005 , 0.20 ± 0.009 and 0.06 ± 0.003 , respectively. These were in general agreement with the ranges of corresponding published estimates. The estimates of both direct (r_a) and maternal (r_m) genetic correlations between all pairs of juvenile growth traits were moderate to high positive. The negative estimates of direct-maternal genetic correlations (r_{am}) of each of the growth traits were evident. The r_a estimates for WW-CD1 pair of traits was 0.27 indicating unfavorable genetic association, while the corresponding estimates for BW-CD1 and YW-CD1 were both low, -0.02 and 0.06, respectively. The r_{am} estimates for CD1-WW and CD1-YW were -0.71 and -0.74, respectively, indicating the favorable association between the traits, while that for CD1-BW was very low (0.05). Thus, the genetic associations of the CD1 with WW and YW suggested significant values of the trait in the selection programs.

4.2. INTRODUCTION

Body weights at birth (BW), weaning (WW) and one year of age (YW) are easily measurable direct indicators of juvenile growth performance. They are most invariably recorded by beef cattle breeders, and selection programs practiced by the breeders have focused mainly on these traits (Meyer et al. 1991; Swalve 1993). The abundant information on genetic parameters is available for birth and subsequent weights or gain reported from a large number of genetic evaluation studies in various breeds of beef cattle around the world that have been reviewed from time to time (Woldehawariat et al. 1977; Mohiuddin 1993; Davis 1993; Koots et al. 1994a, b; Rust et al. 1998).

Early calving is reported to be associated with biological and economic efficiencies in beef cattle (Marshall et al. 1990; Johnston and Bunter 1996). Consequently, the day when calving occurs has been considered as an useful indicator trait of female reproductive efficiency for producers practicing a time-limited breeding season in beef cows (Bourdon and Brinks 1983; Rege 1985; MacGregor and Casey 2000). The first calving date (CD1) recorded for a heifer bears particular economic importance for making herd management and culling decisions early in the life of heifers such that the production from their calving crops in the subsequent years could be maximized. Hence, the CD1 deserves consideration as a potentially important trait for its genetic evaluation to assess its potential merit in the selection programs.

The knowledge of genetic association between the juvenile growth traits and the first calving date is valuable for predicting possible consequence of selection applied to any one or more of these traits. The genetic basis of this association is not yet clearly

understood, as little information on the direct genetic correlations between them (Smith et al. 1989b), and no information on their direct-maternal genetic correlations are available in the literature. The purpose of this study is to estimate genetic parameters of BW, WW, YW and CD1 providing insight into the genetic associations between these traits.

4.3. MATERIALS AND METHODS

4.3.1. Sources of Data

Data from five Canadian Angus herds, one from Manitoba (herd A), three from Alberta (herds B, C and D) and one from Saskatchewan (herd E) were obtained from the Canadian Angus Association. All herds represented the typical breeders' cow/calf operations in the Canadian Prairie Region. The numbers of animals born and their sires and dams from each herd are given in Table 4.1.

Records of calves for the period from the year 1984 to 2001 relating to their own juvenile body weights and their dams' calving events in the herds during their juvenile age up to one year were pooled. Among the three juvenile growth traits, the value of WW was adjusted to 205 days as $[(BW) + (\text{pre-weaning average daily gain in weight}) \times 205]$, and the value of YW was adjusted to 365 days as $[(WW) + (\text{average daily gain in weight from 205-day weaning to one year old}) \times 160]$. A heifer's first calving date, CD1 was calculated as the number of days counting from a fixed day, the first of January in the present study, in a year to the day of that year when the first event of calving occurred in the life of the heifer. Since beef females under the prevailing production systems in Canada are subjected to a time-limited summer breeding season, the small number of calvings (approximately 4% of the calving records) that occurred in the summer (June 21 - September 22) and fall (September 23 - December 20) were edited out of the CD1 records. All values of each trait falling outside the range of four standard deviations

above or below its overall mean in the combined population of five herds were edited out following the Beef Improvement Federation guidelines (BIF 1996).

4.3.2. Development of the Animal Model for Four Trait Analysis

4.3.2.1 *Fixed effects and Covariates*

The descriptive statistics of three juvenile growth traits and first calving date are given in Table 4.2. The effects of various factors on each of BW, WW, YW and CD1 were analysed using SAS programs (SAS 1998) to determine their significance for inclusion in the model of analysis. The contemporary groups of calves for records of juvenile growth traits were formed with the effects of herd- year of calves' birth. Additional factors namely, season of birth, type of birth and sex of the calf at birth which were assumed to be similar in their effects across all herds were also considered. The fixed effects of herd-year with season, type of birth (singleton and multiple birth), and sex at birth were highly significant ($P < 0.01$) for all three juvenile growth traits. The age of dam at birth was highly significant ($P < 0.01$) as both linear and quadratic covariates for each of the three juvenile growth traits representing the curvilinear relationship between them. In case of CD1, the fixed effects of herd- year of calving representing the contemporary groups for the calving heifers was significant, while the type of calving was also a factor ($P < 0.05$) influencing the first calving date. The fixed effects and covariates finally included in the analysis of the multiple-trait animal model are presented in Table 4.3.

4.3.2.2 Genetic groups

For the population of the present study, in which there is significant genetic change occurring over the course of several generations, it is necessary to define the base population, for this is the group which the genetic parameters refer to. The unknown parents of animals from the first generation in the data represent the base population. All unknown parents of animals with records and those of the known parents which did not have their own records and had only a single record of their offspring were considered as “Phantom” parents. These were grouped into genetic groups as described by Westell et al. (1988) and used by Shrestha et al. (1995), by assigning them identification numbers that were simple integer starting from “1” to “N” based on their year of birth in order to eliminate the possible biases from selection that might have occurred in the base population. A total of 36 such genetic groups were identified for the pooled data set from the population of five herds. The pooled pedigree of 6,886 animals involving all four trait records provided nearly a complete pedigree of the respective herds minimizing further effects of selection on the animal model analysis. There were only 793 inbred animals with a very low average inbreeding coefficient of 0.03.

4.2.2.3 The Animal model

The mixed animal model assumed for the analysis of four traits, BW, WW, YW and CD1, as adapted from the bivariate full model given by Quaas and Pollak (1980), is represented as follows:

$$\begin{pmatrix} Y_1 \\ Y_2 \\ Y_3 \\ Y_4 \end{pmatrix} = \begin{pmatrix} X_1 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 \\ 0 & 0 & X_3 & 0 \\ 0 & 0 & 0 & X_4 \end{pmatrix} \begin{pmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \end{pmatrix} + \begin{pmatrix} Z_{a1} & 0 & 0 & 0 \\ 0 & Z_{a2} & 0 & 0 \\ 0 & 0 & Z_{a3} & 0 \\ 0 & 0 & 0 & Z_{a4} \end{pmatrix} \begin{pmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \end{pmatrix} + \\
\begin{pmatrix} Z_{m1} & 0 & 0 & 0 \\ 0 & Z_{m2} & 0 & 0 \\ 0 & 0 & Z_{m3} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} m_1 \\ m_2 \\ m_3 \\ 0 \end{pmatrix} + \begin{pmatrix} W_{m1} & 0 & 0 & 0 \\ 0 & W_{m2} & 0 & 0 \\ 0 & 0 & W_{m3} & 0 \\ 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} p_{m1} \\ p_{m2} \\ p_{m3} \\ 0 \end{pmatrix} + \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \end{pmatrix}$$

where,

Y_1, Y_2, Y_3 and Y_4 = Vectors of records for BW, WW, YW and CD1, respectively,

b_1, b_2, b_3 , and b_4 = Vectors of fixed effects (including covariates) affecting records of BW, WW, YW and CD1, respectively,

X_1, X_2, X_3 and X_4 = Known incidence matrices relating BW, WW, YW and CD1, respectively to corresponding fixed effects,

a_1, a_2, a_3 and a_4 = Random vectors representing direct genetic effects for BW, WW, YW and CD1, respectively,

m_1, m_2 and m_3 = Random vectors representing maternal genetic effects for BW, WW and YW, respectively,

p_{m1}, p_{m2} and p_{m3} = Random vectors representing permanent maternal environmental effects for BW, WW and YW, respectively,

Z_{a1} , Z_{a2} , Z_{a3} and Z_{a4} = Known incidence matrices relating BW, WW, YW and CD1,

respectively to corresponding elements of a_1 , a_2 , a_3 and a_4 ,

Z_{m1} , Z_{m2} and Z_{m3} = Known incidence matrices relating BW, WW and YW, respectively to

corresponding elements of m_1 , m_2 and m_3 ,

W_{m1} , W_{m2} and W_{m3} = Known incidence matrices relating BW, WW and YW, respectively

to corresponding elements of p_{m1} , p_{m2} and p_{m3} ,

e_1 , e_2 , e_3 and e_4 = Random vectors representing residual errors peculiar to each record of

BW, WW, YW and CD1, respectively.

The first (E) and second (V) moments assumed for the animal model were as the following:

$$E \begin{pmatrix} Y \\ a \\ m \\ p_m \\ e \end{pmatrix} = \begin{pmatrix} Xb \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix}, \quad \text{and} \quad V \begin{pmatrix} a \\ m \\ p_m \\ e \end{pmatrix} = \begin{pmatrix} G_a \otimes A & G_{am} \otimes A & 0 & 0 \\ G'_{am} \otimes A & G_m \otimes A & 0 & 0 \\ 0 & 0 & D_{pm} \otimes I_{pm} & 0 \\ 0 & 0 & 0 & R_e \otimes I_e \end{pmatrix}$$

where,

$$a' = [a_1 \ a_2 \ a_3 \ a_4],$$

$$m' = [m_1 \ m_2 \ m_3],$$

$$p_m' = [p_{m1} \ p_{m2} \ p_{m3}],$$

$$e' = [e_1 \ e_2 \ e_3 \ e_4],$$

\otimes = Direct matrix product operator,

A = Numerator relationship matrix,

G_a = Direct genetic (co)variance matrix,

G_{am} = Matrix of covariances between direct and maternal genetic effects,

G_m = Maternal genetic (co)variance matrix,

D_{pm} = Matrix of (co)variances among permanent maternal environment effect,

I_{pm} = Incidence matrix corresponding to (co)variances among permanent maternal environment effects,

R_e = Matrix of (co)variances among residual environmental effects,

I_e = Incidence matrix corresponding to (co)variances among residual environmental effects.

4.3.3. Computing Strategies of MTDFREML Method

The data for the four trait mixed animal model was analysed using the Multiple-Trait Derivative Free Restricted Maximum Likelihood (MTDFREML) set of programs developed by Boldman et al. (1995) to obtain estimates of (co)variances. The mixed model equations were of the order of 52,893 comprising a total of 6,886 animal genetic effects for each of the four traits, 6,886 maternal genetic effects for each of the three growth traits and 1,480 permanent maternal environment effects for the three growth traits, and the fixed effects. The “MTDFRUN” part of the MTDFREML programs was executed for an initial 5,000 rounds of iterations with the “cold start”, i.e. the fresh run. The estimates of

(co)variances obtained from the previous bivariate analyses (Rasali et al. 2001a; Rasali et al. 2001b) and also some estimates extrapolated from the literature were used as the starting values of (co)variance matrices required for initializing the iterative process used in the analysis. The convergence criterion for maximization of the likelihood Simplex function assigned for the model was set at 1.0×10^{-8} . This run was followed by subsequent 5,000 rounds of “continuation” run, if the desired convergence level was not achieved. The procedure right from the “cold start” was executed repeatedly using the (co)variance estimates obtained from the preceding run as the starting values each time in order to realize the global convergence across the components of (co)variances such that there was no difference in the estimates of the genetic parameters from the last two consecutive runs.

The MTDFREML programs were run on the High Performance Computing (HPC) platform using the machine named “Polaris” at the University of Manitoba. The machine runs on the Solaris 8 Operating System from Sun Microsystems, equipped with twenty 1050 MHz Ultra Sparc II CPUs. Approximately 5% of the memory of one of the CPUs was utilized during each run. Each run lasted for a period from 24 h to 7 days.

4.3.4. Gibbs Sampling of Four Trait Animal Model

MTGSAM, a set of programs developed to apply Gibbs sampling to animal models for variance component estimation (Van Tassell and Van Vleck 1995; Van Tassell and Van Vleck 1996) is a Bayesian method of Monte Carlo numerical integration that allows inferences to be made about joint or marginal distributions. The programs were implemented for the data set and the mixed animal model for the four traits, BW, WW,

YW and CD1 that were identical to those used for the MTDREML runs described above. The Gibbs Sampling was used as an iterative scheme to draw samples from full conditional distributions of genetic, permanent maternal environmental and residual error effects as defined in the animal model for the four traits, based on the "informative" or proper priors for the random effects of (co)variances that followed Inverted Wishart (IW) distributions and the "non-informative" or flat priors for the fixed effects that followed multivariate normal distributions. The details about these distributions are described by Wang et al. (1993, 1994), and Van Tassell and Van Vleck (1996). The fully conditional distributions of the (co)variance matrices of genetic, permanent environmental and residual effects were derived from their joint distributions as described by Van Tassell and Van Vleck (1996).

All starting values used for Gauss-Seidel iterations of mixed animal model equations in the Gibbs Sampling procedure were the (co)variance estimates obtained from the MTDFREML analysis that had attained global convergence. The convergence criterion for maximization of the likelihood function of the model in the Gauss-Seidel iterations that run as an initial part of the MTGSAM programs was set at 1.0×10^{-8} . The Gibbs Sampling process used in the present study involved drawing random samples from distributions of parameter levels for each fixed effect factor and also from distributions of variance components. This process can be controlled by several criteria; among them is an integral variable referred to as the "shape parameter", which represents the degree of certainty for the prior distribution (Van Tassell and Van Vleck 1996). The values of the shape parameters for the (co)variance matrices were set to reflect a very high "degree of

belief” in the corresponding prior values. There were two reasons for this. Firstly, the use of flat priors for random effects in the present study led to improper posteriors due to some of the genetic variances from the Gibbs sampler being improper or even “trapped at zero” as discussed by Hobert and Casella (1996). Secondly, the starting values used for initial Gauss-Seidel iterations were the (co)variance estimates that were presumably precise and globally converged in the MTDFREML analysis resulting in all prior (co)variances as being known (Wang et al. 1994).

Initially, a number of trial sets of Gibbs samples were generated to check if the Gibbs Sampling was running towards attaining the desired convergence as indicated by the posterior distributions of the (co)variance components. Based on the experience gained from these trials, a total of 360,000 rounds of Gibbs sampling iterations with the initial 60,000 rounds discarded as burn-in were carried out. For analysis purpose, one sample of each (co)variance was taken every 60 rounds to minimize the level of autocorrelation among samples to a negligible level. This yielded a final total of 5,000 Gibbs samples which were assumed to behave as if they were drawn independently. Under the HPC platform of Polaris machine, approximately 30,000 to 40,000 rounds of Gibbs Sampling were generated per day showing the highly demanding, though not unfeasible, computational requirements for the iterative process of Gibbs sampling.

4.3.5. Convergence Analysis of Gibbs Samples

The determination of the length of a Gibbs sample chain to be generated is usually a challenging task due to the uncertainty of its adequacy in attaining its convergence. A

Gibbs sampling process can be said to have achieved this convergence or “stationarity” when the samples drawn independently follow the expected distribution. A combination of summary statistic estimations, graphical representations and convergence diagnostics of the single chain of Gibbs samples generated was performed for this purpose, using the Bayesian Output Analysis (BOA) software. The program was a version improved by Smith (2001) based on previous Convergence Diagnosis and Output analysis (CODA) software developed by Best et al. (1995), and is available under General Public License of Free Software Foundation. The simple statistics, graphical representations, namely density plots, running mean plots and trace plots and the results of quantitative analyses derived from the software provided intuitive as well as empirical evidences of convergence.

Theories and procedures of the various convergence diagnostic methods have been summarized by Cowles and Carlin (1996), Brooks and Roberts (1998) and Smith (2001). Briefly, three quantitative methods were used for the analysis of individual chains of Gibbs samples generated in the present study. The basic purpose of using these methods was to diagnose if the sampled values of the (co)variances were drifting away from their stationarity in the iterative sampling process. Autocorrelation analysis available in the convergence diagnostic software provided the assessment as to whether the Gibbs samples are drawn independent of each other. Using Geweke’s spectral density diagnostic method, the two fractions comprising the first fraction ($n_A = 0.1n$) and the last fraction ($n_B = 0.5n$) of iteration samples (n = number of samples) from the Gibbs chain were compared for diagnosis of its convergence. The null hypothesis was tested using a Z-statistic calculated as the difference between the means of two fraction samples divided by the asymptotic

standard error of their difference. If the null hypothesis is rejected, it indicates that the chain has not converged by the start of the sample chain, n_0 . Using Heidelberger and Welch's (H-W) convergence diagnostic method, the null hypothesis of stationarity was tested using the Cramer-von-Mises statistic. The program carried out an iterative procedure, based on repeated hypothesis tests of the statistic discarding first 10% of the Gibbs samples at every instance until the resulting chain passed the test, or failed when more than 50% of the samples were discarded. In addition, a H-W halfwidth test was performed on the sample chain, portion by portion, for passing the stationarity test. Raftery and Lewis's Convergence Rate Estimator method was used in order to test the convergence distribution and to estimate the run-lengths of the Gibbs sample chains needed to accurately estimate quantiles of functions of the parameters.

4.4. RESULTS AND DISCUSSION

4.4.1. Convergence of Gibbs Sample Chains

There were a number of diagnostic tests used to assess the convergence of the Gibbs sample chain for each genetic parameter. Some of the several quantitative and qualitative tests were applied in combination, as any one such diagnostic test should not be individually relied upon (Brooks and Roberts 1998). The results of autocorrelation analyses of Gibbs sample chains for all estimated genetic parameters revealed negligible autocorrelation coefficients in the range from -0.01 to 0.09 at lag 1 as illustrated in Figure 4.1 indicating that the final Gibbs chain of 5,000 samples (drawn as one in 60 original samples) behaved as having drawn independently of one another. It was necessary for these samples to be independent, as the autocorrelated samples tended to result in slow convergence of the sample chain (Smith 2001). The probability density plots of the Gibbs posterior samples showed a fairly smooth distribution curve of the samples for each genetic parameter as illustrated in Figure 4.2. Their cumulative running mean plots (Figure 4.3) and trace plots (Figure 4.4) indicated satisfactory level of a “stationarity” with the trend of no significant drift in the parameter values in the sample chains. Geweke’s diagnostic test of the Gibbs samples showed nothing against the convergence ($P > 0.05$), while H-W tests of convergence “passed” for all of the genetic parameters. Similarly, Raftery and Lewis’s diagnostic test showed adequacy in run-lengths of Gibbs sample chains generated in terms of estimating the 2.5% quantile of the parameter distribution with the desired accuracy of ± 0.005 . These diagnostic tests have shown improvement over

a smooth distribution curve, which Wang et al. (1994) considered as the evidence of convergence.

4.4.2. The Estimates and Confidence Measures of Genetic Parameters

Estimates of direct and maternal genetic (co)variances for three juvenile growth traits and first calving date, and their corresponding estimates of heritabilities and genetic correlations derived from MTDFREML analysis are presented in Table 4.4. The corresponding genetic parameter estimates derived from the MTGSAM Gibbs sampling with their measure of confidence are presented in Table 4.5. The estimated values of all genetic parameters from these two methods were fairly consistent. The Gibbs sampling method provided the lower and upper bounds of 95% confidence intervals of the estimated parameters. For the purpose of discussion, the MTGSAM estimates of genetic parameters with their confidence measure are referred to, in subsequent sections.

4.4.2.1 Direct heritabilities

The moderate to high estimates of direct heritability (h^2) for BW, WW and YW (Table 4.5) were generally well within the ranges of their numerous literature estimates that have been abundantly reviewed (Meyer 1992; Swalve 1993; Mohiuddin 1993; Davis 1993; Koots et al. 1994a and Rust et al. 1998). The individual estimates in the literature varied widely because they were estimated for various herds or breeds of beef cattle under varying environments using various models of analyses with differing number and types of fixed and random effects.

The h^2 estimate for BW (0.51 ± 0.015) was close to the mid-point of the wide range of h^2 literature estimates (0.14 to 0.78) cited by three major reviews (Meyer 1992; Mohiuddin 1993; Davis 1993) for the trait, although it was somewhat higher than the weighted mean (0.31) of some 167 literature estimates summarized by Koots et al. (1994a). The present h^2 estimate was also very close to a literature estimate (0.48) for the Angus cattle in Canada (Trus and Wilton 1988). A number of estimates reported in the past decade by Rege and Famula (1993), Swalve (1993), Meyer (1994), Meyer (1995b), Robinson 1996), Mostert et al. (1998) and Mwansa et al. (2002) were either in agreement with or very close to the present estimate. Meyer (1993) and Burrow (2001), both of whom included direct and maternal genetic effects, permanent maternal environmental effects and direct-maternal genetic correlation (r_{am}) for the trait in their models of analysis similar to the present study, also reported fairly comparable estimates between 0.38 and 0.67.

The h^2 estimate for WW (0.70 ± 0.019) was well within, and somewhat closer to the upper limit of, the widely variable range of literature estimates (0.06 to 0.88) that were reviewed by Mohiuddin (1993). Some of the individual h^2 literature estimates that were in agreement with the estimate in the present study were reported by Meyer (1992) and Meyer (1994) with maternal effects and direct-maternal genetic correlation included in the univariate model of analysis for Zebu cattle. The other estimates close to the estimate in the present study were in the range from 0.50 to 0.66 reported by Meyer (1993), Meyer (1994), Brown et al. (1990 as cited by Meyer 1992) and Skrypzeck et al. (2000). The present estimate, however, was much higher than several of the literature estimates reviewed by Meyer (1992), Swalve (1993) and Mohiuddin (1993). It was, also, much

higher than the estimate of 0.30 reported by Rust et al. (1998), the average estimate of 0.22 reported by Davis (1993), and the weighted mean of 234 literature estimates, 0.24 (Koots et al. 1994a).

The h^2 estimate for YW (0.52 ± 0.016) in the present study was close to an estimate (0.50) reported by Rege (1985) for yearling weight as a calf's trait, while somewhat higher literature estimates from 0.66 to 0.80 were also reported by Rege (1985) using the yearling weight as the dam's trait. The present estimate is also fairly comparable to the average (0.45) of the literature estimates reviewed by Woldehawariat et al. (1977). However, the present estimate was somewhat higher than the average of 35 literature estimates (Mohiuddin 1993) and the weighted mean, 0.35 of some 147 literature estimates summarized by Koots et al. (1994a). Other individual literature estimates that were somewhat lower but comparable to the estimate in the present study were in the range from 0.36 to 0.40 obtained by univariate analysis and 0.49 by bivariate analyses both reported in Angus cattle (Meyer 1994), and an estimate of 0.37 reported by Swalve (1993). It was also higher than a more recent estimate (0.31) reported by Burrow (2001).

