

DISSERTATION

DIFFERENTIAL RESPONSE FROM SELECTION FOR LOW BIRTH WEIGHT VERSUS
HIGH CALVING EASE IN BEEF CATTLE

Submitted by

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ABSTRACT

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The economic importance of calving ease is derived from the reduction in costs associated with dystocia. However, the genetic improvement of calving ease did and still does rely upon the downward selection for a trait with no direct economic relevance (i.e., birth weight). Given the antagonistic genetic relationship between calving ease and postnatal growth traits, such a strategy could result in production of lighter animals with uncertain gain in calving ease. Therefore, we hypothesized that direct selection for high calving ease would reduce performance losses associated with selection for low birth weight. Thus, the main objective of our study was to compare two selection approaches: 1. selection for high calving ease; and 2. selection for low birth weight. To evaluate these approaches, we used both simulated data and American Simmental Association field data. Another complicating factor was the approach to evaluation of calving ease with a threshold versus a linear model. The advantages of the threshold model over the linear model, in the analysis of ordered categorical traits, were investigated in the literature. Results are varied with some supporting and others discounting the superiority of the threshold model. Therefore, another goal of the current study was the predictive ability of the threshold and linear methodologies used in the genetic evaluation of calving ease as an example of ordered categorical traits.

Data on calving ease, birth weight, weaning weight, and yearling weight were obtained from the American Simmental Association (ASA). Given the multi-breed nature of the ASA

database, only animals with $\geq 87.5\%$ Simmental composition (to avoid heterosis) were included in our study with data constructed from the base population of 2 year old dams as they provide the most relevant calving ease observations (N=95,791). Weaning and yearling weights were adjusted for age to 205 and 365 *d*, respectively. Further, 160-*d* postweaning gain was calculated from the adjusted weights. Four-generation pedigrees were constructed to estimate sire and maternal grandsire (co)variance components for calving ease (CE), birth weight (BWT), and 205-*d* weight (205-*d* WT), and sire (co)variance components for 160-*d* postweaning gain (160-*d* gain) using threshold-linear sire and sire-maternal grandsire models with a Gibbs sampling algorithm. Following variance component estimation, the direct and maternal EBV for CE, BWT, and 205-*d* weight and direct EBV for 160-*d* gain and 365-*d* weight for 465,710 animals were calculated using a threshold-linear multivariate maternal animal model. Calving ease was modeled as a threshold trait (*i.e.*, underlying continuous liability was assumed) with 3 observed categories (1 = Unassisted calving, 2 = minor assistance, and 3 = major assistance + caesarean). The 365-*d* weight direct EBV were calculated as the summation of the estimated EBV for 205-*d* weight and 160-*d* gain. A subpopulation of 2 year old (first-calf) Simmental heifers (n = 277,897) was extracted under the restriction of including only progeny of first-calf heifers. This subpopulation was used for estimating genetic trends of Simmental, and was also used as a pool of data (control scenario) for different selection scenarios. Therefore, six selection scenarios, for low birth weight as opposed to selection for high calving ease, were created. Using the first-calf heifer data (the control), data for each selection scenario were created by selecting sires, within each year of birth, with EBV \geq the average, then the top 75% of dams with progeny were selected. Six selection scenarios were evaluated with two single trait selection scenarios for both high calving ease (HCE) and low birth weight (LBWT) in addition to four different selection

indices. The indexes were the all-purpose selection index ($API = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT$) adopted by the ASA, two derivative sub-indices: ($API_1 = 1.3 CE + 0.20 YWT$) and ($API_2 = -1.8 BWT + 0.20 YWT$), and lastly Dickerson's selection index ($DSI = -3.2 BWT + YWT$). For each selection scenario, EPD were standardized and then expressed as a deviation from the average EPD, within birth year, from the control scenario. Comparison between various selection scenarios involved that of the direct and maternal genetic trends of studied traits and the net profit from these scenarios. Here, the net profit was calculated for all selection scenarios using the API. Furthermore, we examined the threshold model suitability for the analysis of categorical traits as opposed to linear with the first-calf Simmental heifer calving ease as the trait of interest. We also addressed, not only the linearity of the trait, but also the number of trait categories, the number of fitted traits, and extended the comparison to include the animal model versus the sire model. Only direct (or sire effects in the sire model) genetic effects were fitted in all models. Using a balanced data with herd size ≥ 50 animals, the efficiency of models were determined by the predictive ability of each model using a cross validation "data splitting" technique. The model's predictive ability was estimated using the correlations (Pearson's and Spearman's) between predicted CE EPD obtained from two complementary subsets.

Two simulated data sets were created under two selection scenarios. Selection scenarios were first, selection for high calving ease (HCE) and second, selection for low birth weight (LBW). In both simulated populations, observations on calving ease (CE), birth weight (BWT), weaning weight (WWT), and postweaning gain (PWG) were created. Each population consisted of a base generation of 1,200 sires and 36,000 dams. The first generation was produced by random mating of founders (1,200 sires and 36,000 dams). Each of the three subsequent generations was produced by selecting the top 5% and 80% of sires and dams, respectively, from

previous generations. Parameter estimation was carried out using a multivariate threshold-linear model with Gibbs sampling algorithm. Fixed effects were herd ($n = 120$) and sex of calf. For both selection scenarios, direct genetic trends for CE, BWT, WWT, PWG, and YWT were estimated. Using the HCE data, the predictive ability of the threshold and linear models was compared using the same cross validation procedure described for Simmental field data.

Results from simulated data using single trait selection for low birth weight versus high calving ease showed that the rate of genetic change of CE (% unassisted calving/yr) from the high calving ease selection scenario was higher ($P < 0.001$) than that from the low birth weight scenario. Both selection scenarios have reduced growth rate. However, genetic trends of growth traits obtained under the high calving ease selection scenario were higher ($P < 0.001$). Selection for high calving ease increased ($P < 0.001$) the annual genetic change for CE, WWT, and YWT over the low birth weight selection scenario by 0.37%, 1.65 kg, and 1.77 kg, respectively. Therefore, selection for high calving ease produced animals with better calving ease EPD and with higher growth rates at later ages. Both threshold and linear models had similar predictive ability (i.e., similar correlations). The similar predictive ability might be a result of the highly balanced data used in current study. Nonetheless, both models exhibited substantial increases in the accuracy of prediction for CE when BWT was incorporated as a correlated trait.

Results from the American Simmental beef cattle field data resulted in direct heritabilities for CE (on the underlying scale), BWT, 205-*d* WT, 160-*d* gain, and 365-*d* WT within the literature estimates of the Simmental beef cattle. Maternal heritability estimates for CE, BWT, and 205-*d* WT were also in agreement with the Simmental estimates reported in the literature. The high negative genetic correlation between CE and BWT (-0.67) and the high heritability of BWT (0.52) justified the importance of incorporating BWT in the genetic evaluation of CE. The

moderate positive genetic correlations between BWT and subsequent growth traits exposed the genetic antagonistic relationship between CE and postnatal growth traits when selection for low birth weight is applied.

Results obtained from the Simmental field data showed that all selection scenarios, for high calving ease versus low birth weight, compared to the control scenario, have reduced growth rate but increased ease of calving. Generally, the calving ease-based selection scenarios (HCE, API, and API₁) had the highest net profit and showed higher genetic trends for calving ease and growth-related traits compared to the birth weight-based selection scenarios (LBWT, DSI, and API₂). The calving ease-based selection scenarios shifted the intercept of the net profit of the control scenario by 13, 11.6, and 11.1 \$, respectively; whereas, the birth weight-based selection scenarios showed lower intercepts of 8.2, 7.3, and 8.8 \$, respectively. The single trait, HCE, selection scenario substantially improved calving ease and growth-related traits and resulted in a shift of the intercept of the net profit over the LBWT by 58%.

The comparison of models predictive ability using threshold and linear or animal and sire approaches revealed that the threshold model outperformed the linear model. The highest predictive ability among all compared models was obtained from the threshold-linear sire model with calving ease fitted as a binary trait. The inclusion of linear trait(s) improved the prediction of categorical traits. Furthermore, the analysis of categorical traits with two continuous traits resulted in small differences between the threshold and linear models. The higher the number of categories, the better the linear model prediction; in contrast, the threshold-linear models showed better predictive ability when calving ease was fitted as a binary outcome.

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CHAPTER I.

INTRODUCTION AND OBJECTIVES

1.1. Introduction

Traits measured on farm animals can be categorized into two groups. First, a trait that has a direct effect on profitability by being associated with a specific cost of production or income. Traits in this class are known as economically relevant traits or “ERT” (Golden et al., 2000). Second, a trait that does not affect profitability, as it indirectly influences profitability through a correlation with the ERT, is called an indicator trait. However, indicator traits (*e.g.*, birth weight) are included in genetic evaluations to help predict the genetic merit of ERTs (*e.g.*, calving ease) and improve accuracy of genetic prediction (Golden et al., 2000; Enns, 2010). An example of an economically relevant trait is calving difficulty which describes the difficulty of birth experienced by a cow. Calving difficulty is measured by a scoring system that gives subjective scores ranging from 1 (*i.e.*, unassisted calving) to 5 (*i.e.*, mal-presentation) where the higher the score the more difficult the birth (BIF, 2010). Calving ease is, by definition, the opposite of calving difficulty meaning that the lower the score the more likely the birth process to become easier. Basically, both are the same trait from two perspectives; therefore, they will be referenced synonymously and used interchangeably throughout this document. Numerous publications described the economic importance of calving difficulty resulting from the cost associated loss of calf, death of dam, labor and veterinary charges, and poor subsequent reproductive performance (Wiltbank et al., 1961; Laster et al., 1973; Meijering, 1984). In Holseins cattle, estimated costs associated with categories of calving difficulty were \$0.00, \$50.45, \$96.48, \$159.82, and