Clearly, the h^2 estimates of three juvenile growth traits in the pooled population of five herds in the present study were found more towards the upper bounds of their corresponding ranges of literature estimates. Previous bivariate analyses of the largest subset (herd A) of the five herds had revealed comparable h^2 estimate for BW (Rasali et al. 2001a; Rasali et al. 2002), but relatively low estimates for WW and YW (Rasali et al. 2002). Relatively much higher estimates for WW and YW in the present study are attributed at least partly to improvement in the model of analysis with the inclusion of

genetic groups and multiple traits removing possible bias from the selection in the “base” population, and increasing the sample size by pooling of whole-herd data from the larger herd with other four smaller herds. Further complexity in the model through partition of direct and maternal genetic effects in the analysis of four traits might have also contributed to the higher estimates. However, the results in the present study are not surprising considering the well known nature of moderate to highly heritable growth traits. Meyer (1992, 1994) showed how h^2 estimates of BW, WW and YW changed depending upon the inclusion of maternal genetic and permanent maternal effects in the models. In general, the estimates reported by these authors from the models with inclusion of maternal effects tended to be somewhat lower than the estimates from the models without these effects.

The h^2 estimate for CD1 (0.18 ± 0.009) (Table 4.5) was consistent with the heritability estimate for first calving date (0.17) reported by Meacham and Notter (1987), and close to the estimate (0.20) reported by Buddenberg et al. (1990). However, it was relatively higher than other literature estimates, 0.09, 0.09 and 0.10 reported for the trait in other three studies (Azzam and Nielsen 1987; Smith et al. 1989b; Johnston and Bunter 1996, respectively). The present estimate of direct heritability for CD1 was somewhat higher than the average (0.07) of 10 literature estimates for the repeated records of calving date of older cows (Koots et al. 1994a). First calving date is a function of puberty, date of breeding and the gestation length of the beef heifer, and is likely a trait different from the calving date expressed by older cows.

4.4.2.2 Maternal heritabilities

The maternal heritability (m^2) estimates for BW, WW and YW, 0.10 ± 0.005 , 0.20 ± 0.009 and 0.06 ± 0.003 , respectively (Table 4.5), were proportionately much smaller than the corresponding direct heritability (h^2) estimates. The m^2 estimate for WW was the highest followed by that for BW and YW. This pattern in magnitudes of the estimates for the three traits could be collated with physiological phenomena in that the maternal effects were the largest for weaning weight via the post-natal effects (mainly through the dam's milk) as well as carry-over pre-natal effects provided through the dam's uterine environment. On the other hand, only pre-natal effects were present for birth weight, and both these effects were reduced drastically after weaning but had still some carry-over effects on yearling weight. This pattern of the m^2 estimates was in agreement with numerous literature estimates extensively reviewed (Meyer 1992; Swalve 1993; Davis 1993; Mohiuddin 1993; Koots et al. 1994a; Rust et al. 1998; Mostert et al 1998). These literature estimates varied widely with their ranges from 0.03 to 0.82 for BW and from 0.04 to 0.52 for WW (Meyer 1992; Mohiuddin 1993). The m^2 estimate for BW in the present study was in agreement with the mean of 38 literature estimates (Mohiuddin 1993). Similarly, the estimate for WW was consistent with the mean (0.20) of 38 literature estimates for the trait reviewed by Koots et al. (1994a). On the other hand, the maternal heritability of YW in the present study was slightly lower than the mean (0.11) of 23 literature estimates for YW as reviewed by Mohiuddin (1993) and the mean of estimates (0.11) as reported by Koots et al. (1994a).

Among the individual estimates of m^2 for BW, WW and YW from the literature, several estimates reported (Rege 1985; Trus and Wilton 1988; Meyer 1992; Meyer 1993; Meyer et al. 1993; Swalve 1993; Meyer 1995a; Robinson 1996; Mwansa et al. 2002) were either in agreement with, or very close to the corresponding estimates found in the present study. Some of the other estimates reported by these authors also varied considerably depending upon the breeds, sets of data, methods of analysis used, and the fixed and random effects included in the models (Meyer 1992; Meyer 1994; Meyer 1995a). Meyer (1992) reported estimates for Australian Angus cattle for BW, WW and YW to be 0.102, 0.177 and 0.058, respectively using a model of analysis that included direct and maternal genetic effects and direct-maternal genetic correlations. Skrypzeck et al. (2000) found similar estimates for BW and WW, 0.14 and 0.21, respectively. Another recent study (Burrow 2001) found the estimates for BW, WW and YW to be relatively higher, 0.18, 0.34 and 0.11, but they still followed an order of magnitude similar to that found in the present study. More recent estimates, 0.14, 0.18 and 0.10 reported for BW, WW and YW, respectively (Rasali et al. 2001), from the largest subset of the present data were also consistent with the present estimates.

4.4.2.3 Direct genetic correlations

The direct genetic correlations (r_g) for the trait pairs, BW-WW, BW-YW and WW-YW were 0.31 ± 0.021 , 0.41 ± 0.023 and 0.90 ± 0.007 , respectively (Table 4.5), which are well within the corresponding ranges of literature estimates, from 0.36 to 0.83, 0.26 to 0.57 and 0.16 to 0.92, respectively summarized by Mohiuddin (1993). The order of

magnitude and direction of estimates in the present study for the three trait pairs were in agreement with numerous literature estimates extensively reviewed by Mohiuddin (1993), Davis (1993) and Koots et al. (1994b).

The positive r_a estimates among three juvenile growth traits were in general agreement with several individual corresponding estimates reported by Rege (1985), Nelsen et al. (1986), Smith et al. (1989b), Swalve (1993), Robinson (1996), Mostert et al. (1998) and Burrow et al. (2001). However, these published estimates were somewhat higher figures than the corresponding values for BW-WW and BW-YW pairs of traits in the present study. A number of studies (Rust et al. 1998; Mostert et al. 1998; Burrow et al. 2001) reported the direct genetic correlation estimates between WW and YW approaching unity in agreement with the present study. On the other hand, Rust et al. (1998) reported low and negative estimates of direct genetic correlations, -0.10 and -0.12 for BW-WW and BW-YW pairs, respectively, in contrast to the general trends across the literature estimates as well as the results of the present study; this substantial discrepancy was assumed by the authors to be due to various reasons including differences in selection history indicating the true genetic differences in the population studied, differences in testing schemes and the four trait model of analysis used.

Estimates of correlations of direct genetic effects (r_a) of first calving date (CD1) was low negative (-0.01 ± 0.031) with BW, moderate positive (0.28 ± 0.031) with WW and low positive (0.04 ± 0.034) with YW. The latter two estimates in the present study were comparable to positive but relatively low genetic correlation estimates of days to first calving with weaning weight ($r_a = 0.10 \pm 0.20$) and yearling weight ($r_a = 0.08 \pm 0.18$)

reported by Johnston and Bunter (1996) considering the standard errors in their estimates. On the other hand, the present results were in contrast to other published r_a estimates for CD1-WW and CD1-YW, -0.53 and -0.13, respectively, reported by Smith et al. (1989b) who had reported a positive estimate, but exceeding unity between CD1 and BW. Similarly, a more recent study (Burrow et al. 2001) also reported moderate negative r_a estimates, -0.18 and -0.34 for genetic correlations of days to calving with WW and YW, respectively, while the r_a estimate between days to calving and BW reported by Burrow (2001) was positive and moderate, 0.22. However, none of these published estimates had used the models to separate direct genetic effects from the maternal genetic effects of growth traits to estimate their genetic correlations. The estimates in the present fairly robust analysis have taken account of bias from selection in the base population and used more information to account for the interrelationships among the multiple traits resulting in more reliable estimates. Clearly, the animals selected for direct genetic effects of WW had direct genetic tendency to delay the first calving.

4.4.2.4 Maternal genetic correlations

The estimates of maternal genetic correlations (r_m) between trait pairs, BW-WW and BW-YW were moderate, 0.20 ± 0.032 and 0.32 ± 0.021 , respectively, while that between WW and YW was high positive approaching unity (0.98 ± 0.002). Koots et al. (1994b) reviewing six literature estimates corresponding to r_m for BW-WW trait pair found their mean to be 0.33 which was fairly comparable to the value in the present study. The range of 26 individual literature estimates of r_m published for BW-WW trait pair (Swalve 1993;

Meyer 1993; Meyer et al., 1993; Meyer 1994; Meyer 1995a; Mostert et al. 1998; Rust et al., 1998) was from 0.14 to 0.83 averaging 0.50 ± 0.19 . This excluded a negative but negligible estimate (-0.04) and an another estimate near zero reported for the trait pair (Meyer 1993; 1995a). The figures close to the estimate in the present study were 0.28 and 0.24 reported from a pooled data set (Meyer 1993) and from a four trait animal model (Rust et al. 1998), respectively. On the other hand, 27 published estimates of r_m for BW-YW pair of traits ranged from 0.10 to unity (Swalve 1993; Meyer 1993; Meyer et al. 1993; Meyer 1994; Meyer 1995a; Mostert et al. 1998; Rust et al. 1998) averaging 0.58 ± 0.23 ; this again excluded a negative estimate (-0.126) reported by Meyer (1994) from a data set for Angus cattle. Despite this wide range in the literature estimates, a number of figures very close to the estimate in the present study were 0.318, 0.32 and 0.31 reported by Swalve (1993), Mostert et al. (1998) and Rust et al. (1998), respectively; the latter two estimates, in particular, were derived from four trait animal models similar to the present study. The r_m estimate for the WW-YW trait pair was in agreement with the most of the 28 published estimates that were approaching unity, with an average of 0.93 and standard deviation of 0.10 (Swalve 1993; Meyer 1993; Meyer et al. 1993; Meyer 1994; Meyer 1995a; Mostert et al. 1998; Rust et al. 1998).

4.4.2.5 Direct-maternal genetic correlations

The estimates of direct-maternal genetic correlations (r_{am}) for each of three juvenile growth traits analysed in the present study were all negative; the values for BW, WW and YW were -0.09 ± 0.029 (the lowest) -0.61 ± 0.020 (the highest), and -0.30 ± 0.030 ,

respectively (Table 4.5). These results were in the same direction as the numerous negative published estimates extensive reviewed Meyer (1992), Mohiuddin (1993), Koots et al. (1994b) and Rust et al. (1998), although these reviews also included a few positive estimates. Mohiuddin (1993) reviewed 27 published estimates for r_{am} of BW which ranged from -1.05 to 0.55 averaging -0.35, 26 estimates for r_{am} of WW which ranged from -0.91 to 0.26 averaging -0.15, and 10 estimates for r_{am} of YW which ranged from -0.91 to 0.49 averaging -0.26. Among these estimates, a number of estimates were also equal to or very close to the corresponding estimates in the present study. The individual published estimates that were comparable with the present study were -0.05, -0.59 and -0.41 reported for BW, WW and YW, respectively, in Australian Hereford cattle (Meyer 1992), and -0.04, -0.39 and -0.22, respectively, reported in Australian Simmental cattle (Swalve 1993). Several other studies (Trus and Wilton 1988; Meyer 1993; Tawah et al. 1993; Meyer 1994; Robinson 1996; Mostert et al. 1998; Rust et al. 1998; Skrypzeck et al. 2000; Burrow et al. 2001) showed also negative estimates for these traits, but in a wide range of magnitudes. On the other hand, Meyer (1992), and Meyer (1994) found positive values of these parameters particularly from data sets for Australian Angus cattle. Overall, the present study reiterated an antagonistic genetic association between calf's growth and its future maternal ability for growth of its offspring, which is consistent with the corresponding negative literature estimates for direct-maternal genetic correlations of growth traits (Meyer 1993). Willham (1972) gave an explanation to the negative genetic correlation between the direct and maternal genetic effects as the dam either giving her offspring a "plus" set of genes for the direct effects and "poor" maternal effect or the

reverse. There is an alternative explanation for the observed negative correlation between direct and maternal genetic effects on growth traits. Daughters that are reared in a superior maternal environment appear to be compromised in their own abilities of being good mothers. This may be the result of the faster growing daughters depositing adipose tissues in the udder early in life, at the expense of mammary gland secretory tissues (Mangus and Brinks 1971). Meyer (1992) and Meyer et al. (1993) have discussed downward bias in the direct-maternal genetic correlations that may result from the environmental correlation between generations.

There were generally negative direct-maternal genetic correlations between all combinations of pairs of three juvenile growth traits in the present study except for the positive estimates that were found when the maternal genetic effects of birth weight (BW_m) was involved. The present low negative estimate (-0.08 ± 0.030) between BW_a and WW_m (Table 4.5) was in close agreement with that reported by Meyer (1993). This was comparable with the mean (-0.12) of five literature estimates reviewed by Koots et al. (1994b), and with the individual low estimate (-0.031) reported by Swalve (1993). Several other studies (Meyer et al. 1994; Mostert et al. 1998; Mwansa et al. 2002) reported the estimates in various breeds ranging from -0.55 to -0.14 , while a few positive and moderate literature estimates were also reported particularly in Angus cattle (Meyer 1994, Rust et al. 1998). Similarly, the negative r_{am} estimate between BW_a and YW_m (-0.20 ± 0.029) from the present study was in close agreement with a few estimates between -0.17 and -0.26 reported by Mostert et al. (1998). The other published estimates varied in the wide range

from -0.56 (Mostert et al. 1998) to near zero (Meyer 1993; Meyer 1994), except for an estimate of 0.086 reported by Meyer (1994).

The moderately high negative r_{am} estimate (-0.58 ± 0.021) between WW_a and YW_m (Table 4.5) in the present study was in general agreement with the estimates, -0.58 in Simmental cattle reported by Rust et al. (1998), and -0.52 in Zebu Cross cattle reported by Meyer (1994); it was also comparable to a range of estimates from -0.68 to -0.37 reported by Mostert et al. (1998). A few corresponding moderate negative estimates from -0.42 to -0.24 were reported by Meyer (1993) and Meyer (1994), while the estimates of much lower magnitude (Meyer 1994; Mostert et al. 1998) up to -0.01 and much higher magnitude (Mostert et al. 1998; Rust et al., 1998) up to -0.79 were also reported.

The moderate negative r_{am} estimate, -0.30 ± 0.030 between YW_a and WW_m (Table 4.5) in the present study was in close agreement with the corresponding two estimates, -0.30 and -0.28 among a range of estimates from -0.75 to -0.28 reported by Mostert et al. (1998). The present estimate was also comparable to other estimates in the literature, -0.21 reported by Meyer (1993) and -0.42 ± 0.15 reported by Meyer (1994). In contrast, a few estimates were either much lower negative estimate, -0.047 (Swalve 1993) or even a low positive estimate, 0.14 (Meyer 1994).

The r_{am} estimate, 0.27 ± 0.031 between BW_m and WW_a (Table 4.5) in the present study was comparable with the corresponding estimates reported in the range from 0.34 to 0.39 for the trait pair (Meyer 1994), was relatively higher than the estimate (0.13) reported by Rust et al. (1998). The present r_{am} estimate between BW_m and YW_a pair, 0.38 ± 0.028 (Table 4.5) was much lower than the corresponding estimate, 0.72 reported by Meyer

(1994), while Rust et al. (1998) also reported positive but relatively low estimate, 0.09 for the corresponding trait pair. These results indicated that when the maternal genetic effects of BW mainly through pre-natal effects is involved, it might not necessarily have antagonistic relationship with the post-natal growth traits which receive maternal genetic effects mainly through dam's milk. However, these results were inconsistent with other studies (Swalve 1993; Meyer 1993; Mostert et al. 1998), which reported corresponding estimates to be negative in the ranges from -0.42 to -0.07 and from -0.47 to -0.01 to -0.47, respectively for $BW_m - WW_a$ and $BW_m - YW_a$, indicating the possibility of the sampling errors also playing a significant role in r_{am} between any two different growth traits.

The r_{am} estimates between $CD1_a - BW_m$, $CD1_a - WW_m$ and $CD1_a - YW_m$ pairs of traits, were 0.02 ± 0.033 , -0.73 ± 0.016 and -0.75 ± 0.015 , respectively (Table 4.5). These results indicated a negative genetic association particularly between the post-natal maternal genetic effects of juvenile growth traits and the direct genetic effects of CD1. These r_{am} results can be viewed mainly as the favorable genetic relationship that existed between the cows' own efficiency in attaining successful early calvings and cows' contribution mainly through their milk to faster growth during post-natal juvenile stages of their calves. However, this being the first study to partition these genetic effects in the mixed animal model of genetic analysis, there are no other published estimates available for comparison.

4.4.3. Permanent Maternal Environmental Effects

The proportions of permanent maternal environmental effects (c^2_{pm}) estimated for three juvenile growth traits and their correlations (r_{pm}) along with their corresponding

(co)variances are presented in Table 4.6. These effects of all individual juvenile growth traits were found to be negligible possibly with not much consequence to the animal performance for the trait. These results are generally in agreement with other studies which reported lesser significance of the estimates (Robinson 1996). Similarly, the estimates of correlations between BW-WW and BW-YW pairs of traits were negative but low, -0.009 and -0.12, respectively, while the estimate between WW and YW was approaching unity. These correlations are likely to be of minimal consequence, however, due to low magnitude of the permanent maternal environmental effects.

4.4.4. Residual Environmental Effects

The proportions of residual environmental effects (e^2) estimated for the three juvenile growth traits and the first calving date and their correlations (r_e) along with their corresponding (co)variances are presented in Table 4.7. The e^2 estimates for BW, WW and YW were moderate, 0.38, 0.37 and 0.51, respectively, while that for CD1 was very high, 0.84. The estimates of the residual environmental correlations among the three juvenile growth traits were moderate to high and positive in direction. These results indicated that the residual environmental effects on the performance of growth traits were not antagonistic to the direct as well as maternal genetic effects which have similar trends in their corresponding correlations. The residual correlation coefficient between BW and CD1 was also positive but very low (0.02). On the other hand, the corresponding coefficients between WW-CD1 and YW-CD1 pairs of traits were negative and moderate

in magnitude, -0.19 and -0.15, respectively indicating their favorable residual environmental relationships.

4.4.5. Pertinent Issues Arising from the Present Analysis

Literature relating to genetic parameters in beef cattle is enormously rich, particularly in the estimates of heritabilities and genetic correlations of various growth traits. They have been sufficiently reviewed and summarized on an international scale from time to time by various researchers (Woldehawariat et al. 1977; Meyer 1992; Mohiuddin 1993; Davis 1993; Koots et al. 1994a, b; Rust et al. 1998). Therefore, the quest for new knowledge does not demand further investigation into these parameters especially for three juvenile growth traits, BW, WW and YW. In the present study, however, this area of research has been revisited primarily as a part of the inquiry seeking insight into their genetic association with CD1, a measure of reproductive efficiency in beef cows, which has not been reported to any great extent in the literature. The end result is that the estimates of heritabilities and genetic correlations among the juvenile growth traits from the present study are very similar to numerous corresponding estimates published in various countries, and these can be considered to be valid estimates. This lends support to the new genetic parameters relating to CD1 and their association with the growth traits that have been estimated from the same model analysed in the present study.

The five herds analysed in the present study represent a small sample of cattle compared to the total pedigreed population of Angus cattle in Canada. It was, however, a justifiably adequate sample of herds considering the mixed animal model, the

computational demands and the available software. It was comparable or even larger in size to the data sets analysed in several studies using similar animal models (Meyer 1992, 1993, 1994, 1995a; Mostert et al. 1998 and Rust et al. 1998; Mwansa et al. 2002). The four trait animal model fitted with appropriate fixed and random effects and the inclusion of genetic groups to fix the possible selection bias in the base population has made the present analysis fairly robust. The use of high performance computing facilities of the University of Manitoba in the present study has demonstrated that the multi-trait genetic analysis with inclusion of appropriate fixed effects, direct genetic, maternal genetic and permanent maternal environmental effects is feasible with the current advancement in computing technology.

The pooled population analysed here was composed of a large breeder's herd and four smaller herds of Angus cattle from three provinces in Western Canada. This pooled population might not be very different from the total Canadian population in terms of types of herds pooled. However, the smaller herds had a somewhat discontinuous database of records of animal performance over time. There appeared to be substantial scope and need of improvement in animal recording in the smaller herds.

In the present study, apart from the estimates of direct and maternal heritabilities and genetic correlations among juvenile growth traits, a set of estimates for new parameters of interest have been estimated. In particular, as the first calving date has been found to be a moderately heritable trait, the direct genetic effects of CD1 was found to have favorable association with maternal genetic effects of growth traits, mainly WW and YW but was unfavorable with their direct genetic effects. These new information could be

a useful consideration in multi-trait selection efforts or in determination of correlated responses in selection programs.

4.5. CONCLUSION

The estimates of both direct and maternal heritabilities of three juvenile growth traits were in general agreement with the ranges of corresponding published estimates, and the first calving date was found to be a moderately heritable trait. The direct genetic correlation between weaning weight and the first calving date appeared to be important but in a direction unfavorable to the industry, while the direct genetic correlations of birth and yearling weight with the first calving date did not show much importance. More importantly, the relationships of maternal genetic effects of the juvenile growth traits with the direct genetic effect of the first calving date that have not been reported previously were in a direction favorable to the industry. As a result, heifers with capability for providing more positive maternal genetic effects on juvenile growth of their calves tended to have genetic capabilities for her earlier first calving. The confidence measures of all genetic parameter estimates demonstrated their high precision.

Table 4.1. The numbers of animals with birth or calving records and their sires and dams in the pooled population of five Angus herds.

Herd	Province of herd location	Number of animals with birth records	Number of sires	Number of dams
A	Manitoba	3601	87	754
B	Alberta	779	87	236
C	Alberta	600	39	228
D	Alberta	967	37	211
E	Saskatchewan	495	63	160

Table 4.2. Descriptive statistics of three juvenile growth traits and first calving date in the pooled population of five Angus herds.

Trait	Number of records	Mean	CV, %
Birth weight (BW, kg)	6116	38.84	13.79
Weaning weight (WW, kg)	5360	278.35	15.40
Yearling weight (YW, kg)	4430	439.35	15.85
First calving date (CD1, days from Jan 1)	1153	67.21	46.52

Table 4.3. Covariates, fixed effects and random effects in the multiple-trait mixed model for three juvenile growth traits, BW, WW, YW, and a calving trait, CD1.

Covariates, fixed effects and random effects	Trait			
	BW	WW	YW	CD1
<u>Covariates:</u>				
Age of Dam (AOD)	✓ ^z	✓	✓	-
AOD ²	✓	✓	✓	-
<u>Fixed effects:</u>				
Herd-Year of birth	✓ (61) ^y	✓ (55)	✓ (47)	-
Season of birth	✓ (4)	✓ (4)	✓ (4)	-
Type of birth	✓ (2)	✓ (2)	✓ (2)	-
Calf sex at birth	✓ (2)	✓ (2)	✓ (2)	-
Herd-Year of calving	-	-	-	✓ (60)
Type of calving	-	-	-	✓ (2)
<u>Random effects:</u>				
Direct genetic	✓ (6886)	✓ (6886)	✓ (6886)	✓ (6886)
Maternal genetic	✓ (6886)	✓ (6886)	✓ (6886)	-
Permanent maternal environmental	✓ (1480)	✓ (1480)	✓ (1480)	-

^z A check mark (✓) denotes the presence of the corresponding factor in the model for a trait.

^y The figure in the parenthesis indicates the number of levels for each of fixed and random effects.