\$379.61 for scores 1 to 5, respectively, (Dematawewa and Berger, 1997). These costs were estimated from losses in milk yield, fat yield, protein yield, days open, number of services, and calf deaths. However, the total cost associated with dystocia (i. e., within-parity sum of costs associated with dystocia scores weighted by the probability of occurrence) was \$28.53 for an average heifer and about \$10.00 for an average older cow.

The most influential factors contributing to the incidence of calving difficulty are calf birth weight followed by pelvic area of dam (Bellows, 1993). Increasing birth weight by 1 kg increased the incidence of calving difficulty by (2.3%; Laster et al., 1973) and (13% “Odds ratio”; Johanson and Berger, 2003). Birth weight accounted for 50% of total variance of calving difficulty while pelvic area accounted for 10% (Meijering, 1984). The undesirable combination of both factors is called feto-pelvic disproportion or incompatibility (FPD) which is the main cause of calving difficulty (Meijering, 1984).

Calving ease has a high *negative* genetic correlation with birth weight (Koots et al., 1994b; Eriksson et al., 2004, among others). Therefore, in most genetic evaluations of calving ease, birth weight was incorporated as a correlated indicator trait. Over the years, in order to improve calving ease, animal breeders have put significant emphasis on selection for low birth weight. Nonetheless, a genetic antagonistic relationship may arise given the fact that birth weight has high *positive* genetic correlations with subsequent growth traits. Further, Burfening et al. (1978b) stated that selection for low birth weight would not be as effective in improving the ease of calving. MacNeil et al. (1998) suggested that direct selection for calving ease may be more effective than selecting for the indicator trait, birth weight. Hence, we hypothesize that selection for low birth weight would result in lower growth rates at later ages than would selection on calving ease. Calving ease has lower genetic correlations with later growth traits than birth

weight, and therefore we believe direct selection for high calving ease will improve the ease of calving and reduce the performance loss in postnatal growth traits. If true, the preferable approach would be to use calving ease as selection criteria as opposed to birth weight.

The best linear unbiased prediction (BLUP), given its appealing properties, is considered the method of choice for the genetic evaluation of data that follow multivariate normal distribution. Nonetheless, when analyzing ordered categorical responses (*e.g.*, calving ease) via linear methodology like BLUP, assumptions of: normality, homogeneous variance, and additivity of effects are violated. Gianola and Foulley (1983) described a method called the threshold methodology to be used for the analysis of such traits. The threshold methodology has been validated, theoretically and by simulation studies, to be more suitable for analysis of ordered categorical traits than the linear approach. However, there have been relatively few citations comparing threshold and linear methodologies using field data which press the need to investigate and verify the superiority of the threshold model over the linear model using field data. The combination of the need to compare both methods of calculation and both approaches to selection using field data from the ASA is the motivation for this dissertation.

1.2. Objectives

The primary focus of this dissertation was to investigate the effect of selection for high calving ease compared to selection for low birth weight on other performance traits (*e.g.*, yearling weight) and profitability in terms of net profit.

Objectives of simulation studies and field data analyses are outlined as follow:

Simulated data:

1. Identify the best approach to reduce calving difficulty through quantifying performance losses using estimation of genetic trends for calving ease, birth weight, weaning weight,

postweaning gain, and yearling weight under two selection scenarios: selection for low birth weight versus high calving ease.

2. Comparison of different animal models used in the genetic evaluation of calving ease where calving ease was fitted as a binary or polychotomous trait. Compared models included: univariate animal model fitted to calving ease (Threshold vs. linear), bivariate animal model fitted for calving ease and birth weight (threshold-linear vs. linear-linear), multivariate animal model fitted for calving ease, birth weight, and weaning weight (threshold-linear vs. linear-linear), and multivariate animal model fitted for calving ease, birth weight, weaning weight, and postweaning gain (threshold-linear vs. linear-linear).