Table 4.4. MTDFREML estimates of genetic variances (lower diagonal), covariances (below off-diagonal), direct and maternal heritabilities (upper diagonal) and corresponding genetic correlations (upper off-diagonal) among three juvenile growth traits and first calving date.

Trait parameter	BW _a ^z	WW _a	YW _a	CD1 _a	BW _m	WW _m	YW _m
BW _a	0.52 11.04	0.31	0.42	-0.02	-0.11	-0.07	-0.20
WW _a	25.04	0.59 601.12	0.90	0.27	0.26	-0.59	-0.57
YW _a	40.39	639.55	0.44 841.87	0.06	0.35	-0.31	-0.31
CD1 _a	-0.69	64.39	17.46	0.16 92.46	0.05	-0.71	-0.74
BW _m	-0.52	9.45	15.05	0.67	0.10 2.17	0.20	0.33
WW _m	3.13	-194.89	-120.01	-91.47	3.97	0.18 180.12	0.97
YW _m	-6.68	-142.86	-92.27	-72.42	4.92	133.47	0.05 104.41

^z The traits with subscripts, _a and _m indicate the direct and maternal genetic effects, respectively for corresponding traits.

Table 4.5. The MTGSAM Gibbs sampling posterior means and confidence measures for genetic parameters estimated among BW, WW, YW and CD1.

Genetic parameters ^z	MTGSAM Gibbs samples		
	Mean \pm SE	95% Confidence interval ^y	
		Lower bound	Upper bound
$h^2_{(BW)}$	0.509 ± 0.015	0.480	0.540
$h^2_{(WW)}$	0.700 ± 0.019	0.632	0.705
$h^2_{(YW)}$	0.520 ± 0.016	0.490	0.552
$h^2_{(CD1)}$	0.184 ± 0.009	0.165	0.200
$m^2_{(BW)}$	0.104 ± 0.005	0.095	0.113
$m^2_{(WW)}$	0.198 ± 0.009	0.180	0.215
$m^2_{(YW)}$	0.063 ± 0.003	0.057	0.069
$r_{a(BW-WW)}$	0.311 ± 0.024	0.261	0.355
$r_{a(BW-YW)}$	0.414 ± 0.023	0.364	0.455
$r_{a(WW-YW)}$	0.891 ± 0.007	0.876	0.903
$r_{a(BW-CD1)}$	-0.014 ± 0.031	-0.074	0.045
$r_{a(WW-CD1)}$	0.282 ± 0.031	0.219	0.340
$r_{a(YW-CD1)}$	0.041 ± 0.034	-0.030	0.103
$r_{m(BW-WW)}$	0.204 ± 0.032	0.139	0.264
$r_{m(BW-YW)}$	0.321 ± 0.029	0.260	0.376
$r_{m(WW-YW)}$	0.976 ± 0.002	0.974	0.979
$r_{am(BW-BW)}$	-0.091 ± 0.029	-0.150	-0.035
$r_{am(BW-WW)}$	-0.078 ± 0.030	-0.138	-0.021
$r_{am(BW-YW)}$	-0.195 ± 0.029	-0.252	-0.139
$r_{am(WW-BW)}$	0.268 ± 0.031	0.208	0.326
$r_{am(WW-WW)}$	-0.606 ± 0.020	-0.648	-0.569
$r_{am(WW-YW)}$	-0.584 ± 0.021	-0.625	-0.543
$r_{am(YW-BW)}$	0.377 ± 0.028	0.323	0.432
$r_{am(YW-WW)}$	-0.297 ± 0.030	-0.356	-0.240
$r_{am(YW-YW)}$	-0.296 ± 0.030	-0.356	-0.239
$r_{am(CD1-BW)}$	0.018 ± 0.033	-0.051	0.079
$r_{am(CD1-WW)}$	-0.726 ± 0.016	-0.759	-0.696
$r_{am(CD1-YW)}$	-0.753 ± 0.015	-0.782	-0.726

^z The h^2 , m^2 , r_a , r_m and r_{am} are the direct heritability, maternal heritability, direct genetic correlation, maternal genetic correlation and direct-maternal genetic correlation, respectively of corresponding traits given in the parenthesized subscripts.

^y The highest probability density intervals at ($p < 0.05$) given by Bayesian Output Analysis (Smith 2001), corresponding to 95% confidence intervals.

Table 4.6. The estimates of permanent maternal environment variances (lower elements of diagonal), covariances (lower off-diagonal), their proportions of total phenotypic variances (upper elements of diagonal) and correlations (upper off-diagonal) among BW, WW and YW (estimates from MTDFREML analysis).

Trait parameter	BW _{pm}	WW _{pm}	YW _{pm}
BW _{pm} ^z	0.025 0.53	-0.009	-0.120
WW _{pm}	-0.05	0.057 57.97	0.990
YW _{pm}	-0.79	67.45	0.041 79.49

^z The trait with subscript, _{pm} indicates permanent maternal environmental effect for corresponding trait.

Table 4.7. The estimates of variances (lower elements of diagonal), covariances (lower off-diagonal), the variance proportions (upper elements of diagonal) and correlations (upper off-diagonal) of residual environmental effects BW, WW, YW and CD1 (estimates from MTDFREML analysis).

Traits	BW	WW	YW	CD1
BW	0.38 7.99	0.39	0.36	0.02
WW	21.31	0.37 374.33	0.70	-0.19
YW	31.83	427.29	0.51 988.12	0.15
CD1	0.96	-80.40	-105.56	0.84 493.71

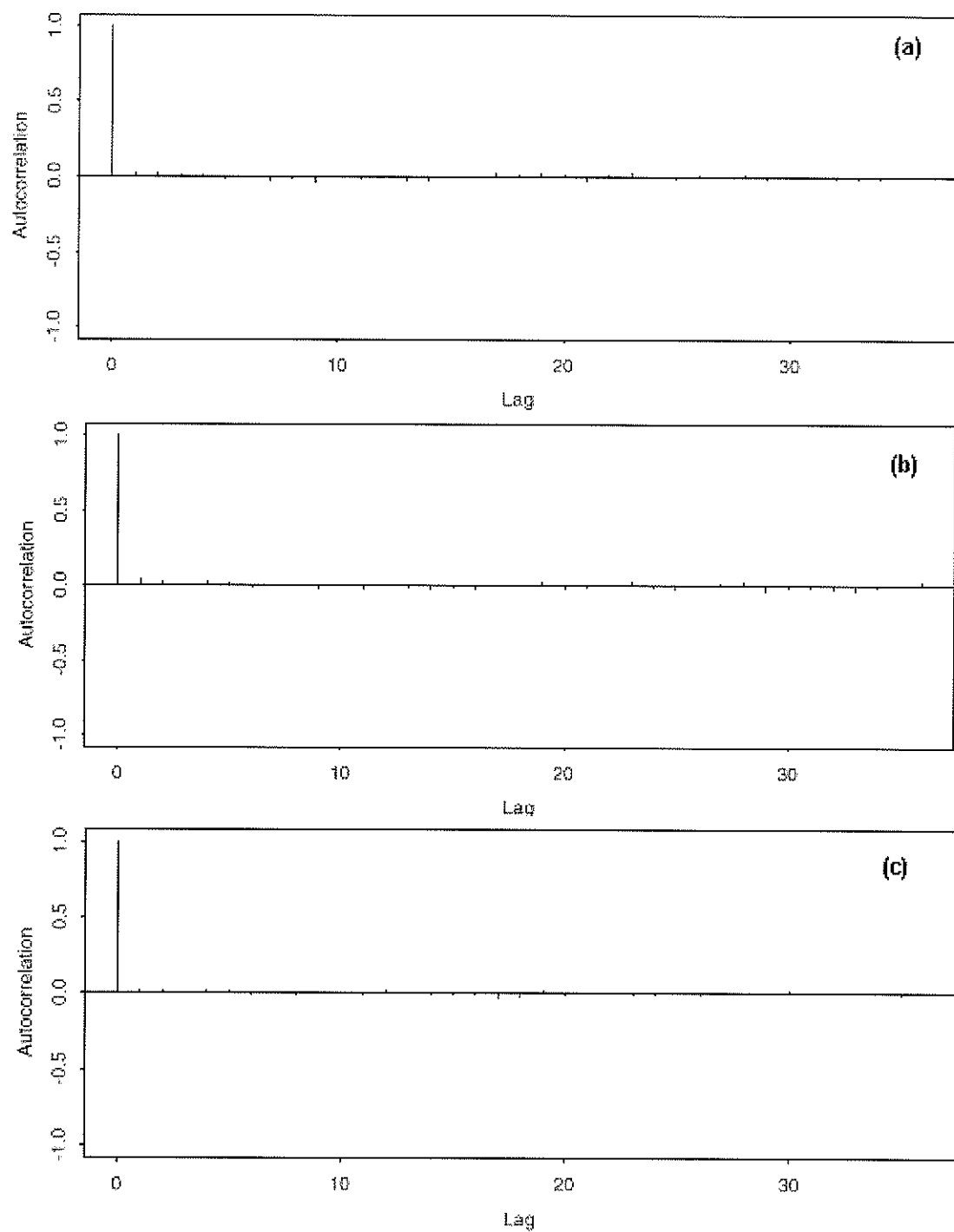


Figure 4.1. Autocorrelation plots of Gibbs iteration samples of three genetic parameters (for examples): (a) $r_{am(WW)}$, (b) $r_a(WW-CD1)$ and (c) $r_{am(CD1-WW)}$. Plots show no significant autocorrelations at lag of 1 or greater.

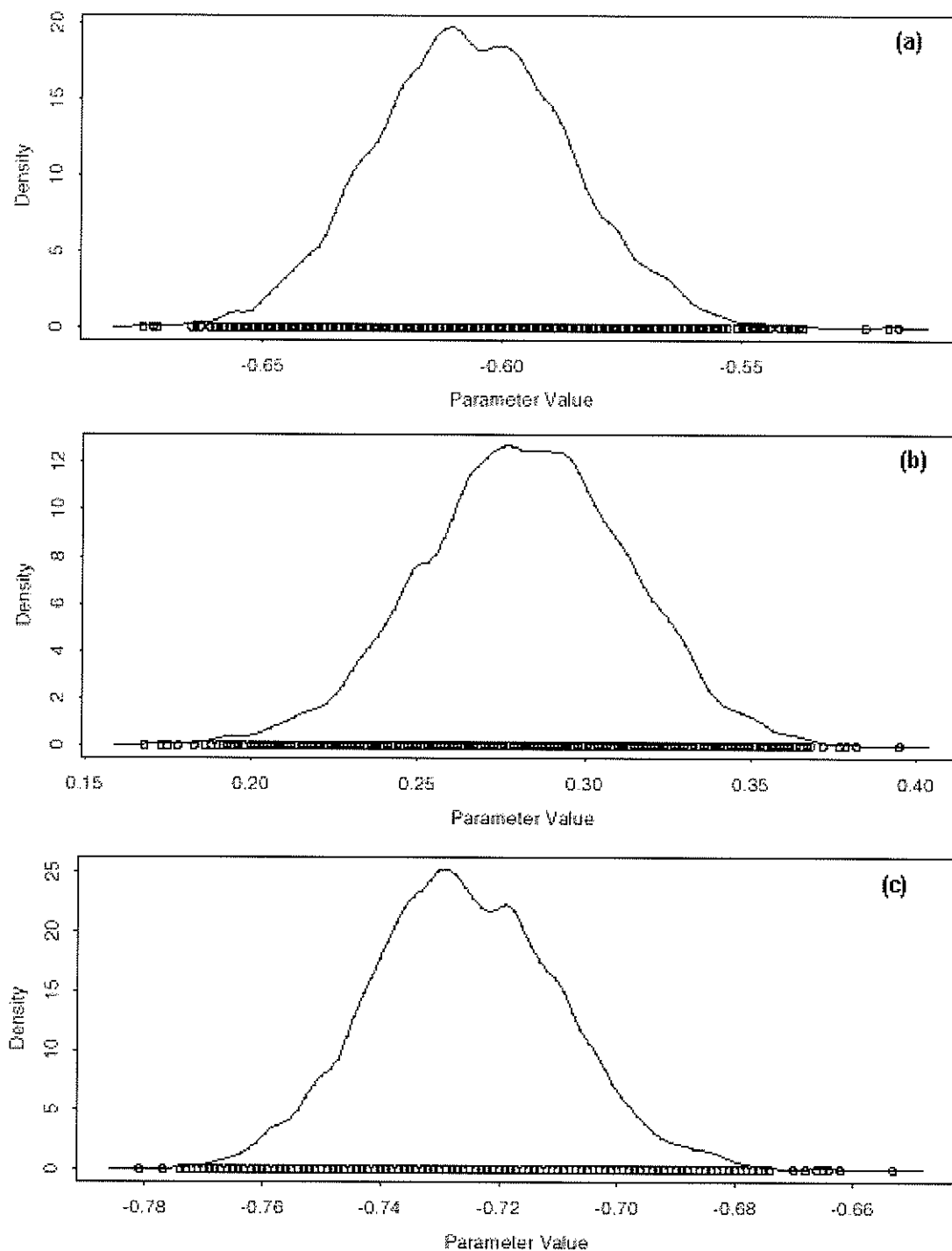


Figure 4.2. Probability density plots of Gibbs iteration samples of three genetic parameters (for examples): (a) $r_{am}(WW)$, (b) $r_a(WW-CD1)$ and (c) $r_{am}(CD1-WW)$.

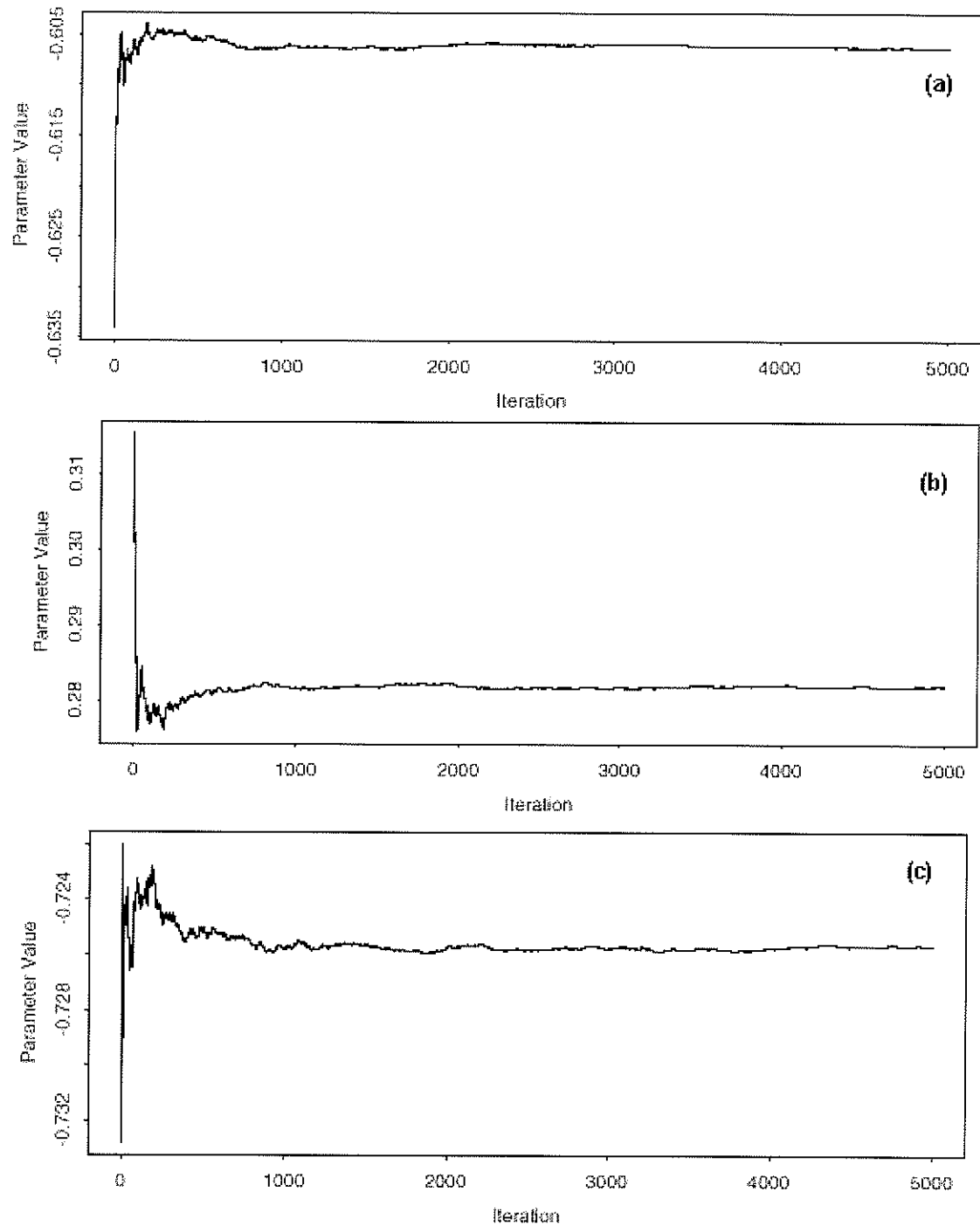


Figure 4.3. Running mean plots of Gibbs iteration samples of three genetic parameters (for examples): (a) $r_{am(WW)}$, (b) $r_{a(WW-CDI)}$ and (c) $r_{am(CDI-WW)}$.

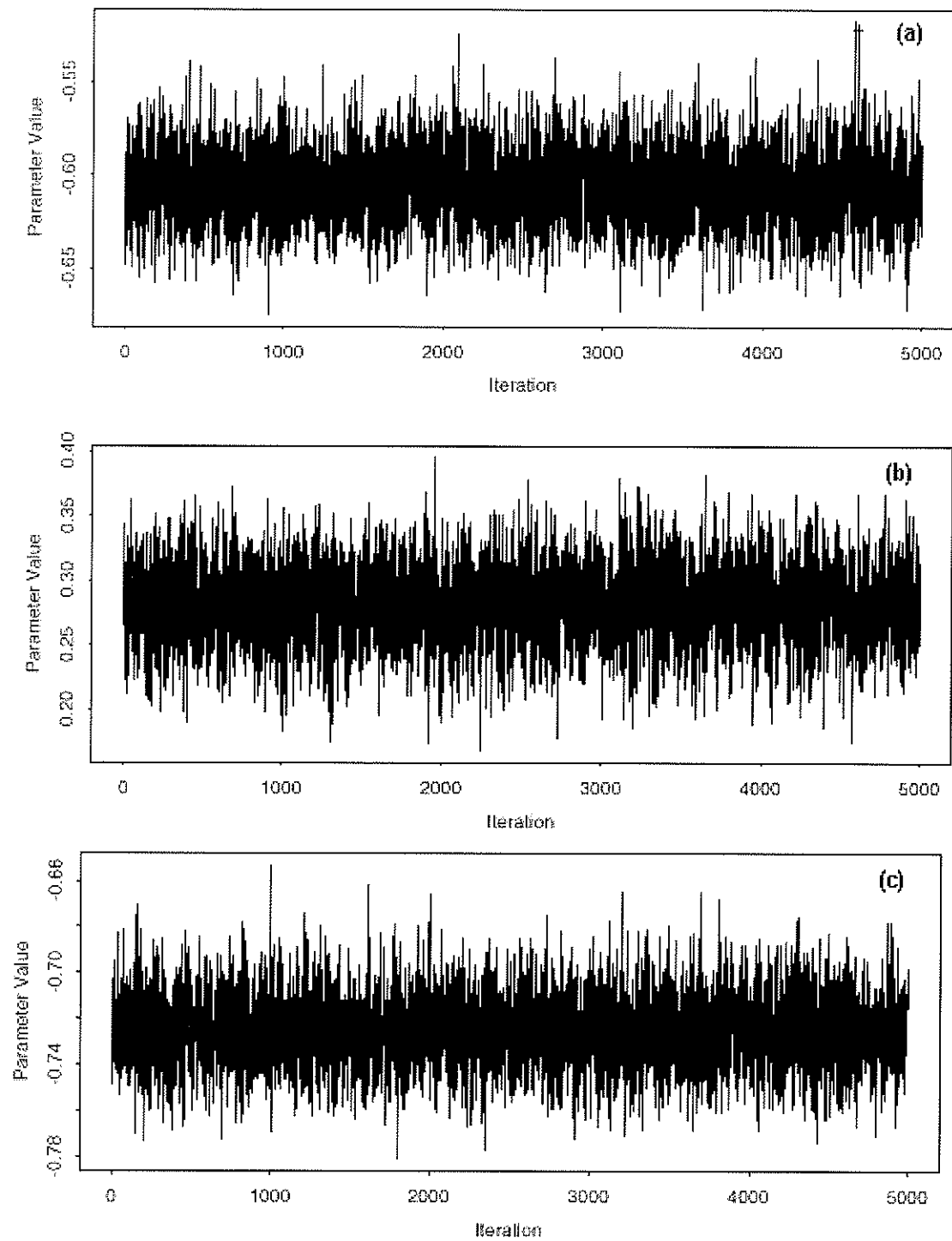


Figure 4.4. Trace plots of Gibbs iteration samples of genetic parameters (for examples):
(a) $r_{am}(WW)$, (b) $r_a(WW-CD1)$ and (c) $r_{am}(CD1-WW)$.

5. STUDY - II:

**MULTIPLE-TRAIT ANIMAL MODEL ANALYSIS OF JUVENILE GROWTH
TRAITS AND REPEATED RECORDS OF CALVING TRAITS OF COWS IN
CANADIAN ANGUS HERDS**

5.1. ABSTRACT

An analysis of records from five Angus cattle herds with 7,171 animals in the pooled pedigree was carried out for weight at birth (BW), at weaning (WW) and at one year of age (YW) of calves born between 1984 and 2001, and repeated records of the cows' calving date (CD) and calving interval (CI) with the objective of determining the genetic association among them. A multiple trait animal model that included a set of significant fixed effects (including Herd-Year contemporary groups), direct (α) and maternal (α_m) genetic effects and permanent environmental effects was applied to the data using MTDFREML. The results showed that the direct heritability (h^2) estimates of BW, WW, YW, CD and CI were 0.45, 0.70, 0.79, 0.25 and 0.10, respectively, while the maternal heritability (m^2) estimates of BW, WW, and YW were 0.18, 0.24 and 0.12, respectively. The positive estimates of direct genetic correlations (r_a , from 0.54 to 0.86) and maternal genetic correlations (r_m , from 0.12 to 0.68) among three juvenile growth traits, and their negative direct -maternal genetic correlation estimates (r_{am} , from -0.30 to -0.06) were in agreement with several literature estimates. The estimates of correlations of CD_a with direct genetic effects for the growth traits ranged from -0.31 to -0.19, and are thus favorable. Similarly, favorable genetic correlation estimates ranging from -0.36 to -0.02 were found for CD_a with maternal genetic effects on growth traits. The genetic correlations of CI_a with direct genetic effects of growth traits ranged from -0.65 to -0.29, indicating a favorable genetic association between them. Corresponding correlation estimates of CI_a with BW_m and WW_m were 0.00 and 0.07, respectively, while that with YW_m was 0.51. The genetic trends of all traits in the pooled population were significant,

and in favorable directions except for CI_a , BW_m and WW_m . The annual average genetic changes in most traits in the pooled population were generally less than the theoretically expected responses in these traits, when assuming single-trait truncation selection for either WW_a and YW_a , but higher response was observed in CD_a in both cases. These results indicate that selection practices likely involved more than one trait.

5.2. INTRODUCTION

Female reproductive efficiency is of high economic importance in beef cattle production systems (Bourdon and Brinks 1983; Rege 1985; Bruns 1994). Under a cow-calf operation, cows should normally calve every year, and wean heavier calves to produce outputs beyond the breakeven point of their replacement cost for the herd profitability. Calving traits such as calving date (CD) and calving interval (CI) measured as repeated records in the herd life of beef cows are indicators of their reproductive efficiency. These traits are generally considered as lowly heritable (Koots et al. 1994a), and have not been given adequate emphasis for their potential use in selection programs. On the other hand, the growth traits of juvenile beef animals, namely body weight at birth (BW), weaning (WW) and one year of age (YW), that are most invariably recorded in beef cattle are sufficiently well documented as moderately to highly heritable traits (Woldehawariat et al. 1977; Mohiuddin 1993; Davis 1993; Koots et al. 1994a, b; Rust et al. 1998). Many selection programs have focused mainly on these traits at various stages in the animal's life from birth to slaughter age at least for the past three decades (Trus and Wilton 1988; Meyer et al. 1991; Swalve 1993).

The association between economically important juvenile growth and reproductive efficiency traits has not been well documented. In particular, the published research results are lacking in information on relationships among direct and maternal genetic components of these traits which could have potential bearing in the selection programs. In the Study I of this thesis, first calving date (CD1) was shown to have significant genetic association with juvenile growth traits. Further investigation into the possible genetic

association between juvenile growth traits and repeated records of calving traits was imperative due to the fact that reproductive efficiency of beef cows is crucial for their life time productivity.

In order to analyse a number of economically important genetic traits of growth and reproduction, multiple trait genetic analysis is a natural choice due to advantages of accounting for certain biases in the data imposed by past selection of breeding animals (Schaeffer 1984; Henderson, 1984; Pollak et al. 1984; Thompson and Meyer 1986), and due to the approach particularly being optimal for the repeated records of certain traits included in the analysis (Simianer 1986). The present study is the first attempt to analyse five economically important traits of growth and female reproduction incorporating their potentially important direct and maternal genetic effects in a single model. The purpose of the study is to estimate genetic parameters among direct and maternal genetic effects on three juvenile growth traits and direct genetic effects on repeated records of two calving traits in Angus cattle, and their respective genetic trends, for establishing the genetic association among them.

5.3. MATERIALS AND METHODS

5.3.1. Sources of Data

A sizeable whole-herd database of Angus cattle (herd A) in Manitoba, and an additional database of relatively smaller four herds of Angus cattle, three from Alberta (herds B, C and D) and one herd from Saskatchewan (herd E), comprising their records of performance were obtained from Canadian Angus Association. All herds represented the typical commercial cow/calf operations in the Canadian Prairie Region. The numbers of animals born and their sires and dams from each herd are given in Table 5.1.

Records of calves born during the period from the year 1984 to 2001 relating to their own juvenile growth traits and their dams' calving events in the herds during their juvenile age up to one year were pooled. Among the traits, BW, WW and YW considered, the latter two were adjusted to the weights at 205 and 365 days, respectively as described in Study I. The records of CD and CI were extracted from the database of consecutive calvings by cows in their respective herds as illustrated in the SAS programming (Appendix 1). The record of CD refers to the number of days counting from a fixed day, January 1 in the present case, to the day of calving in the year of calving. Since beef cows under the prevailing production systems had a time-limited window of their breeding season, less than 4% of 6,115 calving records that occurred in the summer (June 21 - September 22) and fall (September 23 - December 21) not representing the contemporary calving events occurring in main calving periods of winter (December 22 - March 19) or spring (March 20 - June 20) were edited out for this calving trait records. Those calving

dates between December 22 and 31 were given negative values accounting for the backward counting of days. The missing records in the data set were represented by zeros; all non-zero values of each trait record falling outside the range of four standard deviations above or below its overall mean in the pooled population of five herds were edited out following the Beef Improvement Federation guidelines (BIF 1996).

5.3.2. Development of the Animal Model for Five Trait Analysis

5.3.2.1 *Fixed effects and Covariates*

The descriptive statistics of three juvenile growth traits, BW, WW and YW, and repeated records of two calving traits, CD and CI are presented in Table 5.2. The effects of various factors on each of the juvenile growth traits and the calving traits were analysed using SAS programs (SAS 1998) in order to select the significant factors for including them as fixed effects in the final model of genetic analysis. The effects of different fixed effects factors namely herd, year of birth, season of birth, type of birth, sex of calves at birth were significant on BW, WW and YW, and have been discussed elsewhere (Study III in this thesis). The contemporary groups (CG) of calves for records of these juvenile growth traits were formed by the effects of herd- year of calves' birth combining herd and year into a single factor on the consideration that year effects could vary from herd to herd. Additional factors namely, season of birth, type of birth and sex of the calf at birth were included to account for their fixed effects on the growth traits. The age of dam at birth was modeled as polynomial (linear and quadratic) covariates representing its curvilinear

relationship with each of the three juvenile growth traits as suggested by BIF (1996). The effect of herd and year of calving on both of CD and CI were highly significant ($P < 0.01$). In case of these calving traits, the fixed effects of herd- year of calving represented the CG of cows calving in the same year of calving. The season of calving was not included in the model despite being significant ($P < 0.05$) for both the calving traits, because of the possible confounding with the numerical value of CD and CI. The fixed effects and covariates finally included in the analysis of the five trait animal model are presented in Table 5.3.

5.3.2.2 Genetic groups

For a population such as the present one, in which there is significant genetic change occurring over the course of several generations, it is necessary to define the base population, for this is the group, which the genetic parameters refer to. The “base” animals, the unknown parents of animals with records or those of the known parents which did not have their own records and had only a single record of their offspring were considered as “Phantom parents”. These were grouped into genetic groups as described by Westell et al. (1988) and used by Shrestha et al. (1995), by assigning them identification numbers that were simple integer starting from “1” to “N” based on their year of birth in order to eliminate the possible biases from selection that might have occurred in the base population. A total of 36 such genetic groups were identified for the data set of pooled population of five herds. The pooled pedigree of 7,171 animals involving all five trait records provided almost a complete whole-herd pedigree of the respective herds

minimizing further possible effects of selection on the animal model analysis. There were only 973 inbred animals with the negligible average inbreeding coefficient of 0.03.

5.3.2.3 The Animal model

The mixed animal model assumed for analysis of five traits, BW, WW, YW, CD and CI, as adapted from the bivariate full model given by Quaas and Pollak (1980), and further developed from the previous four-trait analysis (Study I in this thesis) is represented as the following:

$$\begin{pmatrix} Y_1 \\ Y_2 \\ Y_3 \\ Y_4 \\ Y_5 \end{pmatrix} = \begin{pmatrix} X_1 & 0 & 0 & 0 & 0 \\ 0 & X_2 & 0 & 0 & 0 \\ 0 & 0 & X_3 & 0 & 0 \\ 0 & 0 & 0 & X_4 & 0 \\ 0 & 0 & 0 & 0 & X_5 \end{pmatrix} \begin{pmatrix} b_1 \\ b_2 \\ b_3 \\ b_4 \\ b_5 \end{pmatrix} + \begin{pmatrix} Z_{a1} & 0 & 0 & 0 & 0 \\ 0 & Z_{a2} & 0 & 0 & 0 \\ 0 & 0 & Z_{a3} & 0 & 0 \\ 0 & 0 & 0 & Z_{a4} & 0 \\ 0 & 0 & 0 & 0 & Z_{a5} \end{pmatrix} \begin{pmatrix} a_1 \\ a_2 \\ a_3 \\ a_4 \\ a_5 \end{pmatrix} +$$

$$\begin{pmatrix} Z_{m1} & 0 & 0 & 0 & 0 \\ 0 & Z_{m2} & 0 & 0 & 0 \\ 0 & 0 & Z_{m3} & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 \end{pmatrix} \begin{pmatrix} m_1 \\ m_2 \\ m_3 \\ 0 \\ 0 \end{pmatrix} + \begin{pmatrix} W_{m1} & 0 & 0 & 0 & 0 \\ 0 & W_{m2} & 0 & 0 & 0 \\ 0 & 0 & W_{m3} & 0 & 0 \\ 0 & 0 & 0 & W_4 & 0 \\ 0 & 0 & 0 & 0 & W_5 \end{pmatrix} \begin{pmatrix} p_{m1} \\ p_{m2} \\ p_{m3} \\ p_4 \\ p_5 \end{pmatrix} + \begin{pmatrix} e_1 \\ e_2 \\ e_3 \\ e_4 \\ e_5 \end{pmatrix}$$

where,

Y_1, Y_2, Y_3, Y_4 and Y_5 = Vectors of records for BW, WW, YW CD and CI, respectively,

b_1, b_2, b_3, b_4 and b_5 = Vectors of fixed effects (including covariates) affecting records of BW, WW, YW, CD and CI, respectively,

X_1, X_2, X_3, X_4 and X_5 = Known incidence matrices relating BW, WW, YW, CD and CI, respectively to corresponding fixed effects,

a_1, a_2, a_3, a_4 and a_5 = Random vectors representing direct genetic effects for BW, WW, YW, CD and CI, respectively,

m_1, m_2 and m_3 = Random vectors representing maternal genetic effects for BW, WW and YW, respectively,

p_{m1}, p_{m2} and p_{m3} = Random vectors representing permanent maternal environmental effects for BW, WW and YW, respectively,

p_4 and p_5 = Random vectors representing permanent environmental effects for repeated records of CD and CI, respectively,

$Z_{a1}, Z_{a2}, Z_{a3}, Z_{a4}$ and Z_{a5} = Known incidence matrices relating BW, WW, YW, CD and CI, respectively to corresponding elements of a_1, a_2, a_3, a_4 and a_5 ,

Z_{m1}, Z_{m2} and Z_{m3} = Known incidence matrices relating BW, WW and YW, respectively to corresponding elements of m_1, m_2 and m_3 ,

W_{m1}, W_{m2} and W_{m3} = Known incidence matrices relating BW, WW and YW, respectively to corresponding elements of p_{m1}, p_{m2} and p_{m3} ,

W_4 and W_5 = Known incidence matrices relating to repeated records of CD and CI, respectively to corresponding elements of p_4 , and p_5 ,

e_1, e_2, e_3, e_4 and e_5 = Random vectors representing residual errors peculiar to each record of BW, WW, YW, CD and CI, respectively.

The first (E) and second (V) moments assumed for the animal model were as the following:

$$E \begin{pmatrix} Y \\ a \\ m \\ p_m \\ p \\ e \end{pmatrix} = \begin{pmatrix} Xb \\ 0 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

and,

$$V \begin{pmatrix} a \\ m \\ p_m \\ p \\ e \end{pmatrix} = \begin{pmatrix} G_a \otimes A & G_{am} \otimes A & 0 & 0 & 0 \\ G_{am} \otimes A & G_m \otimes A & 0 & 0 & 0 \\ 0 & 0 & D_{pm} \otimes I_{pm} & 0 & 0 \\ 0 & 0 & 0 & D_p \otimes I_p & 0 \\ 0 & 0 & 0 & 0 & R_e \otimes I_e \end{pmatrix}$$

where,

$$\mathbf{a}' = [a_1 \ a_2 \ a_3 \ a_4 \ a_5],$$

$$\mathbf{m}' = [m_1 \ m_2 \ m_3],$$

$$\mathbf{p}_m' = [p_{m1} \ p_{m2} \ p_{m3}],$$

$$\mathbf{p}' = [p_4 \ p_5],$$

$$\mathbf{e}' = [e_1 \ e_2 \ e_3 \ e_4 \ e_5],$$

\otimes = Direct matrix product operator,

A = Numerator relationship matrix,

G_a = Direct genetic (co)variance matrix,

G_{am} = Matrix of covariances between direct and maternal genetic effects,

G_m = Maternal genetic (co)variance matrix,

D_{pm} = Matrix of (co)variances among permanent maternal environment effects,

I_{pm} = Incidence matrix corresponding to (co)variances among permanent maternal environment effects,

D_p = Matrix of (co)variances among permanent environment effects,

I_p = Incidence matrix corresponding to (co)variances among permanent environment effects,

R_e = Matrix of (co)variances among residual environmental effects,

I_e = Incidence matrix corresponding to (co)variances among residual environmental effects.

5.3.3. Computing strategies using MTDFREML method

The pooled data set for the five trait mixed animal model was analysed using the Multiple-Trait Derivative Free Restricted Maximum Likelihood (MTDFREML) set of programs to obtain estimates of (co)variances (Boldman et al. 1995). The mixed model equations were of the order of 65,205 comprising a total of 7,171 animal and 7,171 maternal effects for each of five traits, 1,480 effects of permanent maternal environment for each of three juvenile traits, and 1,545 effects of permanent environment for repeated records of each calving trait. The estimates of (co)variances obtained from the previous bivariate to four trait animal model analyses (Rasali et al. 2001a; Rasali et al. 2001b; Study I in this thesis) and some estimates extrapolated from the literature were used as the

starting values of (co)variance matrices required for initializing the iterative process of the analysis. The “MTDFRUN” part of the MTDFREML programs was set to execute a maximum 30,000 rounds of iterations, as the desired convergence level was achieved within this maximum limit of rounds. The procedure right from the freshly started program run, referred to as “cold start” (not a continuation of the previous run) was executed repeatedly using the (co)variance estimates obtained from the preceding run as the starting values. This was done to realize the global convergence across the components of (co)variances such that no difference in the first two decimals of the estimates of each genetic parameter was found between the last two consecutive runs. The convergence criterion for maximization of the variance function values ($-2 \times \text{Log } L$, the logarithm of the likelihood function) of the simplex iterations was set at 1.0×10^{-8} for first several runs, and at 1.0×10^{-6} for the last few rounds for reducing the computing needs.

The MTDFREML programs were run on the High Performance Computing (HPC) platform using the machine named “Polaris” at the University of Manitoba. This machine runs the Solaris 8 Operating Systems from Sun Microsystems, equipped with twenty 1050 MHz Ultra Sparc II CPUs. Approximately 5% of the memory of one of these CPUs were utilized in each run lasting for a period of about 3 to 7 days.

5.3.4 Estimation of Genetic Trends

The estimated breeding value (EBV) of each animal with its standard error of prediction (SEP) and accuracy (r_{TI}) for each of the direct and maternal genetic effects on BW, WW, YW, and direct genetic effects on CD and CI was derived from the

MTDFREML analysis as the solution of their best linear unbiased prediction (BLUP) from the mixed model equations. The mean EBVs of the juvenile growth traits for each year of calf birth and cow's calving traits for each year of calving were computed, and were regressed on the respective years for each herd, similar to the "Procedure 1" as described by Shrestha et al. (1996). The linear regression coefficients thus obtained represented the realized average annual genetic change (ΔG) of each trait over the years for each herd.

The estimates of realized responses were compared to those expected assuming single-trait truncation selection for either WW_a (direct genetic effect of WW) or YW_a according to Falconer and Mackay (1996). The selection intensity of male and female animals used in the calculation of these theoretically expected maximum responses to selection were 1.858 and 0.966, respectively, based on the proportions, 0.081 and 0.403 of animals, respectively (Van Vleck et al. 1987) that could be selected as parents annually in the pooled population of five herds. A generation interval of four and six years for male and female animals, respectively, was assumed. The estimates of heritability, genetic variances and genetic correlations used in these calculations were those derived from the present analysis.

5.4. RESULTS AND DISCUSSION

5.4.1. The Estimates of Genetic Parameters

The estimates of genetic (co)variances, heritabilities and genetic correlations among three juvenile body weights and two calving traits in the pooled population of five Angus herds are presented in Table 5.4. The genetic (co)variance estimates represent the covariance matrix computed by simultaneous partitioning of variance components of all five traits from a single analysis. The direct (subscript, a), maternal (m) and direct-maternal (am) genetic correlations among the traits analysed simultaneously using more information about the animals with records from later stages of life could have eliminated the possible bias of selection history for these traits (Schaeffer 1984; Pollak et al. 1984).

5.4.2.1 *Direct heritabilities*

The estimate of direct heritability ($h^2 = 0.45$) for BW (Table 5.4) in the present study, which is fairly close to the corresponding estimate from four trait model in the Study I in this thesis. The estimate is in agreement with at least five corresponding literature estimates reviewed or estimated by Meyer (1992), is consistent with, or close to, more than one-third of 45 corresponding published estimates ranging from 0.14 to 0.61 (Mohiuddin 1993), and is in agreement with three published estimates reviewed by Davis (1993). Among the h^2 estimates of BW from the published studies, numerous individual estimates (examples, Rege 1985; Winder et al. 1990; Meyer 1993; Meyer 1994; Meyer 1995b; Robinson 1996; Mostert et al. 1998; Mwansa et al. 2002) are in agreement with or

very close to the estimate in the present study, while relatively higher estimates are reported in several other studies (examples, Rege 1985; Meyer 1993; Skrypzeck et al. 2000; Rasali et al. 2002; Burrow 2001). The present estimate, though somewhat higher than the weighted mean of 0.31 from 167 published estimates reviewed by Koots et al. (1994a), represents an improvement over the past estimates considering the modeling rigors imposed in its estimation.

The direct heritability estimate ($h^2 = 0.70$) of WW (Table 5.4) in the present study was consistent with the corresponding estimate from the four trait model fitted with the same data set for growth traits (Study I in this thesis). This was not surprising given that Mohiuddin (1993) reviewed the 53 published estimates ranging from 0.07 to 0.66, and despite their much lower average (0.22), several of these published estimates were individually close to the present estimate. Furthermore, a number of moderately high h^2 estimates of WW around 0.50 have been reported (Knights et al. 1984; Rege 1985; Johnson et al. 1992; Meyer 1993; Skrypzeck et al. 2000), while a few corresponding published estimates are as high as 0.66 (Johnson et al. 1992) and 0.75 (Meyer 1993). This present estimate, though relatively higher than the mean, 0.35 of some 239 published estimates reviewed by Koots et al. (1994a), represented the improvement from the past estimates, considering the modeling rigors of its estimation and the number of traits used in the multiple trait analyses as being advantageous in terms of accounting for the sampling errors and possible selection biases.

The h^2 estimate of YW in the present study was high, 0.79 (Table 5.4), but fairly close to the corresponding estimate of 0.70, reported in one large scale analysis in the

United States (Rege 1985). The present estimate is much higher than the weighted mean, 0.33 of 154 published corresponding estimates that were reviewed by Koots et al. (1994a), and the average, 0.31 of 35 literature estimates that were in the range from 0.12 to 0.50 reviewed by Mohiuddin (1993). While considerable variation in these literature estimates for YW was evident similar to BW and WW, most published estimates tended to cluster around the moderate value range from 0.25 to 0.50 (examples, Knights et al. 1984; Meyer et al. 1993; Meyer 1995a; Mostert et al. 1998; Rust et al. 1998; Burrow 2001; Rasali et al. 2001a). The very high estimate derived in the present study represent the improvement from the past estimates owing to the model of analysis that utilized more information to evaluate the animal model through genetic and environmental correlations across traits, and rigorously eliminated various types of biases caused by selection history across herds in the population (Schaeffer 1984; Pollak et al. 1984). This was evident from the fact that a relatively simpler four trait model of analysis for the same population of Angus cattle yielded a relatively lower h^2 estimate of 0.44 for YW (Study I in this thesis), and the single trait model yielded an even lower estimate (Study III in this thesis), indicating that the estimate of heritability is at least partly dependent on the model of analysis as discussed by Meyer (1994).

The h^2 estimate of CD as a trait with repeated records in the present study was found to be moderate, 0.25 (Table 5.4). This estimate is in agreement with Azzam and Nielsen (1987) who reported the estimate for the third parity cows to be 0.24 ± 0.06 . A few other published estimates comparable to the present estimates were the estimates for second parity cows that were 0.17 ± 0.03 and 0.36 ± 0.18 reported by Azzam and Nielsen

(1987) and Smith et al. (1989b), respectively. Similarly, the heritability for parity 1 was estimated as high as 0.20 ± 0.16 and 0.39 ± 0.21 from two data sets of Hereford cattle with the low estimates for subsequent parity classes in another study (Buddenberg et al. 1990). Several other published studies (Meacham and Notter 1987; Rege 1985; Lopez de Torre and Brinks 1990; Meyer et al. 1990; MacNeil and Newman 1994; Johnston and Bunter 1996; Gutierrez et al. 2002) have shown the h^2 estimates for calving date to range from 0.11 to 0.20. Furthermore, the present estimate is somewhat much higher than either the unweighted or weighted mean of published estimates falling less than 0.10 as reviewed by Davis (1993) and Koots et al. (1994a). A number of individual studies also showed that the heritability estimates of CD and other analogous traits were less than 0.10 (Ray et al. 1989; Meyer et al. 1990; Brown et al. 1990; Burrow 2001), which tend to support the general notion that the reproductive traits are generally lowly heritable. However, the relatively higher estimate in the present study could be attributed mainly to improvement in the model of analysis by simultaneous inclusion of five traits eliminating possible bias from selection (Schaeffer 1984; Pollak et al. 1984). The differential genetic variation across parities, with most of the repeated records of the trait coming from later parities of cows, might have also contributed to the higher estimate for CD as compared to the corresponding estimate for first calving date (0.16) in Study I of this thesis. Clearly, the present estimate and several of the published estimates suggest that the calving date as a measure of reproductive efficiency is a heritable and useful in the selection programs.

The h^2 estimate of CI in the present study was 0.10 (Table 5.4), which is in agreement with the mean, 0.10 of four published estimates for older beef cows and 0.09 of

seven published estimates for beef heifers both reviewed by Koots et al. (1994a). Similarly, a recent estimate reported for CI in dairy cattle was 0.09 ± 0.02 (Haile-Mariam et al. 2003). These estimates are all comparable with the estimate, 0.15 in Kenya Sahiwal breed reported by Wakhungu et al. (1991). Furthermore, several other studies in the literature (examples, Meacham and Notter 1987; Lopez de Torre and Brinks 1990; Frazier et al. 1999; Khan et al. 1999; Ojango and Pollot 2001; Veerkamp et al. 2001) have shown the estimate in both beef and dairy cattle to be less than 0.07. Clearly, the trait CI is less heritable than CD.

5.4.2.2 Maternal heritabilities

The estimates of maternal heritability (m^2) of BW, WW and YW, 0.18, 0.24 and 0.12, respectively found in the present study were in agreement with or very close to the means, 0.18, 0.20 and 0.11, respectively of the large numbers of corresponding literature estimates reviewed by Koots et al. (1994a), and were also well within the wide ranges of their corresponding literature estimates reviewed by Meyer (1992) and Mohiuddin (1993). Meyer (1995a) reported estimates that were lower than the estimates in the present study for all three juvenile growth traits. Estimates of these parameters in the literature varied depending upon the models, number of traits included in the model and breeds of beef cattle used (Meyer 1993; Meyer et al. 1993; Swalve 1993; Meyer 1994; Mostert et al. 1998; Rust et al. 1998; Skrypzeck et al. 2000). The four trait model analysed for the same population (Study I in this thesis) yielded m^2 estimates that were relatively lower than the present values. This shows how the number of traits included in their simultaneous

analysis can influence the heritability estimates. The order of magnitudes of the present estimates indicate that the pre-natal and post-natal maternal genetic effects on weaning weight (WW_m) was the highest, followed by the pre-natal maternal genetic effects on birth weight (BW_m). On the other hand, the maternal genetic effects on yearling weight (YW_m) was the lowest as being progressively tapering from the carry-over effects of both BW_m and WW_m .