Simmental (field) data:

1. Estimate genetic and residual parameters ((co)variances) for calving ease, birth weight, weaning weight, postweaning gain, and yearling weight of American Simmental beef cattle by means of the threshold methodology.
2. Compare different models fitted to calving ease (binary versus polychotomous) using first parity Simmental heifer data including: threshold versus linear; animal model versus sire model.
3. Compare genetic trends for calving ease, birth weight, weaning weight, postweaning gain, and yearling weight of American Simmental beef cattle under six different artificial selection scenarios: High calving ease (HCE), low birth weight (LBWT), Dickerson's selection index (DSI), all purpose selection index recommended by the American Simmental Association (API), API₁: includes only yearling weight and calving ease, and API₂: includes only yearling weight and birth weight.
4. Compare profit between all selection scenarios applied to Simmental data.

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CHAPTER II.

LITERATURE REVIEW

In this chapter, literature on topics considered the most relevant and essential for the study of ordered categorical traits (*e.g.*, calving ease) were reviewed. These topics included: ordered categorical traits, factors influencing calving ease, the threshold model, Markov Chain Monte Carlo (MCMC) and the Gibbs sampling algorithm, model comparisons (threshold versus linear; and animal versus sire), genetic and residual parameters for calving ease and growth traits, selection index, and genetic trends estimated from selection trails for calving ease and birth weight.

2.1. Ordered categorical traits

Ordered categorical traits are traits that have phenotypes that can be assigned into ordered classes. Traits with only two categories are known as binary traits (*e.g.*, disease susceptibility “infected vs. healthy” and pregnancy status as pregnant vs. non-pregnant). Calving ease is a traditional example of ordered categorical traits which has an observed distribution based on the discrete nature of its phenotype (Fig. 2.1) which is assigned to animals following a scoring system based on the degree of calving difficulty which ranges from 1 for unassisted calving to 5 for mal-presentation. Since most ordered categorical traits in the field of animal science are in essence quantitative traits, categories of this kind of traits can be ordered along a hypothetical underlying continuous distribution in which the observed categories are transformed to an underlying continuous variate known as liability.

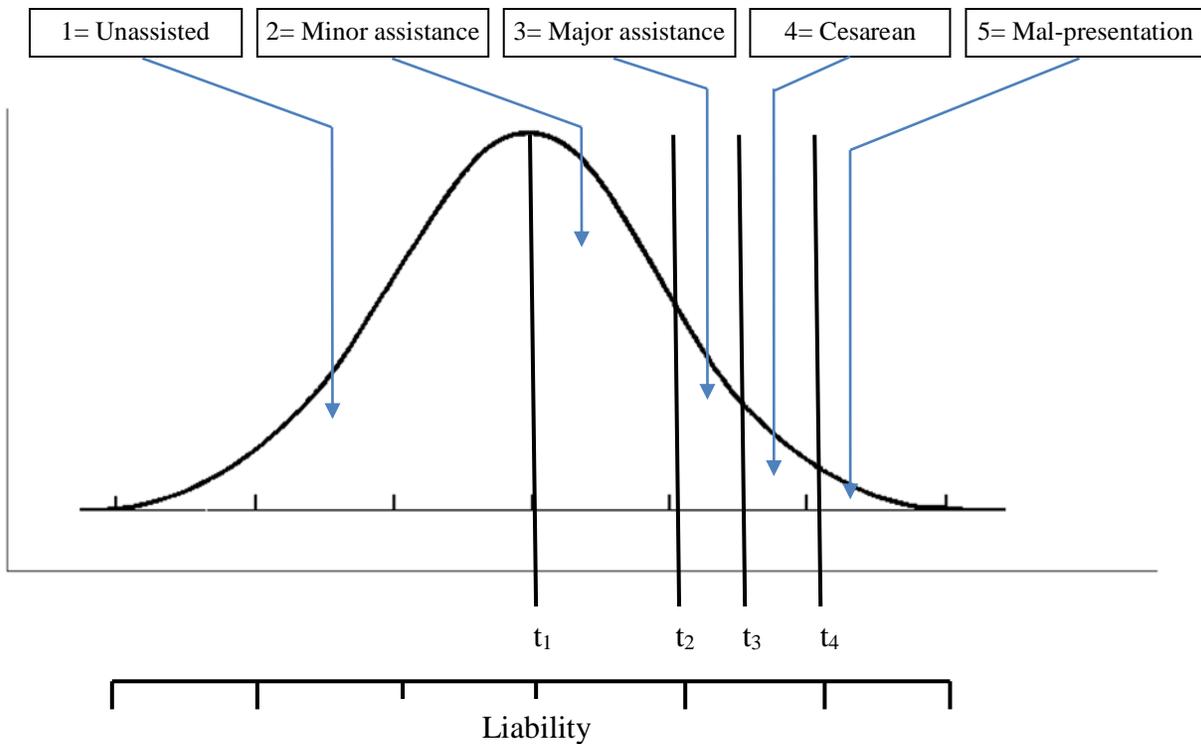


Figure 2.1: The underlying continuous variate (liability) and the discrete observed scores of calving ease