5.4.2.3 Direct genetic correlations

The estimates of direct genetic correlations (r_a) for three juvenile growth traits in pairs, BW-WW, BW-YW and WW-YW in the present study were 0.54, 0.56 and 0.86, respectively (Table 5.4), which are in close agreement with the means of the corresponding literature estimates reviewed by Davis (1993), Koots et al. (1994b) and Mohiuddin (1993), and with the corresponding estimates from individual studies particularly in Angus cattle (Winder et al. 1990; Mostert et al. 1998) and in other breeds (Rege 1985; Burrow 2001). The r_a estimates for BW_a - WW_a and BW_a - YW_a pairs of traits in the present study were somewhat higher than the corresponding estimates from the four trait animal model analysis of the same population (Study I in this thesis), but the corresponding estimate for WW-YW pair in present study was in agreement with that in Study I. Some differences in the parameter estimates can be attributed mainly to the fact that the five trait model used more information from (co)variances by additional records of calving traits as compared to the four trait model. The ranges of r_a estimates found in the literature for the pair of BW-WW, BW-YW and WW-YW were wide, -0.36 to 0.83,

0.26 to 0.57 and 0.16 to 0.92, respectively as reviewed by Mohiuddin (1993). Higher estimates of 0.63 ± 0.42 , 0.88 ± 0.32 and 0.97 ± 0.01 , respectively were also reported for the three correlations in an individual study (Nelsen et al. 1986). Rust et al. (1998) even reported negative values for BW-WW and BW-YW, while the corresponding estimate for WW-YW pair was approaching unity (0.96). Several other studies have also shown moderate to high estimates for the three trait pairs (Smith et al. 1989b; Swalve 1993; Robinson 1996). In general, the moderate to high direct genetic correlations were evident in the correlations for the three trait pairs, with the tendency of the estimate for WW_a - YW_a approaching unity.

The r_a estimate of BW_a - CD_a and WW_a - CD_a and YW_a - CD_a pairs of trait effects were -0.19, -0.31 and -0.21, respectively (Table 5.4) indicating that the animals with breeding values for heavier weights of calves at birth, weaning and at one year of age tended to have breeding values for early calving. This favorable relationship of juvenile growth traits with the calving date was not found in the analysis of a four trait model of the same population (Study I in this thesis), in which case the calving trait was the first calving date. The present negative estimates of the correlations between growth traits and the CD were close or comparable to several literature estimates (Rege and Famula 1993; Smith et al. 1989b; Meyer 1991; Burrow 1999 as cited by Newman and Coffey 1999). Smith et al. (1989b) reported high standard errors (SEs) of the negative estimates, r_a , -0.53 ± 0.79 for WW-CD and -0.13 ± 0.60 for YW-CD. On the other hand, there was one study (Burrow 1999 as cited by Newman and Coffey 1999) which reported a positive estimate of 0.22 between BW_a and CD_a . Similarly, the estimates for WW-CD and YW-CD pairs, 0.10 ± 0.20 and

0.08±0.18, respectively, were reported by Johnston and Bunter (1996). Overall, the present estimate in agreement with a number of available literature estimates tend to suggest the negative direct genetic correlation of CD with growth traits, particularly WW and YW.

The r_a estimates of BW, WW and YW with CI in the present study were -0.23, -0.38 and -0.65, respectively (Table 5.4). These indicated that the genetic association between any one of three growth traits and CI was favorable to the producers, if CI was to be proved as an useful measure of reproductive efficiency in beef cows. Among a very few studies available in the literature that showed the genetic association of growth traits with CI, Uchida et al. (1998) reported a negative genetic correlation estimate (-0.41) between BW and CI, which is comparable to the corresponding present estimate. In contrast, Frazier et al. (1999) reported that BW and WW are predictors of CI ($P<0.001$) with increase in BW resulting in longer CI in mature cows.

The estimate of direct genetic correlation between CD and CI in the present study was found to be zero. There are only a few corresponding estimates in the literature for comparison. The result in the present study is comparable to positive but very low r_a estimate, 0.06 between the two traits reported by Lopez de Torre and Brinks (1990), and the low negative estimate (-0.09±0.88) reported for the pair of traits by Meacham and Notter (1987). This indicated negligible possibility of realizing any substantial correlated response in CI through selection for CD and vice versa. Lopez de Torre and Brinks (1990) found that their estimate of correlation changed from near zero to a moderate value of 0.25 using adjusted calving interval indicating that their adjustment was a factor influencing the records of CI. On the other hand, van der Westhuizen et al. (2001) found positive and

very high estimate of genetic correlation between the two traits (0.79), while a moderate negative estimate, -0.28 was also reported in the literature (Gutierrez et al. 2002).

Meacham and Notter (1987) reported very high negative estimate (-0.83) of genetic correlation of CI with the first calving date indicating that higher genetic potential for early first calving tend to lengthen the subsequent calving intervals. However, these results could be valid only when calving interval represents an unbiased measure of reproductive efficiency.

5.4.2.4 Maternal genetic correlations

The estimates of maternal genetic correlations (r_m) of BW-WW, BW-YW and WW-YW pairs of traits were 0.32, 0.12 and 0.68, respectively (Table 5.4) indicating the respective magnitude of their positive relationships that could influence their correlated responses to selection among the maternal genetic traits. An estimate of maternal genetic correlation between BW-YW trait pair (0.11) and that of WW-YW (0.64) reported by Swalve (1993) are in agreement with the corresponding estimates of the present study. However, the present estimates are somewhat lower than their corresponding estimates from the four trait model analysed for the same population (Study I in this thesis). There are also much higher values of numerous estimates reported in the literature (Meyer et al. 1993; Swalve 1993; Meyer 1994; Meyer 1995a; Mostert et al. 1998; Rust et al. 1998). All these estimates are indicative of the part-and-whole relationships of the maternal genetic effects among the three juvenile growth traits. The relatively high positive correlation between WW_m and YW_m is the evidence that the maternal genetic effects of YW are the

carry-over effects of WW_m controlled by mostly the same set of genes and, to a very little extent, of BW_m . On the other hand, the maternal genetic effects of WW are comprised of the pre-natal maternal genetic effects carried over from BW_m and the post-natal maternal genetic effects from birth to weaning mainly contributed by dam's milk. While there was as a substantial maternal genetic effects carried over from birth to weaning, there was only a limited pre-natal maternal genetic effects carried over to YW_m resulting in lower r_m estimate between BW_m and YW_m as compared to the estimate between BW_m and WW_m .

5.4.2.5 Direct-maternal genetic correlations

The direct-maternal genetic correlation (r_{am}) estimate of individual trait WW was moderate negative (-0.30), while that of BW and YW were also negative but low, -0.08 and -0.06, respectively (Table 5.4) in the present study. The present r_{am} estimate for BW was in agreement with, and that for WW and YW were higher than the corresponding estimates from the four trait analysis of the same population (Study I in this thesis). Several studies reported in the literature have documented these estimates consistently to be negative albeit variable in magnitudes (Koots et al. 1994b; Mohiuddin 1993; Meyer 1993; Tawah et al. 1993; Trus and Wilton 1988), while a few positive estimates are also reported (Meyer 1992; Meyer 1994; Trus and Wilton 1988). Koots et al. (1994b) and Mohiuddin (1993) reviewed large numbers of literature estimates of r_{am} which averaged -0.35 and -0.35, respectively for BW, -0.16 and -0.15, respectively for WW, while the latter author reported the literature average for YW to be -0.26. The specific published r_{am} estimates that were consistent with or close to the present estimate of r_{am} for BW was -

0.04 (Swalve 1993). The estimates for WW reported by Meyer (1993) and Rust et al. (1998) were -0.30 and -0.32, respectively, while the estimates reported by Meyer (1993) for YW was -0.05. In general, the present results along with many other published studies support the antagonistic genetic relationships between animals' genetic potential for "growth" and their genetic potential for nursing their offspring mainly through milk. This phenomenon is considered logical from an evolutionary standpoint in that there are checks and balances between direct and maternal genetic effects for growth and milk yield respectively (Cundiff 1972). These relationships were at least partly due to the dam transmitting to her progeny a 'plus' set of genes for direct effects on growth and a 'poor' maternal effect, or vice versa as postulated by Willham (1972).

In the present study, the estimate of direct-maternal genetic correlation (r_{am}) between direct genetic effects on any of three juvenile traits and the maternal genetic effects of the other trait was generally low ranging from -0.04 to 0.04 except for the moderate positive estimates of the correlation between WW_a and BW_m , and between YW_a and BW_m , 0.28 and 0.47, respectively (Table 5.4). The latter two estimates are comparable to the estimates from the four trait model analysis of the same population (Study I in this thesis), and also to the corresponding estimates reported by Meyer (1994). Rust et al. (1998) reported low positive estimates for these two pairs of traits. These results indicate that there might not be antagonistic genetic relationships between pre-natal maternal genetic effects and post-natal direct genetic effects of growth traits. However, in contrast to these results, the negative estimates in variable magnitudes have also been reported in

some cases (Swalve 1993; Meyer 1993; Koots et al. 1994b) indicating some inconsistencies of the estimates reported particularly between two different growth traits.

The direct genetic effect of CD was found in the present study to be associated favorably with maternal genetic effects of the three juvenile growth traits. The r_{am} estimates were moderate, -0.18 and -0.39, respectively for CD_a - WW_m and CD_a - YW_m , while the corresponding estimate between CD_a and BW_m was very low negative, -0.02. These results indicate that the cows with a genetic potential to calve early tend to have genetic potential for a higher level of mothering ability providing more milk to their calves resulting in their higher weaning and yearling weight. However, such a favorable association was not the case for CI_a , which had r_{am} estimates next to zero and very low, 0.00 and 0.07 with BW_m and WW_m , respectively. The corresponding estimate between CI_a and YW_m was 0.51, but might not be of any consequence due to low heritabilities of both traits. No corresponding estimates were found in the literature for comparison to these results from the present study.

5.4.2. Permanent and Residual Environmental Effects

The variance ratios (c^2_{pm}) and correlations (r_{pm}) of permanent maternal environmental effects of three juvenile growth traits and permanent environmental effects (c^2_p) of repeated records of two calving traits in a pooled population of five Angus herds are given in Table 5.5.

The low c^2_{pm} estimate of BW (2.6% of phenotypic variance) in the present study is comparable to a few corresponding estimates between one and four percents reported in

the literature (Meyer 1992; Meyer 1993; Meyer 1994), while somewhat wide range of several estimates from 0.11 to 25% have been reported by the same authors and others (Meyer et al. 1993; Meyer et al. 1995a; Robinson 1996; Swalve 1993; Skrypzeck et al. 2000). Similarly, the estimates of c^2_{pm} for WW and YW found to be extremely low or negligible, 0.4 and 0.1 % of their phenotypic variances, respectively in the present study were comparable with the corresponding literature estimates, 0.2 for WW (Robinson 1996) and zero for YW (Meyer et al. 1993; Swalve 1993). Several other estimates reported by these authors and others (Meyer 1992; Meyer 1993; Meyer 1994; Meyer et al. 1995a; Robinson 1996; Skrypzeck et al. 2000) were somewhat higher estimates as high as up to 34% for WW (Meyer 1993) and up to 14% for YW (Meyer 1994).

The correlations between permanent maternal environmental effects of the three growth traits were substantial; the r_{pm} estimate for BW-WW and BW-YW pairs of traits were negative indicating their antagonistic relationships, while that between WW-YW was 0.68, which was comparable to the literature estimates that were very high (Swalve 1993). Even though these correlation estimates were relatively large, the low magnitudes of permanent maternal environmental effects on BW, WW and YW indicated that the importance of these correlations is not high.

The estimates of permanent environmental effects (c^2_p) for repeated records of both calving traits, CD and CI were negligible, indicating that their estimates repeatabilities (Falconer and Mackay 1996) were not very different from corresponding heritability estimates.

Residual error effects (e^2) are unknown environmental effects unique to individual animals. The magnitudes of variation due to these effects on BW, WW, YW, CD and CI relative to their corresponding phenotypic variances and the correlations among them are presented in Table 5.5. These were in the reciprocal order of the direct heritability estimates of the traits, and were highest for CI (90% of its phenotypic variance) followed by CD (74%), while the e^2 estimates for the three juvenile growth traits ranged from 11 to 37%.

The estimate of residual environmental correlation (r_e) between BW and WW was approaching unity, while the estimates of r_e found for BW-WW and WW-YW pairs of traits were 0.35 and 0.46, respectively. These correlations follow the same direction and comparable magnitudes of the corresponding literature estimates (Meyer 1993; Meyer 1994; Meyer et al. 1995a; Mwansa et al. 2003) except for their order in that the estimates were highest for WW-YW pair followed by BW-WW. These correlations among the three juvenile growth traits suggest that the random environmental effects shared their influence on these traits in the comparable magnitudes and directions with the corresponding genetic correlations between the traits.

The r_e estimate for YW-CD was high negative (-0.86), while that for BW-CD was low positive, 0.11 in contrast to the very low corresponding estimates reported by Burrow (2001), indicating that the YW and CD are both important traits of choice to consider their favorable random environmental effects on growth and female reproductive efficiency in beef cattle. The r_e estimate of CI with BW, WW, YW and CD were -0.07, 0.00, 0.07 and

0.02, respectively indicating that the environmental relationships between these trait pairs were not of much importance.

5.4.3. Phenotypic (Co)variances of Traits

The phenotypic (co)variances and phenotypic correlations among BW, WW, YW, CD and CI are presented in Table 5.6. The phenotypic correlation estimates for WW-YW, BW-WW and BW-WW pairs of traits ranged from 0.51 to 0.83, which are consistent with or comparable to the estimates reported in the literature (Koots et al. 1994b; Meyer 1993; Meyer 1994; Meyer 1995a; Nelsen et al. 1986; Rege 1985). The phenotypic correlation estimates of BW, WW and YW with CD were -0.01, -0.14 and -0.37, respectively, while the corresponding estimates with CI were -0.09, -0.09 and -0.14, respectively. These results indicated that the phenotypic relationships of both CD and CI particularly with post-weaning growth were favorable. However, the estimate of phenotypic correlation between CD and CI was found to be very low (0.02).

5.3.4. Genetic Trends of Direct and Maternal Genetic Effects of Traits

The mean estimated breeding values (EBV), standard errors of prediction (SEP) and their accuracy (r_{TP}) for the direct and maternal genetic effects of the three growth traits and direct genetic effects of two calving traits, as derived from the best linear unbiased prediction (BLUP) solutions from MTDFREML analysis, are presented in Table 5.7. The results showed that despite highly variable SEP of these direct and maternal genetic effects, prediction of direct genetic juvenile growth traits, BW_a , WW_a and YW_a have

relatively high accuracy (r_{TI}), while that for BW_m , WW_m , YW_m , CD_a and CI_a are moderate. The value for accuracy, r_{TI} is equal to the square root of heritability of the trait for the situation of mass selection of individual animals evaluated on the basis of their single records (Mrode 1996). In addition, the pedigree structure used for multiple-trait analysis in the present study has provided more genetic information resulting in the increase of the accuracy for the traits (Schaeffer 1984; Simianer 1986). For an illustration, h^2 estimated for CD_a was 0.25 resulting in an accuracy of 0.50 for the animal's breeding values based on their single records, while the mean accuracy as a result of using all available records in the present study was 0.58 ± 0.15 .

The genetic trends of direct and maternal genetic effects of the three juvenile growth traits across year of birth and direct genetic effects of cows' two calving traits across their year of calving in the pooled population of five Angus herds are presented in Figures 5.1 and 5.2, respectively. The results showed that there were steadily increasing genetic trends in direct genetic effects of BW, WW and YW over the years, yielding their overall genetic progress until the later few years when the progress declined. This decline in the later years might have been due to inconsistency in breeding programs particularly in the smaller herds. Wide variations in the EBVs of different traits across years are not surprising as compared to the ranges of breeding values reported by Johnson et al. (1992) for pre-weaning growth traits, particularly 205-d weight that varied considerably. On the other hand, there were more or less stationary genetic trends of maternal genetic effects of BW and WW, while that of YW showed a decline in the later years of calves' birth. There was also a general trend of antagonistic genetic progress between direct and maternal

genetic effects of each of the three juvenile growth traits (Figure 5.1) reflecting on the corresponding negative genetic correlations. The direct genetic effects of CD and CI showed a decline in their genetic trends across years of calving (Figure 5.2) indicating an overall improvement in female reproductive efficiency, although there was some fluctuation evident in the genetic trend of CI in the later years. Overall, the genetic progress was favorable in direct genetic effects of both juvenile growth and female reproductive efficiency particularly in terms of early calving.

The average annual genetic change (ΔG) derived as regression coefficients of the traits on years are presented in Table 5.8. The observed annual ΔG for all traits in the largest herd, A, were significantly different from zero ($p < 0.05$), with the regression coefficients, 0.34, 0.10, 3.91, 0.28, 7.56 and -0.46 kg year⁻¹ for BW_a , BW_m , WW_a , WW_m , YW_a and YW_m , respectively, and -1.09 and -0.41 day year⁻¹ for CD_a and CI_a , respectively, and were in favorable direction except for YW_m . Corresponding estimates in each of the four smaller herds (B, C, D and E) were significant ($p < 0.05$) for BW_a , WW_a , YW_a (0.25, 3.59 and 4.08 kg year⁻¹, respectively) and CI_a (-0.27 day year⁻¹) in herd B, for only CI_a (-0.67 day year⁻¹) in herd C, for BW_m , WW_a and YW_m (0.13, 1.79 and 0.87 kg year⁻¹, respectively) in herd D, and for BW_a (-0.17 kg year⁻¹), BW_m (0.18 kg year⁻¹) and CI_a (-1.94 day year⁻¹) in herd E. Overall in the pooled population, the annual average genetic change in BW_a , WW_a , YW_a , YW_m and CD_a were significantly different from zero ($P < 0.05$), and their corresponding regression coefficients were 0.167 kg year⁻¹, 1.817 kg year⁻¹, 4.394 kg year⁻¹, -0.952 kg year⁻¹ and -1.089 day year⁻¹, respectively. The former three values were fairly comparable to the Angus breed's average genetic changes in

corresponding genetic effects of BW, WW and YW, as derived from the data of the recent report on Canadian Black Angus cattle (Wilson and Hassen 2003), which had 0.01 ± 0.004 , 1.01 ± 0.079 and 2.14 ± 0.105 kg year⁻¹, respectively. The annual average genetic changes in BW_a, WW_a, YW_a in the present study were also comparable to the results found in Hereford cattle for which the regression coefficients of BLUP estimates of 0.08 ± 0.06 , 1.10 ± 0.21 and 8.21 ± 6.00 kg on year of birth for BW, WW and YW, respectively were reported by Sharma et al. (1985).

Further, in an effort to understand breeding objectives and selection practices in relation to the genetic association between growth and calving traits, the observed ΔG values were compared to expected maximum genetic changes resulting from single-trait selection on either WW_a or YW_a as the selection criteria. The results (Table 5.9) showed that the realized genetic progress in each of three growth traits was far less than the theoretically maximum genetic change calculated according to Falconer and Mackay (1996) for each selection criterion. When WW_a was assumed to be the single-trait selection criterion, the observed ΔG values were 40.8, 28.6 and 59.6 % of theoretical expected ΔG values for BW_a, WW_a and YW_a, respectively. Similarly, when YW_a was considered the selection criterion, the corresponding observed ΔG values were 37.1, 31.3 and 42.5 % of their expected ΔG values, respectively. The observed ΔG values for the corresponding maternal traits were negative and negligible. On the other hand, the observed ΔG value for CD was somewhat greater (by 30 to 41 %) than the theoretically expected annual progress in the trait. Since observed ΔG values were generally less than those expected from single trait selection on either WW or YW, the selection criteria

actually used by the breeders must have involved traits different from these, or a variety of traits. These results indicate that more than one trait likely played an important role in selection decisions made within the herds in the pooled population.

5.4. CONCLUSION

The present study showed that calving date is more heritable and a more useful trait than calving interval. This indicated the potential merit of including the former in the multiple-trait selection programs along with the moderately to highly heritable and correlated juvenile growth traits. The negative direct-maternal genetic correlations of individual growth traits showed the antagonistic relationship between direct and maternal genetic effects on growth reiterating what has been documented in the literature. The negative direct genetic correlations of three growth traits with calving date, and the negative correlations of maternal genetic effects of three growth traits with direct genetic effects of calving date indicated their association to be favorable as correlated traits. There were generally positive and favorable trends of direct genetic effects of birth, weaning and yearling weights, and calving date over the years. These findings indicated that a number of growth and female reproductive traits might have played a favorable role as selection criteria in the selection history of the five Angus herds analysed in the present study. However, the stationary or slightly declining trends in maternal genetic effects of juvenile growth traits in the population over the years suggested that selection emphasis using them as the selection criteria might not have been considered important in the selection programs. Similarly, calving interval was not important as a selection criterion in the population.

Based on the results from the present study, it could be suggested that both direct and maternal genetic effects of either WW or YW are deserving selection criteria in a multiple-trait selection program aimed at favorable correlated response in CD.

Table 5.1. The number of animals, their sires and dams in five Angus herds that were pooled for the analysis.

Herds or Traits	Number of animals with records	Number of sires ^z	Number of dams
<u>Herd:</u>			
A	3601	87	754
B	779	87	236
C	600	39	228
D	967	37	211
E	495	63	160

^z Of these, only one sire was common to herds B, C and E; two sires were common to herds, B and E; another two sires were common to herds C and E; one sire was common to B and C; and another one sire was common to D and E.

Table 5.2. The pedigree structure and descriptive statistics of three juvenile growth traits and two calving traits in the pooled population of five Angus herds.

Trait	Number in the pedigree ^z			Mean	CV, %
	Sires	Dams	Animals		
BW, kg	236	1480	6115	38.84	13.78
WW, kg	222	1414	5357	278.26	15.36
YW, kg	194	1278	4430	439.35	15.85
CD, days	264	776	5763	72.93	42.25
CI, days	218	631	4106	373.38	13.26

^z The number of sires and dams include a total of 36 genetic groups (Westell et al. 1988) allocated for parents with no records of their own or with only one offspring with a single record for any of the traits.

Table 5.3. Covariates, fixed effects and random effects in the multiple-trait mixed model for three juvenile growth traits, BW, WW, YW, and two calving traits, CD and CI.