Calving ease is by definition the opposite of calving difficulty which is an ordered categorical trait measured by subjective scoring system in which the degree of calving difficulty is recorded as follow: 1 for unassisted calving, 2 for minor assistance, 3 for major assistance, 4 for caesarian section, and 5 for abnormal presentation (BIF, 2010).

Economically relevant traits (ERT) are “the traits that directly affect profitability by being associated with a specific cost of production or an income stream” (Golden et al., 2000). The economic importance of calving difficulty is documented in the literature (Wiltbank et al., 1961; Anderson and Bellows, 1967; Brinks et al., 1973; Laster et al., 1973). Because of its association with a cost of production such as loss of calf (Nix et al., 1998), death of dam, and the cost of labor and veterinary procedures (Philipsson, 1976b; Philipsson et al., 1979; Meijering, 1980,

1984), calving difficulty can be classified as an ERT. Further, Thompson et al. (1983) reported a reduction in subsequent reproductive performance of cows experiencing calving difficulty. The economic importance of calving difficulty, in dairy cattle, was also confirmed and estimated by Dematawewa and Berger (1997). They evaluated the economic impact of dystocia on different production and reproductive traits. These authors estimated the cost associated with each category of calving difficulty to be \$0.00, \$50.45, \$96.48, \$159.82, and \$379.61 per head for scores 1 to 5, respectively.

2.2. Factors affecting calving difficulty

Some factors have a direct effect on the incidence of calving difficulty such as calf birth weight and pelvic area of dam. Other factors have indirect effect on calving difficulty via affecting either birth weight or pelvic area of dam. Sex of calf, gestation length, and weight of dam during pregnancy are important factors that influence birth weight and consequently calving difficulty. Factors affecting pelvic area of dam are parity and age of dam at first calving. Literature describing the contributing factors that affect the incidence of calving difficulty are reviewed in the succeeding sections.

Calf size: The incidence of calving difficulty is primarily driven by a combination of two major factors: size of calf (consequently, birth weight) and pelvic area of dam (Bellows et al., 1969; Prentiss, 1971; Rice and Wiltbank, 1972). Bellows (1993) reported that the most important factors that affect dystocia were precalving weight and pelvic area of the dam, as well as sex and birth weight of the calf. Further, he concluded that birth weight is the most important factor followed by the dam's pelvic area. The incidence of calving difficulty is greatly influenced by the interactions of birth weight of calf and dam's pelvic area (Fig. 2.2) where birth weight has a higher influence. As birth weight increased by 1 kg, the odds of calving difficulty increased by

13% (Johanson and Berger, 2003). Laster et al. (1973) and Burfening et al. (1978a) estimated increase in the percent of assisted calving as 2.3% (across breeds and different ages of dam) and 4.5% (2 yr old Simmental heifers), respectively, when birth weight increased by 1 kg.

Calf birth weight, as a measure calf size, is widely used in the genetic evaluation of calving difficulty. This is a result of its strong genetic correlation with calving difficulty which ranged from 0.72 to 0.78 (Burfening et al., 1981; Koots et al., 1994b; Eriksson et al., 2004; Phocas and Laloe, 2004; Jamrozik and Miller, 2014). Calf size is a function of genetic and environmental factors. These factors are breed of sire and dam, sex, gestation length, parity, age of dam, and dam's nutrition during gestation. Each of these deserves additional investigation which follows.