Covariates, fixed effects and random effects	Trait ^z				
	BW	WW	YW	CD	CI
<u>Covariates:</u>					
Age of Dam (AOD)	✓	✓	✓	-	-
AOD ²	✓	✓	✓	-	-
<u>Fixed effects:</u>					
Herd-Year of birth	✓ (61) ^y	✓ (55)	✓ (47)	-	-
Season of birth	✓ (4)	✓ (4)	✓ (4)	-	-
Type of birth	✓ (2)	✓ (2)	✓ (2)	-	-
Calf sex at birth	✓ (2)	✓ (2)	✓ (2)	-	-
Herd-Year of calving	-	-	-	✓ (60)	✓ (54)
<u>Random effects:</u>					
Direct genetic	✓ (7171)	✓ (7171)	✓ (7171)	✓ (7171)	✓ (7171)
Maternal genetic	✓ (7171)	✓ (7171)	✓ (7171)	-	-
Permanent maternal environmental	✓ (1480)	✓ (1480)	✓ (1480)	-	-
Permanent environmental	-	-	-	✓ (1545)	✓ (1545)

^z A check (✓) mark denotes the inclusion of the corresponding factor in the model for a trait.

^y The figure in the parenthesis indicates the number of levels for each of fixed and random effects.

Table 5.4. Estimates of direct and maternal heritability (upper diagonal and bold), genetic correlations (upper off-diagonal), genetic variances (lower diagonal) and genetic covariances (lower off-diagonal) among three juvenile growth traits and two calving traits in the pooled population of five Angus herds.

Trait	BW _a ^z	WW _a	YW _a	CD _a	CI _a	BW _m	WW _m	YW _m
BW _a	0.45 10.27	0.54	0.56	-0.19	-0.23	-0.08	-0.04	0.00
WW _a	46.10	0.70 721.81	0.86	-0.31	-0.38	0.28	-0.30	0.00
YW _a	73.76	945.70	0.79 1692.53	-0.21	-0.65	0.47	0.04	-0.06
CD _a	-7.09	-96.47	-101.12	0.25 131.02	0.00	-0.02	-0.18	-0.36
CI _a	-10.61	-149.27	-393.18	0.49	0.10 213.29	0.00	0.07	0.51
BW _m	-0.51	15.12	39.55	-0.53	0.01	0.18 4.19	0.32	0.12
WW _m	-1.81	-129.11	28.60	-31.94	16.11	10.51	0.24 251.24	0.68
YW _m	0.02	0.04	-39.16	-66.51	119.41	4.01	172.25	0.12 259.15

^z Subscripts, _a = direct genetic effects and _m = maternal genetic effects.

Table 5.5. Variance ratios and correlations of permanent maternal, permanent and residual environmental effects fitted for the five-trait mixed model.

Traits	BW	WW	YW	CD	CI
<u>Permanent maternal environmental effects ^z:</u>					
BW	0.026				
WW	-0.93	0.004			
YW	-0.35	0.68	0.001		
<u>Permanent environmental effects ^y:</u>					
CD				0.012	
CI				0	0.3×10^{-6}
<u>Residual environmental effects ^x:</u>					
BW	0.37				
WW	0.98	0.18			
YW	0.35	0.46	0.11		
CD	0.11	0.02	-0.86	0.74	
CI	-0.07	0.00	0.07	0.02	0.90

^z Diagonal elements represent c_{pm}^2 , the proportion of phenotypic variance due to permanent maternal environmental effects, and off-diagonal elements represent r_{pm} , the correlations between these effects.

^y Diagonal elements represent c_p^2 , the proportion of phenotypic variance due to permanent environmental effects, and off-diagonal element represents the correlation between these effects, which was assumed to be zero.

^x Diagonal elements represent e^2 , the proportion of phenotypic variance due to residual environmental effects, and off-diagonal elements represent r_e , the correlations between these effects

Table 5.6. Estimates of phenotypic variances (diagonal) and phenotypic covariances (lower off-diagonal) and phenotypic correlations (upper off-diagonal) among three juvenile growth traits and two calving traits in the pooled population of five Angus herds.

Traits	BW	WW	YW	CD	CI
BW	22.93	0.65	0.51	-0.01	-0.09
WW	100.15	1029.01	0.83	-0.14	-0.09
YW	112.44	1228.18	2146.85	-0.37	-0.14
CD	-1.15	-106.12	-395.72	534.21	0.02
CI	-19.84	-139.53	-288.08	17.08	2119.18

Table 5.7. Mean estimated breeding values (EBVs), standard error of prediction (SEP) and accuracy of prediction (r_{TI}) with their standard deviation (SD) of animals in the pedigree (n=7,135) for juvenile growth and calving traits.

Genetic traits	EBV \pm SD	SEP \pm SD	$r_{TI}\pm$ SD
BW _a	0.53 \pm 2.98	2.48 \pm 0.90	0.62 \pm 0.23
BW _m	0.17 \pm 1.45	1.78 \pm 0.40	0.49 \pm 0.19
WW _a	-5.99 \pm 33.16	17.99 \pm 10.48	0.73 \pm 0.24
WW _m	7.35 \pm 12.48	14.21 \pm 4.46	0.48 \pm 0.19
YW _a	-2.88 \pm 49.60	25.67 \pm 20.08	0.77 \pm 0.24
YW _m	6.49 \pm 13.53	15.74 \pm 9.09	0.41 \pm 0.21
CD _a	-0.31 \pm 7.59	9.34 \pm 2.32	0.58 \pm 0.15
CI _a	-0.89 \pm 20.75	12.27 \pm 4.60	0.56 \pm 0.18

Table 5.8. The average annual genetic gain derived as the regression coefficients relating mean estimated breeding values (EBVs) of juvenile growth traits and calving traits to year of calf's birth and year of calving, respectively, in five Angus herds.

Herd	Average annual genetic change							
	BW _a ^z	WW _a	YW _a	CD _a	CI _a	BW _m	WW _m	YW _m
A	0.335** (0.82) ^y	3.914** (0.97)	7.556** (0.98)	-1.089** (0.97)	-0.407** (0.88)	0.096** (0.73)	0.284** (0.44)	-0.457** (0.50)
B	0.252** (0.62)	3.591* (0.37)	4.0849** (0.83)	-0.171 ^{ns} (0.05)	-0.267* (0.39)	-0.0002 ^{ns} (0.00)	-0.977 ^{ns w} (0.14)	-0.033 ^{ns} (0.01)
C	-0.025 ^{ns} (0.04)	-0.956 ^{ns} (0.15)	3.018 ^{ns} (0.14)	0.016 ^{ns} (0.01)	-0.665* (0.50)	-0.017 ^{ns} (0.02)	0.049 ^{ns} (0.00)	-0.073 ^{ns} (0.01)
D	-0.041 ^{ns} (0.09)	1.79* (0.54)	2.183 ^{ns} (0.35)	-0.017 ^{ns} (0.03)	-0.352 ^{ns} (0.17)	0.132** (0.85)	0.085 ^{ns} (0.01)	0.871** (0.69)
E	-0.173* (0.53)	1.631 ^{ns} (0.19)	2.388 ^{ns} (0.19)	-0.306* (0.45)	-1.938** (0.79)	0.185** (0.83)	-0.096 ^{ns} (0.01)	0.630 ^{ns} (0.29)
Pooled	0.167** (0.53)	1.817* (0.63)	4.394** (0.75)	-1.089** (0.97)	-0.088 ^{ns} (0.15)	-0.015 ^{ns} (0.07)	-0.065 ^{ns} (0.04)	-0.952*** (0.86)

^z _a = direct genetic effects, and _m = maternal genetic effects.

^y The figure in the parenthesis indicates the coefficient of determination (R²) for the corresponding regression.

^x *** = (p<0.01), * = (p<0.05).

^w ^{ns} = not significant (P>0.05);

Table 5.9. Observed annual genetic change in each trait compared to annual genetic change expected with single trait selection on either WW_a or YW .

Direct or correlated response to selection (kg or d year ⁻¹)					
Selection criterion	Correlated trait	r_g^z between selected and correlated traits	Observed annual genetic change in each trait	Expected annual genetic change in the trait	Observed response as percentage of the expected response
WW_a	BW_a^y	0.54	0.167	0.409	40.8
	WW_a	1.00	1.817	6.341	28.6
	YW_a	0.86	4.394	7.367	59.6
	CD_a	-0.31	-1.089	-0.838	129.9
	CI_a	-0.38	-0.088	-1.311	6.7
	BW_m	0.28	-0.015	0.135	-11.1
	WW_m	-0.30	-0.065	-1.124	5.7
	YW_m	0.00	-0.952	0.000	NC ^x
YW_a	BW_a	0.56	0.167	0.451	37.1
	WW_a	0.86	1.817	5.799	31.3
	YW_a	1.00	4.394	10.337	42.5
	CD_a	-0.21	-1.089	-0.770	141.5
	CI_a	-0.65	-0.088	-1.868	4.7
	BW_m	0.47	-0.015	0.241	-6.2
	WW_m	0.04	-0.065	0.159	-40.6
	YW_m	-0.06	-0.952	-0.242	392.7

^z r_g = genetic correlation;

^y Subscripts, _a = direct genetic effects, and _m = maternal genetic effects,

^x NC = not calculated due to zero value of r_g .

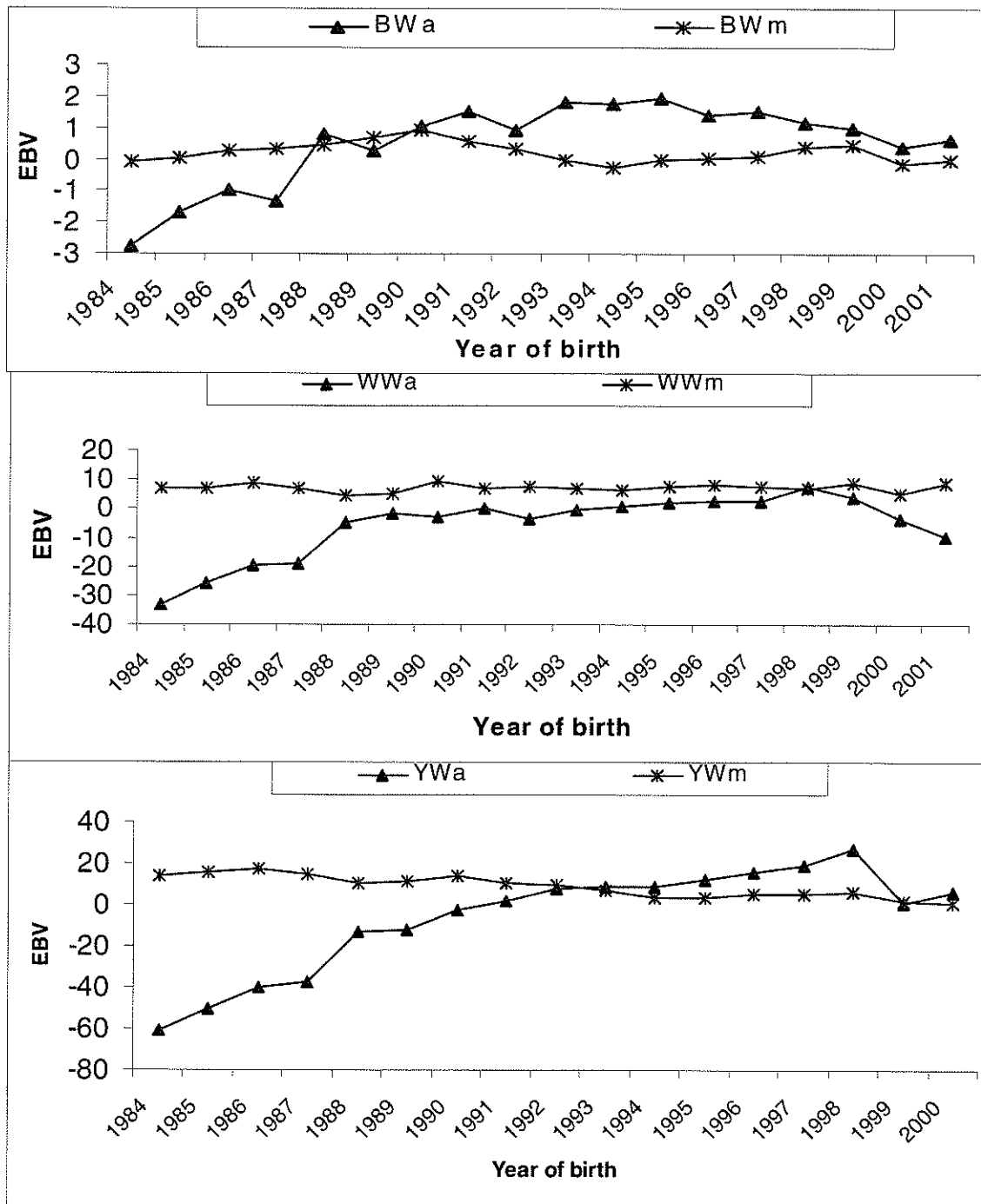


Figure 5.1 Genetic trends across year of birth (as mean EBV, kg) for birth weight (BW, top), weaning weight (WW, middle) and yearling weight (YW, bottom). Suffices a and m with the trait indicate its direct genetic and maternal genetic effects, respectively.

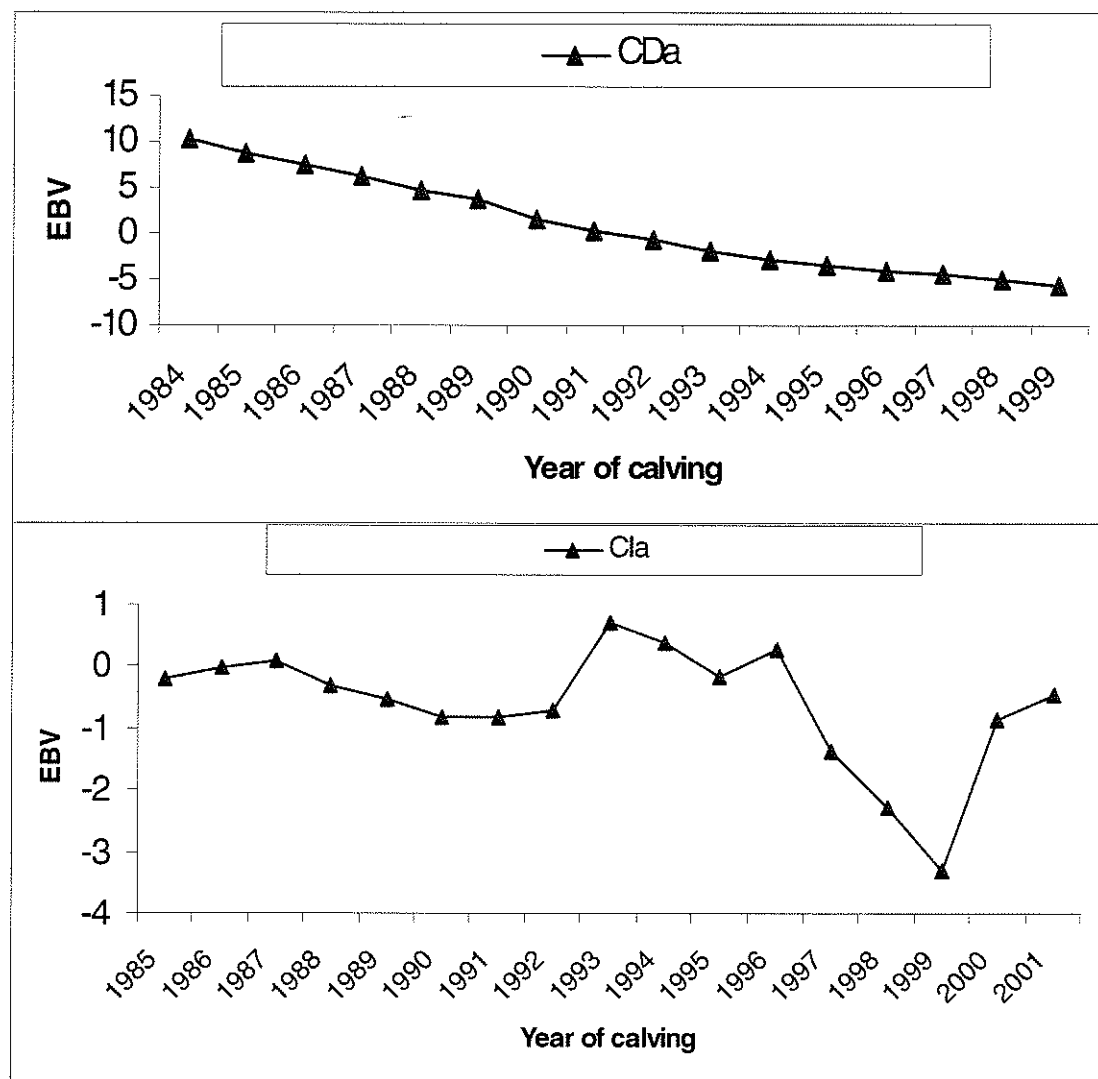


Figure 5.2 Genetic trends across year of calving (as mean EBV, d) of direct genetic effects of calving date (CD_a, top) and calving interval (CI_a, bottom). Suffix a with the trait indicates its direct genetic effects.

6. STUDY - III:
CORRELATION ANALYSIS OF ESTIMATED BREEDING VALUES (EBVS) OF
JUVENILE GROWTH TRAITS AND COWS' STAYABILITY IN ANGUS
HERDS

6.1. ABSTRACT

Data from a pooled population of five herds with a pedigree of 6,864 Angus cattle in western Canada, comprising records of 6,116 animals for juvenile growth traits and 1,073 cows for stayability to 3 years of age (Stay3) were analysed to estimate the rank correlations between their EBVs. Univariate animal models were used to analyse body weights at birth (BW), at 205-d weaning (WW) and at one year of age (YW) using ASREML program. The models included fixed effects due to herd-birth year, birth season, birth type, calf's sex and age of dam (linear and quadratic covariates), and random direct and maternal genetic effects. The study also utilized an ASREML univariate logit animal model that included fixed effects due to cow's herd-birth year, and a random direct genetic effect for Stay3 as a binary scored trait. Survival analysis revealed that the risk of cows being culled from the herd was the highest between two to three years of age over a range of calving ages up to a maximum age of 10 years. The direct heritability (h^2) estimates for BW, WW and YW were 0.49 ± 0.03 , 0.40 ± 0.04 , and 0.37 ± 0.04 , respectively. Corresponding maternal heritability (m^2) estimates were 0.12 ± 0.02 , 0.13 ± 0.02 and 0.08 ± 0.02 , respectively. The h^2 estimate for Stay3 was 0.39 ± 0.10 . Rank correlation estimates among direct EBVs for three growth traits and those among their maternal EBVs were all highly significant, ranging from 0.47 to 0.82, which were consistent with the literature estimates of the genetic correlations between the corresponding traits. The direct EBVs of Stay3 and direct as well as maternal EBVs of growth traits were not correlated except for maternal EBVs of WW ($P < 0.10$), suggesting that the Stay3 may not be influenced by the selection for the growth traits.

6.2. INTRODUCTION

Stayability is defined as the probability of a cow surviving in the herd to a specific age when given the opportunity to reach that age (Hudson and Van Vleck 1981). The trait depends largely on cows being culled for reproductive failure (Snelling and Golden 1994). This trait has recently received interest as an economically relevant trait of reproduction in beef cows, due to its economic benefit in improvement of their reproductive life-span (Golden et al. 2000; Doyle et al. 2000). Formigoni et al. (2002) suggested that the economic importance of the trait is directly related to the fertility of cows in the herd and prevailing production systems. Therefore, it is important that those cows and heifers which are selected as breeding stock for their higher genetic potential are kept in the herd long enough to produce a number of calves at least to cover the large investment of time and resources involved in replacing them (Doyle et al. 2000).

The genetic analysis of such traits relating to cows' longevity has been fairly well documented in dairy cattle (Everett et al. 1976a,b; Hudson and Van Vleck 1981; Van Doormaal et al. 1984). In beef cattle, Snelling and Golden (1994) and Snelling et al. (1995) were the first studies to report the heritability estimates of stayability traits. While the direct selection for a longevity trait like stayability has not been considered worthwhile due to its low heritability (Vega-Murillo et al. 1999), a few other authors (Snelling et al. 1995; Doyle et al. 2000; Silva et al. 2003) have shown that stayability is a moderately heritable trait.

Information on the genetic association between stayability and any of the growth traits is lacking to date. Snelling et al. (1995) pointed out the need for knowledge of the

genetic relationship of this trait with other economically important traits in beef cattle. In fact, the theory relating to direct estimation of the genetic correlation between a normally distributed quantitative trait such as a growth trait and a binomially distributed categorical trait such as stayability has not been established to date (Gilmour, personal communication). Univariate methods of estimating heritability (Thompson et al. 1985), and estimating breeding values (EBVs) using mixed models (Gilmour et al. 2001) for a binary trait on its underlying scale based on its liability derived from its logit or probit transformation have been developed. Gilmour et al. (1995) has also developed a REML based method for application to continuous metric traits such as juvenile growth traits. Having both these procedures at hand, the present study was undertaken with the objective to determine genetic relationships between the juvenile growth and stayability traits by way of estimating correlations between their EBVs for these traits.

6.3. MATERIALS AND METHODS

6.3.1. Sources of Data

A single herd (herd A) database was obtained directly from a sizeable purebred herd of Angus cattle in Manitoba through the arrangement of Canadian Angus Association. An additional database of relatively smaller four herds of Angus cattle, three from Alberta (B, C and D) and one from Saskatchewan (E), was obtained from an Australian institution where Canadian Angus cattle records of performance have been stored, again through arrangement of the Canadian Angus Association. All the five herds represented the typical cow/calf breeder operations in the Canadian Prairie Region. Records of calves relating to their calving events and body weights that were derived from the databases of five herds during the period from the year 1984 to 2001 were utilized. The numbers of animals born and their sires and dams from each herd are given in Table 6.1.

6.3.2. Statistical Analyses

6.3.2.1 Derivation of data sets for specific traits

Juvenile growth traits

Data sets of records for the juvenile body weight traits of calves at birth (BW), 205-d weaning (WW) and one year of age (YW) were derived directly from the database from the pooled population of five Angus herds. The data set for each trait was first

subjected to analysis using General Linear Model Procedure of SAS (1998) to determine the significance of various fixed effects namely Herd, Year of birth, Season of birth, Type of birth and Sex of the calf born and that of linear and quadratic covariates of the age of dam.

Stayability traits

The stayability trait of a cow in the herd is expressed as a binary scored trait based on her calving successes by assigning the value "1" if a cow survived to calve for a given number of times by certain age, or "0" if a cow was culled from its herd before that age. The binary scored values of the trait were derived using SAS programming (SAS 1998) from the calving records of cows for each calving order (sequential parity) of a cow. Calving of twins or triplets was considered as one calving event for the purpose of counting calving orders and deriving the stayability traits. The stayability values for all calving orders in the life of all cows until 10 years of age was first subjected to survival analysis using the LIFETEST procedure (SAS 1998) to estimate their survival distribution function (SDF) and hazard function related to cow age.

Given that a cow survived to an age (t), for small change of Δt the hazard function, $h(t)$ for an age-specific stayability trait was computed by $f(t | X \geq t)$ as suggested by Van Doormaal et al. (1984),

where,

Δt = change in age (time, t),

X = the given condition of age such that $t \leq X < t + \Delta t$,

$S(t)$ = the survival distribution function (SDF),

$F(t) = 1 - S(t)$, the probability that a life-time is shorter than t ,

$f(t)$ = the probability density function (PDF), defined as the derivative of $F(t)$

$h(t) = f(t)|S(t)$.

Based on the visual assessment of the SDF and hazard function curves on the number of calving records available for individual cows, a stayability trait (Stay3) indicating the ability of cows to calve two times remaining in the herd until 3 years of age given that each of them had the opportunity to calve two times, was identified as an important trait for the genetic analysis.

6.3.2.2 Pedigree structure

The pedigree information available for the whole population of five herds was utilized in the genetic analysis of three juvenile growth traits and one stayability trait in order to minimize the possible bias of selection from exclusion of any pedigree relationship. All unknown parents of “base” animals, and any parent which has only one offspring record with no record of its own, were considered as “phantom” parents assigning them as genetic groups in order to minimize any effect of possible selection among the “base” animals on the estimates of genetic parameters and associated breeding values. Sires and dams were grouped according to the year of their birth into a total of 36 genetic groups as proposed by Westell et al. (1988) and used by Shrestha et al. (1995).

6.3.2.3 Univariate animal model for juvenile growth traits

Initially, statistical analyses of three selected juvenile growth traits, BW, WW and

YW were carried out using the GLM procedure (SAS 1998) to ascertain the significance of various fixed effects. The factors, namely Herd-Year of birth representing the contemporary groups of calves born similar to Study I, Season of birth (winter: Dec 22 to March 19; spring: March 20 to June 20; summer: June 21 - September 22 and fall: September 23 - Dec 21), Type of birth (singleton and multiple births) and Sex of the calf born as the fixed effects were included in the animal model for the analyses of data sets of each growth trait from the pooled herd population. The age of dam at calving was included in each model for juvenile growth traits as a linear and a quadratic covariate representing their curvilinear relationship, such that each of the growth traits was either pre-adjusted for these covariate effects or they were fitted directly into the respective models. Any animal record falling below or above the mean by four times its standard deviation was considered as outlier assuming it to have an error of recording, and was edited out as a missing or improper record following the BIF guidelines (BIF 1996).

The direct animal and maternal effects were considered as random for all animals in the pedigree structure for calves born from 1984 to 2001, and their parents in the pooled population. The permanent maternal effects of each of the juvenile growth traits were not included in the model for computational ease, as they were found to be of negligible magnitude in Study I and Study II.

Thus, a univariate mixed animal model for each of the juvenile growth traits analysed using the ASREML programs (Gilmour et al. 2001) was as follows:

$$Y = X\beta + Zu + e$$

Where,

Y = Vector for measurement of the a growth trait;

X = Incidence matrix for fixed effects of a growth trait;

Z = Incidence matrices for random direct and maternal genetic effects of a growth trait;

β = Vector for fixed effects (including covariates);

u = Vector for random effects direct and maternal genetic effects of a growth trait;

e = Vector for random error for the trait.

From this procedure for each of the juvenile growth traits, the heritability and its standard error were estimated, and estimated breeding value (EBV) was derived as the solutions of random effects from the mixed model equations.

6.3.2.4 Univariate binomial animal model for stayability trait

The selected stayability trait, the Stay3, was analysed by the restricted maximum likelihood method using the ASREML program (Gilmour et al. 2001). The logit transformation was applied to the stayability trait to transform the stayability trait variable into its underlying scale based on its liability. This involved fitting a univariate mixed animal model to transformed binary scores (1, 0) of the trait as follows:

$$\text{logit} [\pi] = X\beta + Zu + e$$

with,

$$\text{trait mean, } \mu = 1/(1+e^{(-X\beta)}) \text{ and}$$

$$\text{trait variance, } \sigma^2 = \mu(1-\mu)/N$$

where,

logit [π] = the log of odds of success for a stayability trait,

$$= \log [(probability\ of\ success)/(probability\ of\ failure)]$$

X = Incidence matrix for fixed effects of the stayability growth trait;

Z = Incidence matrices for random direct genetic effects of the stayability trait;

β = Vector for fixed effects;

u = Vector for random effects direct genetic effects of the stayability trait;

e = Vector for random error for the stayability trait.

From this procedure, the heritability and its standard error for Stay3 were estimated, and estimated breeding values (EBVs) of the trait for each animal in the pooled population was derived as the solution of the random effects from mixed model equations.

6.3.2.5 Accuracies and Correlations of EBVs

Accuracies of EBVs for the juvenile growth traits and stayability were determined using standard errors of predictions (SEP) derived as the solutions for individual animal and maternal effects from the Best Linear Unbiased Prediction (BLUP) procedures in the ASREML program (Gilmour et al. 2001). Technically, the value of SEP is the square root of the prediction error variance (Mrode 1996; Gilmour et al. 2001), and hence, the accuracy of prediction is derived as:

$$\text{Accuracy} = \sqrt{1 - (SEP^2 / \sigma_g^2)},$$

where,

σ_g^2 = the genetic variance (animal or maternal) from the animal models.

Finally, the Spearman's rank correlations among the EBVs for individual juvenile growth

traits and the stayability trait were estimated using the CORR Procedure (SAS 1998).

6.4. RESULTS AND DISCUSSION

6.4.1. The Characteristics of Traits

6.4.1.1 *Fixed effects*

The means of BW, WW and YW across various influencing factors are given in Table 6.2. Their least-squares means with standard errors are given in Appendix Table 6.1. The fixed effects factors, namely the herd, year of birth, season of birth, type of birth and sex at birth were highly significant ($P < 0.01$) for all three traits.

Herd A, the largest of the five herds, had the highest mean of BW (36.17 kg), which was 13% higher than the lowest mean observed in one of the smaller herds (D). The second highest mean BW was found in smaller herd C, which recorded heaviest weaned calves as well as heaviest yearlings with their means of 314.3 and 487.4 kg, respectively. These highest means of WW and YW were, respectively 30 and 27% higher than the corresponding lowest means found in one smaller herd, B. The largest herd A ranked second in mean WW that was 21 % lower than the highest mean WW (314.3 kg) for herd C, while the herd A had only 6% lower mean YW than the herd C. These results indicated that the pre-weaning and post-weaning body weights variable across herds.

From the year 1984 to 2001, there was generally an increasing trend in the means of BW, WW and YW with some fluctuations occurring during different years. There was also a slight decline in the mean values in 1987 and 1996 consistently in all three traits. Year effects have been documented by various authors (Azzam and Nielsen 1987; Nelsen

et al. 1987; Tawah et al. 1993) as factors that influence BW, WW and YW.

The majority of the calves were born in the winter and spring seasons with fewer born in summer and fall. The calves born in the fall, winter and spring in order were heavier at birth than those born in summer. On the other hand, the calves born in winter and summer were weaned heavier than those born in the fall and spring. Winter and spring born animals weighed less at one year of age than those born in the summer and fall. Season has been included as the significant fixed effect also in other genetic studies (Assam and Nielsen 1987; Rege and Famula 1993; Tawah et al. 1993) with their variable means across seasons. Rege and Famula (1993) reported that the calves born in spring were the heaviest at birth and at one year of age, while those born in winter were heaviest at weaning. Tawah et al. (1993) reported that the calves born in the wet season were heavier than those born in the dry season.

The singletons were heavier in weights at birth, weaning and one year of their age than the animals born as twins or triplets, likely due to diversion of limited maternal nutritional resources to the one calf vs several. The male calves were heavier than females at birth, weaning and at one year of age in agreement with several other studies (Baker et al. 1991; Burrow 2001; Tawah et al. 1993; Robinson 1996; MacGregor and Casey 2000; Rege and Famula 1993).

The proportional means of Stay3 for five herds and the years of cow's birth from 1982 to 1998 are given in Table 6.3. The highest proportion (86%) of cows having success score for Stay3 was found in the largest herd A followed by the herd D from Alberta (78%). The proportions of cows attaining Stay3 fluctuated across years showing

no specific pattern, although some proportions were relatively higher, 0.76, 0.74 and 0.77 in later years, 1994, 1996 and 1997, respectively. The range of these proportions across all years was comparable to the range of percentages of cows retained in a South African herd of beef cattle at 36 months of age across different years from 1973 to 1991 (van der Westhuizen et al. 2001), but such data were not found in the literature for Canadian herds.

6.4.2. Survival and Hazard Function Curves of the Stayability

The survival analysis revealed that the survival density function (SDF) curve (Figure 6.1) for cows of the pooled population declined sharply between two to three years of their age indicating the disappearance of a large number of first calf heifers before their second calving. This decline in the survival curve became less intense following the second calving at three years of their age until six years of age. The survival analysis revealed further that the hazard rate for cows was highest during the period from two to three years of age, following which the hazard curve showed low and steady level until the occurrence of the second peak hazard between six and seven years of age (Figure 6.2). These results suggested that the stayability of cows to three years of age is important indicating that its genetic analysis for the pooled population of the five herds could be valuable. However, due to a dramatic drop in the sample size for stayability records beyond three years of age, genetic analysis of cows' stayability to higher ages was not pursued.

6.4.3. Heritability Estimates

The heritability estimates and their standard errors for three juvenile growth traits, BW, WW and YW, and one cows' stayability trait, the Stay3, derived from the pooled population of five Angus herds are given in Table 6.4. The estimates of direct heritability (h^2) for BW, WW and YW were 0.49 ± 0.03 , 0.40 ± 0.04 and 0.37 ± 0.04 , respectively. These estimates were all within the ranges of estimates reported in the major literature reviews (Meyer 1992; Mohiuddin 1993; Swalve 1993; Koots et al. 1994). The h^2 estimate of BW was also consistent with the corresponding estimates from the four and five trait models analysed for the same population in Study I and II, respectively in this thesis. The estimates for WW and YW in the present study were somewhat lower than the four and five trait analyses likely due to differences in their models and interactions among the traits included in Study I and II since the present study was based on univariate analysis. Many studies have shown such differences in estimates between univariate and multivariate analyses (Mackinnon et al. 1991; Meyer 1992; Meyer 1993; Meyer 1994). Further discussion on direct h^2 estimates of growth traits in the literature have been held in Study I.

The estimate of h^2 for cows' stayability to three years of age (Stay3) was 0.39 ± 0.10 in the present study. It was not a surprising figure when considering the variable range of estimates reported for stayability traits in the literature for beef cattle, although the estimates reported for various traits of longevity and stayability were low in dairy cattle (Van Doormaal et al. 1984; Weigel et al. 1995; Vollema and Groen 1996) and pigs (Lopez-Serrano et al. 2000). The published estimates for beef cattle ranged from next

to zero (Vega-Murillo et al. 1999) to as high as 0.68 reported by Snelling et al. (1995), and several other estimates fall within this range (Snelling and Golden 1994; Snelling et al. 1995; Doyle et al. 2000; Van der Westhuizen et al. 2001; Silva et al. 2003). Doyle et al. (2000) computed the confidence intervals of h^2 estimates for stayability to five calvings that ranged from 0.001 to 0.288 and from 0.036 to 0.304 from the two series of sub-sample estimates with their mean of 0.23. The results of Snelling and Golden (1994), Snelling et al. (1995) and Doyle et al. (2000) analysing the subsets of data from the same herds of Angus cattle suggested that the stayability was heritable in the populations analysed. Some of these estimates found in the literature were based on the analyses of raw binary (0,1) values of stayability traits, while others were based on a transformation (such as logit or probit) of the binary outcomes. Genetic analysis of the transformed outcomes as done in the present study should give more accurate results.

6.4.3. Estimated Breeding Values (EBVs) and their Accuracies

The mean direct and maternal EBVs for three juvenile growth traits and cows' stayability (Stay3) for the pooled population of five herds studied are given in Table 6.5. The mean direct and maternal EBVs for all three juvenile growth traits were positive values except for a small negative value for maternal BW, while the mean EBV for Stay3 was a small positive value. The prediction error variances (PEV) and accuracies of direct and maternal EBVs for BW, WW, YW and that of direct EBV for Stay3 are given in Table 6.6. The average accuracy of the direct EBV for BW was largest (0.74 ± 0.07) among all traits, followed by 0.68 ± 0.08 and 0.66 ± 0.10 for WW and YW, respectively,

clearly attributed to the magnitude of their h^2 estimates. The average accuracies for maternal EBVs for BW and WW (0.44 ± 0.11 and 0.44 ± 0.12 , respectively), were similar, and that for YW was moderate but slightly lower mainly owing to low maternal heritability of the trait. The average accuracy of the direct EBV for Stay3 of relatively small sample size was moderate and comparable with that of the maternal EBVs for growth traits indicating moderate usefulness of their predictions.

6.4.4. Correlations Between Estimated Breeding Values (EBVs)

The Spearman's rank correlation estimates among direct and maternal EBVs of BW, WW and YW, and direct EBV of Stay3 in the pooled population of five Angus herds of cattle are given in Table 6.7. These correlations, theoretically, reflect the genetic correlations between the corresponding traits with moderate accuracies of their true breeding value predictions. The direct EBVs of three juvenile growth traits were all highly correlated to one another ($P < 0.001$) with the highest correlation coefficient (0.82) between WW and YW, followed by the correlation coefficients of BW with WW and YW that were 0.50 and 0.55, respectively. Similarly, the maternal EBVs of three juvenile growth traits were also highly correlated ($P < 0.001$), with the high correlation coefficient (0.76) between WW and YW, and moderate correlations between EBVs of BW and YW and that of BW and WW. All these correlations estimates showed high consistency with the corresponding genetic correlations between these traits reported in the literature (Mohiuddin 1993; Koots et al. 1994a). These were also in agreement with the corresponding genetic correlations estimated from multiple trait analyses of the same

pooled population reported in Study I and Study II in this thesis. These results indicated that the rank correlations in the present study satisfactorily reflected the correlations between the corresponding true breeding values vis-a-vis their corresponding genetic correlations.

The results also showed that the EBVs for Stay3 and that of direct genetic effects of three growth traits were not correlated ($P>0.05$) indicating that the genetic correlations between these traits were not likely to be significant. The maternal EBVs for WW, on the other hand, had low positive rank correlation with the direct EBV for Stay3 ($P<0.10$). Hence, Stay3 is likely to be unaffected by the selection programs emphasizing growth traits particularly through their direct genetic effects. From a preliminary analysis of a subset of data from the present population, Rasali et al. (2002) reported positive correlations of direct EBVs for BW and maternal EBVs for BW and WW with the direct EBVs for Stay3, but in the present study the model of analysis was improved by incorporating genetic groups and much larger data set. On the other hand, Mwansa et al. (2003) reported negative genetic correlations between early growth and success to 3rd calving, but they used a different definition of the stayability trait.

6.5. CONCLUSION

Stayability to three years of age of cows in the pooled population of Angus cattle is a heritable and an important trait which deserves attention in the selection programs. The rank correlations of direct EBV of Stay3 with the direct or maternal EBVs of birth, weaning and yearling weights indicated that the selection for juvenile growth is not likely to result in any important correlated response in calving success of cows to three years of age. Further research in other herds, both large and small ones, will be necessary to verify universality of this result across other herds in Canada and elsewhere.

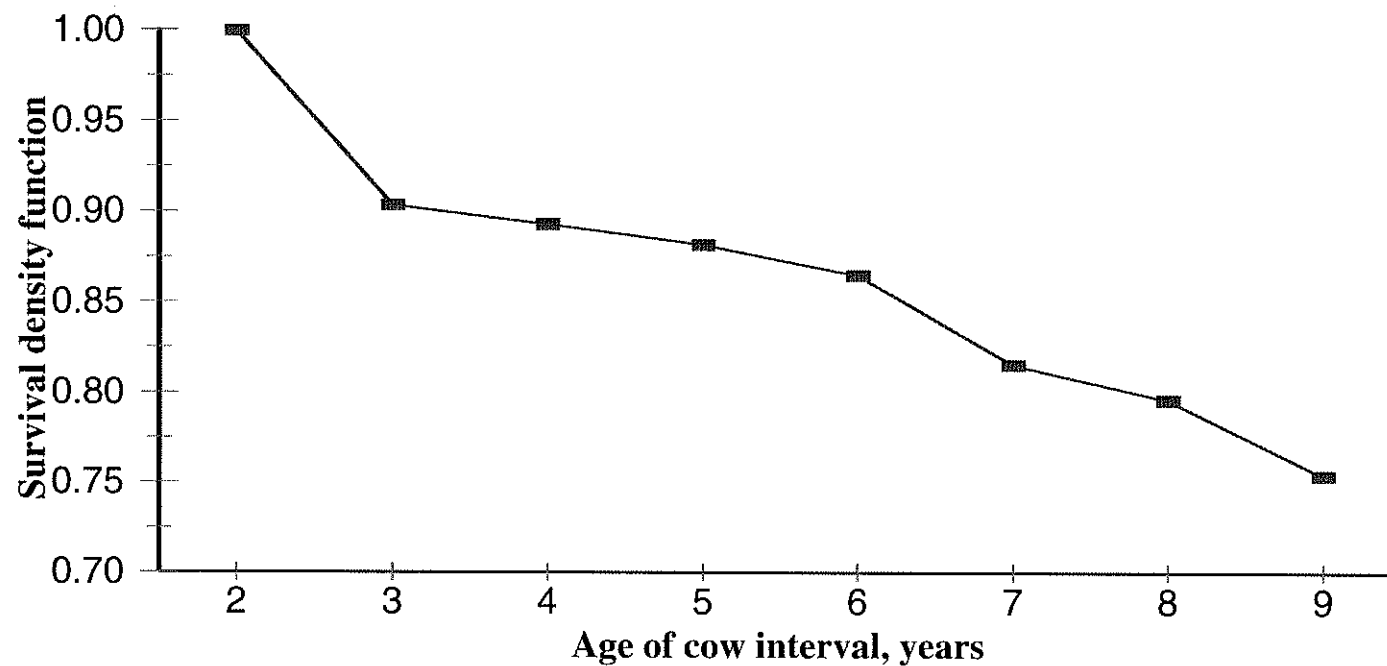


Figure 6.1. Survival density function (SDF) of cows' stayability in their respective herd of the pooled population of Angus cattle given that they had opportunity to calve at least once.

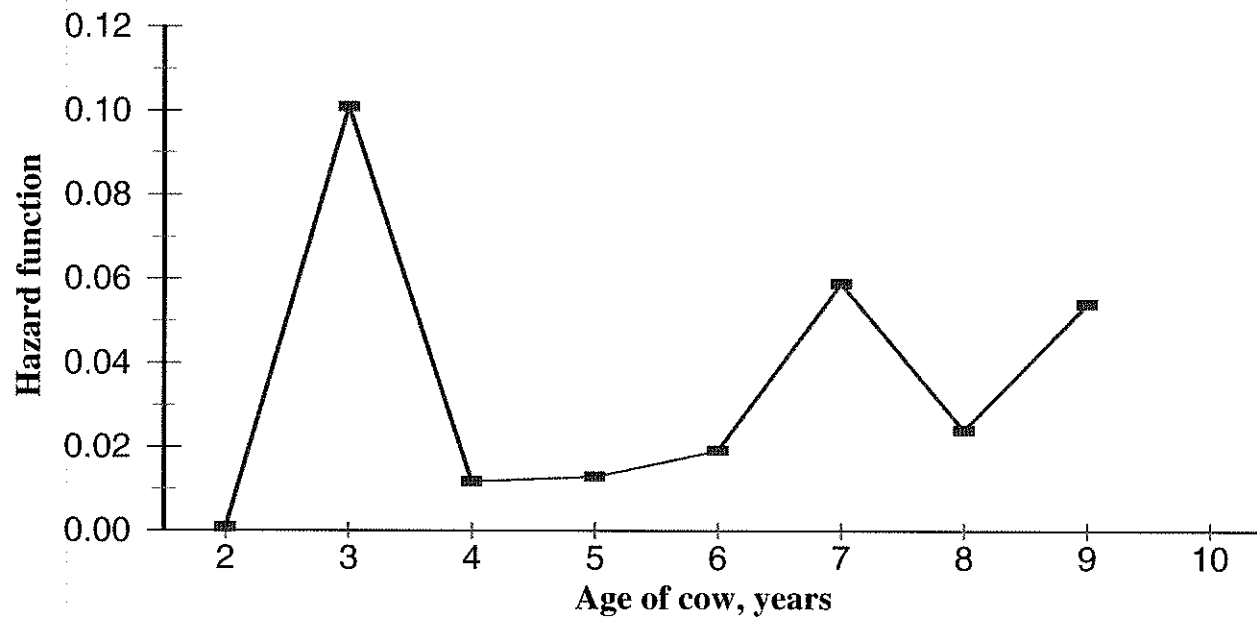


Figure 6.2. The hazard function of cows's stayability across their age in their respective herds of pooled population of Angus cattle given that they had opportunity to calve at least once.

Table 6.1. The numbers of animals with birth records, their sires and dams in the pooled population of five Angus herds.

Herd	Number of animals with birth records	Number of sires	Number of dams
A	3601	87	754
B	779	87	236
C	600	39	228
D	967	37	211
E	495	63	160

Table 6.2. Least squares means of birth weight (BW), weaning weight (WW) and yearling weight (YW).

Factors ^z	BW, kg	WW, kg	YW, kg
Herd:			
A	36.17 (3276) ^y	259.8 (3100)	461.6 (2860)
B	33.18 (779)	242.0 (393)	384.2 (300)
C	34.64 (599)	314.3 (557)	487.4 (237)
D	31.70 (967)	259.3 (830)	407.2 (723)
E	34.49 (495)	266.6 (479)	423.9 (310)
Year of birth:			
1984	31.89 (207)	248.1 (201)	412.1 (191)
1985	32.43 (179)	269.2 (178)	409.4 (169)
1986	33.86 (178)	279.3 (174)	421.8 (174)
1987	32.20 (198)	265.3 (188)	414.7 (186)
1988	32.55 (188)	253.0 (181)	436.2 (178)
1989	33.79 (267)	274.3 (238)	447.0 (183)
1990	34.59 (241)	255.5 (219)	417.5 (205)
1991	34.13 (241)	263.8 (221)	432.0 (212)
1992	34.12 (306)	256.8 (285)	434.1 (220)
1993	34.93 (354)	278.5 (279)	437.1 (258)
1994	34.95 (346)	274.6 (292)	449.3 (282)
1995	35.27 (331)	285.1 (309)	444.7 (303)
1996	34.90 (493)	275.4 (397)	430.5 (338)
1997	34.39 (580)	265.8 (463)	438.2 (431)
1998	34.69 (558)	280.9 (512)	436.6 (418)
1999	34.54 (602)	273.1 (570)	443.2 (318)
2000	34.35 (427)	275.7 (401)	454.8 (364)
2001	35.00 (421)	256.7 (233)	-
Season of birth:			
1. fall	34.19 (141)	259.8 (75)	442.2 (56)
2. winter	34.02 (3137)	275.1 (2759)	408.8 (2061)
3. spring	34.37 (2738)	262.9 (2480)	399.3 (2282)
4. summer	33.55 (100)	275.7 (45)	481.1 (31)
Type of birth:			
1. singleton	37.88 (5903)	279.5 (5193)	448.6 (4298)
2. multiple	30.19 (213)	257.3 (166)	417.1 (132)
Sex at birth:			
1 Female	32.80 (2892)	257.0 (2551)	385.1 (2029)
2 Male	35.27 (3224)	279.8 (2808)	480.6 (2401)
Coefficient of variation, % ^x	12.06	12.09	10.02

^z Effects of all factors shown here were significant at (P<0.001) for all traits.