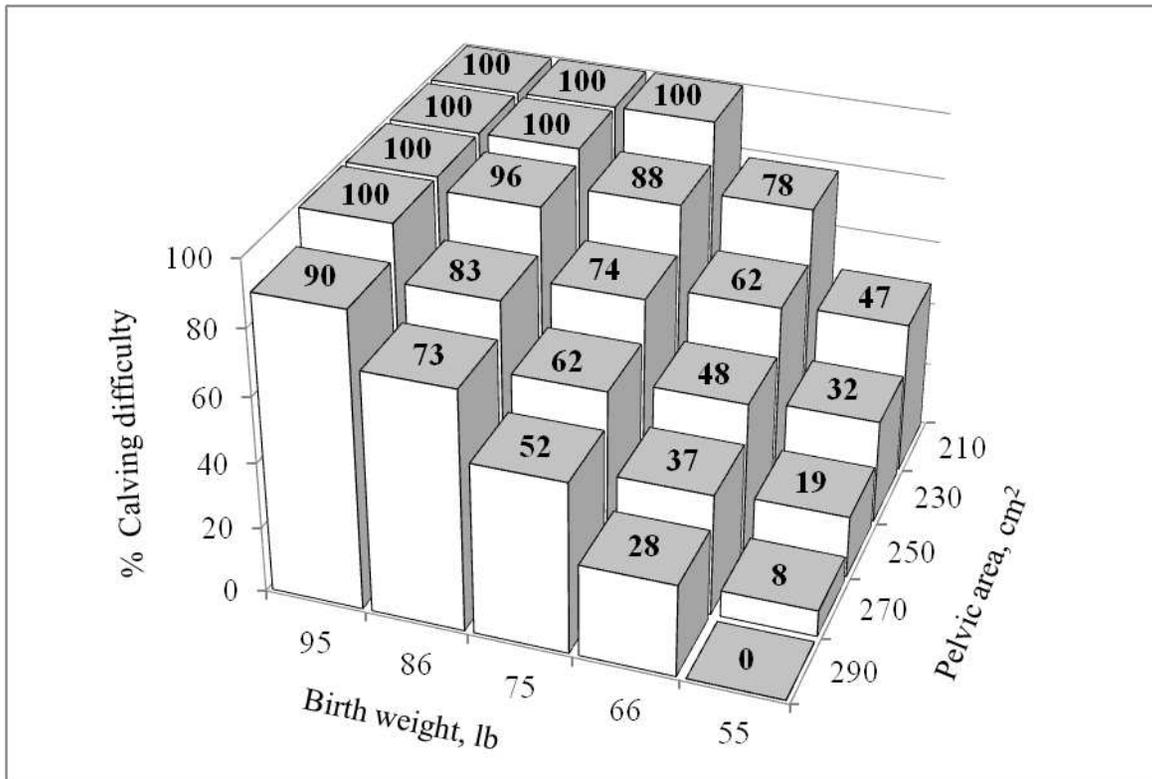


Figure 2.2: Relationships among pelvic area, calf birth weight and percent calving difficulty. Adapted from Bellows (1993).

Sex of calf: Bull calves are typically heavier at birth than heifers. Consequently, a higher incidence of calving difficulty is observed when the calf is a male. Everett and Magee (1965) and Smith et al. (1976) reported that male calves have longer gestation length (0.9 and 1.7 d, respectively) compared to female calves. The longer gestation length was associated with higher birth weight. A corresponding effect of sex on dystocia was confirmed in several studies (Bellows et al., 1971; Brinks et al., 1973; Naazie et al., 1989; Sieber et al., 1989; Klassen et al., 1990; Dekkers, 1994; Johanson and Berger, 2003). Bull calves have a higher incidence of dystocia ($P < 0.05$) compared to heifers, consequently, they have higher mortality within 24 h of birth (Nix et al., 1998). Incidence of unassisted calving for males and females, from first parity heifers, were 48.9% and 55.6%, respectively (Dekkers, 1994). For later parities, the incidence of unassisted calving were 66.5% and 71.3% for their respective sex. Similar results were attained by Steinbock et al. (2003) who found that Swedish Holsteins heifers that gave births to males expressed higher incidence of calving difficulty comparing to heifers with female progeny.

Gestation length: Cows with longer gestation length experienced more calving difficulty (Laster et al., 1973; Philipsson, 1976a). Gestation length has been investigated in relation to both calf size and sex (Everett and Magee, 1965; Smith et al., 1976). On the genetic level, moderate genetic correlations of 0.20 and -0.21 were estimated between gestation length and birth weight and calving ease, respectively, (Lee et al., 2002). This suggests an antagonistic relationship between gestation length and calving ease which is driven by the positive effect of gestation length on birth weight. Similar results were obtained by Jamrozik and Miller (2014) who reported that gestation length had genetic correlation estimates of 0.23 and -0.21 with birth weight and calving ease, respectively. Results from Kemp et al. (1988) showed that as gestation length increased, the incidence of calving difficulty increased. Mujibi and Crews (2009)

estimated strong genetic correlations of 0.43 and -0.38 between gestation length and birth weight and calving ease (transformed to Snell scores), respectively. In summary it appears that gestation length is consistently negatively related to calving ease and positively related to birth weight.