^y The figures in the parentheses indicate number of records.

^x Residual standard deviation as a percent of the mean.

Table 6.3. Cows surviving to 3 years of age having calved two times, as a proportion of all cows surviving to 2 years of age having calved once.

Factors	Proportion for herd and for year of birth of heifers.
Herd:	
A	0.86 (508) ^z
B	0.46 (155)
C	0.44 (102)
D	0.78 (161)
E	0.71 (96)
Year of birth:	
1982	0.59 (22)
1983	0.79 (14)
1984	0.68 (28)
1985	0.69 (30)
1986	0.63 (32)
1987	0.51 (49)
1988	0.68 (53)
1989	0.64 (32)
1990	0.56 (74)
1991	0.60 (74)
1992	0.61 (83)
1993	0.56 (78)
1994	0.76 (85)
1995	0.64 (121)
1996	0.74 (114)
1997	0.77 (76)
1998	0.62 (57)

^z The figure in the parenthesis indicates the number of records of cows.

Table 6.4. The heritability estimates ($h^2 \pm SE$) for juvenile growth traits and cows' stayability to 3 years of age.

Trait	n ^z	Heritability estimates	
		Direct h ² ±SE	Maternal h ² ±SE
<u>Juvenile growth traits:</u>			
BW	6864 (6116) ^y	0.49±0.036	0.12±0.017
WW	6158 (5360)	0.42±0.038	0.12±0.018
YW	5250 (4430)	0.38±0.044	0.08±0.019
<u>Stayability traits:</u>			
Stay3	1428 (1073)	0.39±0.103	-

^z The number of animal effects in the pedigree of animal models.

^y The figure in parenthesis indicates the actual number of records analysed for the trait.

Table 6.5. Means and standard deviations for direct and maternal estimated breeding values (EBVs) for three juvenile growth traits and stayability from univariate analyses.

Trait	Number of animal effects ^y	EBVs (Mean±SD)	
		Direct	Maternal
BW	6864	0.83±2.74	0.05±0.81
WW	6157	4.86±16.32	0.94±5.30
YW	5250	7.97±20.19	1.30±4.81
Stay3	1428	0.04±0.28	-

^y The number of animal effects excluding genetic groups.

Table 6.6. Prediction error variance (PEV) and accuracy for direct and maternal Estimated Breeding Values (EBVs) for three juvenile growth traits and a stayability trait.

Traits	n ^z	Direct EBVs		Maternal EBVs	
		PEV Mean±SD ^y	Accuracy Mean± SD	PEV Mean±SD	Accuracy Mean± SD
Birth weight	6864	4.81± 1.01	0.74±0.07	2.04±0.27	0.45±0.11
Weaning weight	6158	225.13± 45.39	0.69±0.09	100.58±13.34	0.44±0.12
Yearling weight	5250	386.96±79.48	0.66±0.10	129.27±13.36	0.38±0.11
Stayability to 3 years	1428	0.56± 0.04	0.34±0.09	-	-

^z The number of animals in the pedigree.

^y SD= Standard deviation.

Table 6.7. Spearman's rank correlations between direct EBVs of BW, WW and YW and direct EBV of Stay3 (above diagonal) and maternal EBVs of BW, WW and YW and direct EBV of Stay3 (below diagonal) in a pooled population of five Angus herds of cattle.

	BW	WW	YW	Stay3
BW		0.504*** ^z (6157) ^y	0.547*** (5250)	0.042 ^{ns} (1407)
WW	0.472*** (6157)		0.824*** (5232)	-0.022 ^{ns} (1376)
YW	0.466*** (5250)	0.764*** (5232)		-0.021 ^{ns} (1327)
Stay3	0.015 ^{ns} (1407)	0.046 * (1376)	-0.027 ^{ns} (1327)	

^z *** = significant at (P<0.01); * = significant at (P<0.1); ^{ns} = not significant.

^y The figures in the parentheses indicate the number of animals in the pedigree excluding genetic groups.

7. GENERAL DISCUSSION

The primary purpose of the present research was to examine the genetic association between juvenile growth and female reproductive efficiency in beef cattle. Estimation of the genetic parameters including heritabilities and genetic correlations among important traits provided not only quantitative assessment of their genetic relationships, but also the basis to derive implications that may result from selection of one trait on another.

There has been no dearth of genetic parameter estimates particularly for juvenile growth traits in the literature so as to necessitate their separate investigation, but in the present thesis research they have been reexamined as a part of analyses involving interrelationships among growth and reproductive traits in beef cattle. Several of the genetic parameters that were estimated in the present research were comparable to the literature estimates, although some of them (for example direct heritability estimates of WW and YW in Study II) were somewhat higher than the means of estimates found in the literature (Mohiuddin 1993; Koots et al. 1994a, b). The estimates in the present research should be viewed in the context that many estimates of the genetic parameters reported in the literature suffer from their considerable variability for reasons such as the methods of estimation, sampling errors, effectiveness of removing environmental variations, inbreeding, assortative mating and past selection (Barlow 1978). The literature estimates also suffer from poor precision because of the relatively small size of the data sets (Brien 1986). For genetic correlations derived from small studies, Brien (1986) suggested that their signs and the directions of the correlated responses to selection should be considered

together with those from similar studies, instead of relying heavily on the magnitude of estimates of the genetic correlations from the single studies. In the present studies, there were also a few new parameters estimated. Among these, of particular interest are the estimates of direct-maternal genetic correlations between reproductive and growth trait, for which the literature estimates are not available for comparison. In the following discussion, the findings from the present studies relating to the growth and reproductive traits are viewed individually as well as an integrated group of traits.

7.1. GENETIC ANALYSIS OF JUVENILE GROWTH TRAITS

Genetic parameters such as heritabilities and genetic correlations for juvenile growth traits are important elements to consider in the design of selection programs in beef cattle. Moderate to high estimates of direct heritabilities and low to moderate maternal heritabilities of three traits, BW, WW and YW found from the present genetic analyses are comparable to numerous studies reported in the literature (Rege 1985; Meyer 1992; Mohiuddin 1993; Koots et al. 1994a). These results reaffirm the well documented fact that any of these traits have potential for response to selection for growth. Barlow (1978) summarized the literature findings that selection for body size at any stage would result in relatively large concomitant changes in size at all other ages. However, selection for increased BW is detrimental to calving ease due to the known consequence of dystocia, and is avoided. BW may be a trait of importance only for deriving average daily gain to certain ages such as at weaning, yearling or final slaughter. The remaining weight traits, WW and YW have usually been the traits utilized in selection programs (BIF

1996). These two, however, may require a closer examination in the light of realizing optimum correlated responses in one another and other traits of economic importance.

The direct or maternal genetic correlations for the pair combinations of three growth traits analysed in the present research were all moderate to high positive. These estimates of direct and maternal genetic correlations ranged from 0.31 to 0.90, and 0.12 to 0.97, respectively, and were in agreement with numerous previous studies summarized by Mohiuddin (1993), Swalve (1993), Koots et al. (1994b) and many other studies reported more recently in the literature (for examples, Mostert et al. 1998; Rust et al. 1998). It was evident from these results that either direct or maternal genetic correlation between WW and YW, especially, was much higher and close to unity as compared to relatively lower correlations of BW with WW, and with YW.

The high positive direct genetic correlation between WW and YW indicates that most of the same genes control both these traits. On the other hand, fewer genes controlling birth weight are likely to be the same as those controlling body weights at weaning and yearling ages. This phenomenon may be due to the fact that growth in different stages of the animals' life involves development of different tissues and organs, which are each likely under the control of a different set of genes. During the time from conception to birth, growth would be controlled largely by the genes responsible for differentiation of cells as well as cell multiplication followed by development of different organs. Around the time of birth and thereafter, the genes responsible for development of the musculo-skeletal system may play a major role in the process of growth. From weaning to yearling age, the genes responsible for development of muscles and adipose

tissues may be playing a greater role in the body growth of calves. The differential growth of tissues and organs from early stage to maturity of mammals in general have been illustrated by Taylor (1985) and Beitz (1985).

The maternal genetic effects on BW of calves are mainly provided through pre-natal uterine environment, while those on WW are provided mainly through dam's milk and some carry-over pre-natal maternal effects from birth, both of which are also carried over to YW to some extent. The genes responsible for maternal genetic effects on BW are likely to be different from those responsible for maternal genetic effects on WW and YW, which were in turn likely to be controlled by mostly the same genes. This may explain why maternal genetic correlation estimate between WW and YW was very high, and the estimates for BW-WW and WW-YW pairs of traits were relatively lower.

The antagonistic relationship between the individual animal's own genetic capability for a juvenile growth trait and its maternal genetic ability provided to its calves for the same trait when it becomes a dam was evident from the estimates of direct-maternal genetic correlations of BW, WW and YW, ranging from -0.60 to -0.06, with the highest negative value for WW (-0.60), in the present research (Study I and Study II). These consistently negative estimates were in agreement with numerous studies reported in the literature (Meyer 1992; Mohiuddin 1993; Swalve 1993; Koots et al. 1994b; Rust et al. 1998). These results generally indicate that the animals which have a high genetic potential for their own growth tend to have less genetic potential to provide good pre-natal uterine environment and/or post-natal nursing to their calves. There is some controversy over the existence of this negative correlation, with some researchers

suggesting that the negative genetic correlation could arise through an environmental effects not accounted for in most analyses. The explanation for this is that the animals that produce more milk and are, thus, good mothers have calves that grow fast; but if these calves are female, they accumulate adipose tissue in their mammary gland resulting in poor performance through their milk in nursing their own offspring (Mangus and Brinks 1971; Cantet et al. 1988). This results in an environmental covariance between dams and offspring introducing bias into what is estimated as the direct-maternal genetic correlation for the trait (Rege 1985; Meyer 1992). However, Cundiff (1972) considered this antagonistic relationship logical from the evolutionary standpoint of having checks and balances between the growth and milk yield which are due to both genetic and environmental effects.

7.2. GENETIC ANALYSIS OF FEMALE REPRODUCTIVE TRAITS

Calving traits such as those analysed in the present studies, CD1 (Study I), CD and CI (study II) indicate beef cows' reproductive efficiency in terms of their timely calving, which is normally expected once in a year. In most temperate climate production systems, if the cow's fertility is temporarily compromised within a fixed length breeding season for various reasons ranging from the bull's fertility, management problems or the cow herself, breeding and resultant calving will be delayed, and CI will be lengthened.

The present genetic analyses (Study I and Study II) revealed that the two calving traits, CD1 and CD are moderately heritable, and are associated with the genetic capabilities of the cows. These two traits could thus be useful in selection programs.

These results are in agreement with a few studies in the literature (Meacham and Notter 1987; Lopez de Torre and Brinks 1990; Gutierrez et al. 2002) indicating that calving date is preferred over calving interval as a measure of female reproduction in beef cattle. On the other hand, CI was not a good measure of female reproduction not only due to its low heritability but also due to possible bias in its length for beef cows subjected to the time-limited breeding season. Most of the variation in CI was environmental in origin. In addition, its direct genetic correlation with CD was also found to be nil in the present research (Study II).

In the present Study III, the stayability trait (Stay3) has been found to be a moderately heritable trait in agreement with a few other studies reported in beef cattle (Snelling et al. 1995; Doyle et al. 2000; Silva et al. 2003), unlike the results reported in dairy cattle (Van Doormal et al. 1984) and in pigs (Lopez-Serrano et al. 2000) in which cases the traits have been reported to be lowly heritable. The highest culling rate of cows at three years of age as shown by their hazard function and moderately heritable nature of the trait, the Stay3, found in Study III indicated that Stay3 is worth considering in selection programs for reducing the culling of cows from the herds based on their failure in calving, and for contributing, in turn, to the reproductive efficiency of cows.

7.3. GENETIC ASSOCIATION BETWEEN GROWTH AND FEMALE REPRODUCTIVE TRAITS

Growth and female reproduction may have many physiological effects and biochemical pathways in common. This is due to the complexity of the effects of many genes, each with small effects, involved in their inheritance. Brien (1986) stated that the

state of knowledge of these traits is made up of pieces of a puzzle derived from isolated experimental studies carried out mainly in laboratory animals. There has been much work since then, but the situation is not greatly improved in terms of integration of this knowledge. Based on the studies reviewed at that time, Brien (1986) surmised that physiological links underlying the genetic associations between growth and reproduction are mediated by hormones such as prolactin, hormones secreted by adrenal glands and the thyroid hormones. Unraveling these links is rather complex, and linking them to the level of individual traits is a formidable task to be carried out with research in several disciplines including genetics, physiology and molecular biology.

The genetic analyses of female reproductive traits with juvenile growth traits in the present research revealed that the positive direct genetic correlation of CD1 particularly with WW was unfavorable ($r_a = 0.27$) such that the animals with higher direct genetic effects for WW tended to have a genetic tendency for delayed first calvings. This may be due to the occurrence of delayed puberty. Although there is no direct experimental evidence to illustrate this phenomenon in beef cattle, Brien (1986) has summarized several mouse studies showing that mouse lines selected for high body weight or gain show infertility at an age when normal mice would be expected to conceive. Brien (1986) has also concluded in his review that the decline in fertility following directional selection in a growth trait may be at least partly due to loss of homeostatic balance. This could also be viewed in the context of 'Resource Allocation Theory' (Rauw et al. 1998) in that animals selected for juvenile growth traits, particularly the weaning or yearling weight, have to face the challenges of limited food intake

resources being diverted to high growth, in turn, taking away from fitness or reproductive traits such as CD1.

Unlike CD1, the other calving traits CD and CI were measured as repeated records of calvings from cows of all ages, and showed moderate to high negative estimates of direct genetic correlations with juvenile growth traits in agreement with previous studies in the literature (Smith et al. 1989b; Meyer 1991; Rege and Famula 1993). For cows that are already near mature size, and not needing to express growth (unlike younger cows), feed resources for support of reproduction may not be limiting (Rauw et al. 1998). This could be a plausible explanation for favorable direct genetic correlations between these calving traits and juvenile growth traits, allowing cows to calve earlier and at shorter intervals in the later ages.

Negative genetic correlations of direct genetic effects of CD1 and CD with maternal genetic effects of juvenile growth traits particularly WW and YW found in the present research (Study I and Study II) indicated that both heifers and the older cows that calved early tended to have genetic capability to provide good post-natal nursing to their offspring. On the other hand, the genetic correlations of direct CI with maternal BW and maternal WW were found to be near zero, while that with maternal YW was positive but not consequential due to low heritabilities of both direct CI and maternal YW (Study II).

The estimates of rank correlations between direct EBVs of Stay3 and direct EBVs of all three juvenile growth were not significantly different from zero thus showing no evidence of genetic association between these traits. Hence, the correlated response of Stay3 from the selection for direct genetic effects if any of these growth traits would be

negligible. However, the results of a preliminary analysis (Rasali et al. 2002) and the results of correlation between maternal EBVs of WW and direct EBVs of Stay3 showed some favorable tendency in their genetic association. It is necessary to explore further to ascertain these genetic relationships of stayability with a number of economically important traits across populations of different breeds and herds of beef cattle. It is also important that genetic correlations of stayability with the growth traits are estimated with the advancement in feasible methods of their genetic analyses.

8. GENERAL CONCLUSIONS

Based on the genetic analyses carried out in three sets of present studies, the following conclusions are made:

1. Three juvenile growth traits, BW, WW and YW were found to be moderately to highly heritable for their direct genetic effects. Maternal genetic effects were lowly to moderately heritable, and accounted for 5 to 24% of the total phenotypic variation.

2. Two continuous traits of calving, CD1 and CD, and a binomial trait, stayability to three years of age (Stay3) are moderately heritable traits that would be useful in selection programs, while calving interval was lowly heritable.

3. The direct-maternal genetic correlations of BW, WW and YW were moderately negative, indicating the antagonistic relationships between direct genetic and maternal genetic effects for each of these weight traits.

4. The direct genetic correlation estimate between CD1 and WW was moderately positive indicating an unfavorable association between them. On the contrary, the estimates of direct genetic correlations of BW, WW and YW with CD and CI were negative indicating them as favorably correlated traits. Hence, CD1 and CD may not necessarily be the traits controlled by same sets of genes.

5. The correlations between direct genetic effects of CD1 with maternal genetic effects of weaning and yearling weights were negative and favorable. Similarly, the direct genetic correlations of CD and CI with maternal genetic effects of BW, WW and YW were favorable. These results indicate the value of selection for these maternal genetic effects especially in realizing correlated response in CD1 and CD. All direct-maternal

genetic correlations between calving traits with juvenile growth traits estimated in the present studies are new parameters that are not found in previous studies for comparison.

6. The genetic trends and average genetic changes in direct and maternal genetic effects of BW, WW, YW, and direct genetic effects of CD and CI were generally favorable. These were indicative of selection programs in the herds involving selection for a number of traits rather than for a single trait.

7. The correlations of estimated breeding values of Stay3 with direct EBVs of BW, WW and YW were not significant indicating that no substantial correlated response can be expected from the selection for any of three juvenile growth traits on Stay3 and vice versa. However, the highest rate of culling of cows at three years of their age as shown by the hazard function and moderate heritability of the trait Stay3 showed that Stay3 was a trait worth considering in the selection programs.

8. The new genetic parameters estimated from the present research could be valuable for use in beef cattle selection programs in Canadian Angus cattle, and also for their further validation across other breeds and herds of beef cattle.

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Appendix 1: Example SAS Programming used for generating date sets for calving date (CD) and calving interval (CI)

```
Filename Filedat 'directory path/Filedat1';
Filename Filedat2 'directory path/Filedat2';
Filename CIfile 'directory path/CIfile';
Filename CDfile 'directory path/CDfile';

* BDD=Day of month of calf's birth (two digits);
* BMM=Month of calf's birth (two digits);
* BYY=Year of calf's birth (two digits);
* Type of calf's birth (singleton or multiple);
* Ncalves= Number of calves born;

Data A;
  Infile Filedat1;
  Input AnimID $ SireID $ DamID $ BDD BMM BYY Sex BType;
  BD=MDY(BMM,BDD,BYY);
Cards;

Proc Sort Data=A; by Dam BD;

Proc Means Data=One; by Dam;
  Var BD; Output Out=Onem N=Ncalves;

Proc Print Data=Onem;

Data B;
  Merge One Onem; by Dam;
Cards;

Proc sort Data=B; by Dam BD;

Data C;
  Set B;
  File Filedat2;
  Put Tattoo $10. Dam $10. BDD 3. BMM 3. BYY 3. BD 6. Ncalves 3.;
Cards;
```

```

Data D;
  Infile Filedat2;
  Input Tattoo $ Dam $ BDD BMM BYY BD Ncalves;
  CD = BD; CI=.; Output;
  If Ncalves > 1 then Do;
    NC=Ncalves;
    Do I = 1 to NC-1;
      Input Tattoo $ Dam $ BDD BMM BYY BD Ncalves;
      CI=BD-CD;
      Output;
      CD=BD;
    End;
  End;
Cards;

```

```

Proc Sort Data= D; by Dam CD;

```

```

Proc Means Data=Four; by Dam CD;
  Var CI;

```

```

Data E;
  Set D;
  File Cifile;
  If CI > 0;
  If CI <> .;
  Put Dam $10. CI 5.;
Cards;
Proc Print;

```

```

Data F;
  Set D;
  File CDfile;
  Put Dam $10. BDD 3. BMM 3. BYY 3. CD 7.;
Cards;

```

```

Proc Print;

```

```

Quit;

```

Appendix 2. Least-squares means (\pm SE) of birth weight (BW), weaning weight (WW) and yearling weight (YW) across herd, year of birth, season of birth, type of birth and sex at birth in a pooled population of five herds of Angus cattle.

Factors ^z	BW, kg	WW, kg	YW, kg
Herd:			
A	36.17 \pm 0.26	259.8 \pm 2.4	461.6 \pm 3.6
B	33.18 \pm 0.25	242.0 \pm 2.4	384.2 \pm 3.7
C	34.64 \pm 0.33	314.3 \pm 2.8	487.4 \pm 4.8
D	31.70 \pm 0.29	259.3 \pm 2.6	407.2 \pm 4.0
E	34.49 \pm 0.34	266.6 \pm 2.9	423.9 \pm 4.5
Year of birth:			
1984	31.89 \pm 0.41	248.1 \pm 3.3	412.1 \pm 4.8
1985	32.43 \pm 0.43	269.2 \pm 3.4	409.4 \pm 4.9
1986	33.86 \pm 0.43	279.3 \pm 3.4	421.8 \pm 4.9
1987	32.20 \pm 0.42	265.3 \pm 3.4	414.7 \pm 4.8
1988	32.55 \pm 0.42	253.0 \pm 3.4	436.2 \pm 4.9
1989	33.79 \pm 0.37	274.3 \pm 3.2	447.0 \pm 4.8
1990	34.59 \pm 0.39	255.5 \pm 3.2	417.5 \pm 4.7
1991	34.13 \pm 0.39	263.8 \pm 3.2	432.0 \pm 4.7
1992	34.12 \pm 0.36	256.8 \pm 3.0	434.1 \pm 4.5
1993	34.93 \pm 0.34	278.5 \pm 3.0	437.1 \pm 4.4
1994	34.95 \pm 0.35	274.6 \pm 3.0	449.3 \pm 4.4
1995	35.27 \pm 0.35	285.1 \pm 2.9	444.7 \pm 4.3
1996	34.90 \pm 0.31	275.4 \pm 2.8	430.5 \pm 4.2
1997	34.39 \pm 0.30	265.8 \pm 2.7	438.2 \pm 3.9
1998	34.69 \pm 0.30	280.9 \pm 2.5	436.6 \pm 3.8
1999	34.54 \pm 0.30	273.1 \pm 2.5	443.2 \pm 4.0
2000	34.35 \pm 0.32	275.7 \pm 2.7	454.8 \pm 4.2
2001	35.00 \pm 0.33	256.7 \pm 3.1	-
Season of birth:			
1. fall	34.19 \pm 0.46	259.8 \pm 4.5	442.2 \pm 6.8
2. winter	34.02 \pm 0.19	275.1 \pm 1.5	408.8 \pm 2.3
3. spring	34.37 \pm 0.22	262.9 \pm 1.8	399.3 \pm 2.7
4. summer	33.55 \pm 0.53	275.7 \pm 5.5	481.1 \pm 8.7
Type of birth:			
1. singleton	37.88 \pm 0.19	279.5 \pm 1.9	448.6 \pm 2.9
2. multiple	30.19 \pm 0.37	257.3 \pm 3.2	417.1 \pm 4.8
Sex at birth:			
1. Female	32.80 \pm 0.25	257.0 \pm 2.3	385.1 \pm 3.5
2. Male	35.27 \pm 0.25	279.8 \pm 2.3	480.6 \pm 3.5

^z Effects of all factors shown here were significant at ($P < 0.001$) for all traits.