Parity and age of dam at first parity: The total cost associated with calving difficulty was \$28.53 for 2 year old heifers and about \$10.00 for older cows (Dematawewa and Berger, 1997). Parity and age of dam within parity appeared to also influence incidence of calving difficulty; therefore, inclusion of parity in the genetic evaluation of calving difficulty has been emphasized by many researchers (Berger and Freeman, 1978; Harville and Mee, 1984). In general, first parity heifers, in both dairy and beef cattle, expressed higher incidences of calving difficulty than cows at later parities (Berger and Freeman, 1978; Thompson et al., 1983; Fiedlerová et al., 2008). Furthermore, the odds of unassisted calving versus assisted calving with major difficulty were 11.58 times greater in older cows than in heifers (Berger et al., 1992). This trend was further reinforced when Nix et al. (1998) reported primiparous dams had a higher incidence ($P < 0.01$) of calving difficulty (17%) compared to multiparous dams (4%). They found that calf mortality increased as the severity of calving difficulty increased. Further, loss of calves from primiparous dams within 24 h of birth was higher than ($P < 0.01$) those from multiparous dams with mortality rates of 7% and 4%, respectively, leading the authors to conclude that birth weight and parity of dam explained most observed variability in calving difficulty. Steinbock et al. (2003) concluded that first parity Swedish Holsteins heifers showed more variation in calving difficulty than second parity heifers. The incidence of calving difficulty was higher for first parity heifers at calving age < 30 months and they recommended that first parity heifers should be bred at a moderate age (> 21 mo) to reduce the incidence of calving difficulty. Laster et al. (1973) reported that, when birth weight held constant, age of dam was the most important effect

($p < 0.005$) associated with calving difficulty. Similar results were reported by Brinks et al. (1973) in their study on Hereford.

Pelvic area of dam: Calf birth weight and pelvic area of dam are the most important factors influencing the incidence of calving difficulty (Meijering, 1984). The author reported that both factors accounted for 50% and 10% of total variance of calving difficulty. Feto-pelvic disproportion (FPD) occurs when the fetus weight or size is not compatible with pelvic area of the dam. Pelvic area of dam is considered the most important maternal trait that affects calving difficulty (Price and Wiltbank, 1978; Morrison et al., 1985). Incidence of calving difficulty decreased by 11% when pelvic area increased by 1cm^2 (Johanson and Berger, 2003). However, Laster (1974) and Naazie et al. (1991) found weak phenotypic and genetic correlations between calving difficulty and pelvic area of dam; however, in the latter study, authors speculated that the low correlations would be attributed to the above-threshold pelvic area observations (i.e., dams have pelvic area larger than the threshold at which calving difficulty would likely occur). Naazie et al. (1991), in a study on three synthetic breeds, suggested that pelvic area and birth weight combined would be a better predictor for calving difficulty than using only one of them. Johnson et al. (1988) suggested that ratio of heifer pelvic area to calf birth weight should have a minimum of $4.7\text{ cm}^2/\text{kg}$; however, estimation of birth weight will be critical because it is not available before calving. Bellows et al. (1982) reported that heifers are smaller than cows in pelvic height, width, and pelvic area, consequently they experienced more calving difficulty. In summary, estimation of breed-specific pelvic area threshold is not practical since the interaction with birth weight was evident; however, ratio between birth weight and pelvic area would be a viable option to consider. Further, as heifers are growing, age of heifer when pelvic area is measured is another important factor that should be considered.

Dam weight and prenatal nutrition: Level of nutrition during pregnancy affects directly dam weight and body condition score which in turn influence fetal growth. Since birth weight is the final weight of prenatal growth, any change in nutrition will accordingly change weight of dam and calf birth weight and eventually the incidence of calving difficulty. Cows with body condition score (BCS) of 4.7 gave birth to lighter calves (-4.3 kg) than those from cows with BCS of 5 (Houghton et al., 1990). Corah et al. (1975) found that heifers lost 5.8 kg of body weight gave birth to lighter calves (-2 kg) compared to calves produced by cows that gained 36.1 kg in the last 100 d of gestation. Birth weight of calves from heifers with BCS of 2.5 was lower (-4.1 kg) than those from heifers with BCS of 5.5, however, nutrition level did not affect incidence of calving difficulty (Bellows and Short, 1978). Freetly et al. (2000) reported that cows on a low plane nutrition during pregnancy gave birth to calves with lighter birth weight compared to calves from cows with better nutrition. However, in a study on Angus, Hereford, Angus-Hereford, and Simmental-Angus, Morrison et al. (1999) found that weight and BCS of dam did not affect calf birth weight.

Breed of sire and dam: Direct genetic effects, for different beef cattle breeds, can account for significant amounts of variation in birth weight ranging from 26 to 66% of total variance (Koots et al., 1994a; Bennett and Gregory, 1996; Eriksson et al., 2004; Phocas and Laloe, 2004). For calving difficulty, heritability estimates were typically lower (6 to 26%; Kemp et al., 1988; Koots et al., 1994a; Matilainen et al., 2009). The genetic makeup of sire and dam, *i.e.*, maternal grandsire of a calf can affect the incidence of calving difficulty (Laster et al., 1973; Meijering, 1984). Laster et al. (1973) reported that calves sired by continental beef breeds expressed more difficult births than those sired by Hereford, Jersey, and Angus. Furthermore, breed of dam was another determinant factor for calving difficulty where Hereford dams experienced more calving

difficulty than Angus dams. Brinks et al. (1973) reported that line of sire and line of dam significantly influenced incidence of calving difficulty in a study with different Hereford lines. Smith et al. (1976) reported that breed of sire and breed of dam have significant effects on calving difficulty of Hereford and Angus cows with calves sired by Hereford, Angus, Jersey, South Devon, Limousin, Charolais, and Simmental sires. Results showed that interaction between breed of sire and age of dam (parity) had a highly significant effect on calving difficulty, especially for first parity dams.

In summary, all genetic and environmental factors associated with calving difficulty, such as genetic makeup of calf, sex, gestation length, nutrition, parity and age of dam, directly affect birth weight, which is the most important factor influencing incidence of calving difficulty. The second most influential predictor of calving difficulty appears to be pelvic area of dam which interacts with birth weight to form Feto-pelvic disproportion (FPD), which is considered the main cause of calving difficulty.

2.3. The threshold model for categorical traits

Phenotypes of many traits in the field of animal science are recorded as ordered categories (*e.g.*, calving ease and litter size in sheep). Categorical nature of such traits makes it difficult to be analyzed via means of linear methodologies where traits are assumed to follow a normal distribution. One of the earliest papers that provides a procedure to deal with categorical traits was that of Grizzle et al. (1969), who proposed a weighted regression procedure in which weights are based on population frequencies estimated from data. Authors assumed that subclasses, *e.g.* sex, age of dam, sire, and herd, are samples from separate populations; however, Schaeffer and Wilton (1976) reported that those assumptions were not suitable for sire evaluation of calving ease rather they assumed that subclasses are sampled from one population. Berger

and Freeman (1978) transformed a categorical trait into a continuous trait through assigning K ordered numerical values to the K categories and then the transformed trait was treated as a linear trait that followed the general linear mixed model. Linear approaches, such as Henderson's best linear unbiased prediction (BLUP; Henderson, 1953; Henderson, 1973, 1975), assume that data is normally distributed, additive effects, and variances are homogenous; however, when evaluating ordered categorical traits using linear methodologies, those assumptions are violated (Thompson, 1979; Gianola, 1982). It has been suggested that categorical traits have a hypothetical underlying continuous scale "liability" which becomes discrete (observed scale) with fixed thresholds that determine the boundaries of the categories (Wright, 1934; Dempster and Lerner, 1950; Falconer, 1965). The assumption of normal distribution of liability appears true if polygenic inheritance with large number of loci is evident (Foulley et al., 1990). Theory of the threshold model was developed by Wright (1934), Bliss (1935), and Dempster and Lerner (1950); however, the statistical methodology for the model was developed by Gianola (1982), Foulley et al. (1983), Gianola and Foulley (1983), Harville and Mee (1984), Foulley et al. (1987), and Foulley and Manfredi (1991). The application of the threshold methodology from a Bayesian point of view was introduced by Gianola and Foulley (1983). The work of Harville and Mee (1984) provided a procedure for the analysis of ordered categorical traits from the classical BLUP point of view.

Development of the threshold methodology in the Bayesian framework: The work of Gianola and Foulley (1983) of fitting a threshold model in a Bayesian setting was extended by Foulley et al. (1983) to incorporate a continuous trait "birth weight" with equal design matrices (*i.e.*, no missing values). Foulley and Gianola (1984) extended the threshold model of Foulley et al. (1983) to fit multiple categorical traits (calving difficulty and calf viability). Furthermore,

Foulley and Gianola (1986) handled the problem of missing data for sire evaluation of multiple binary traits, but without allowing missing fixed effects. On the other hand, Foulley (1987) derived equations for models with different fixed effects (i.e., unequal design matrices for fixed effects), but those models do not support missing data (as cited in Janss and Foulley, 1993). Janss and Foulley (1993) developed a bivariate model for one continuous “birth weight” and one threshold binary trait “calving difficulty” with unequal design matrices (i.e., unbalanced layout) for both fixed effects and missing data. Hoeschele et al. (1995) extended the model of Janss and Foulley (1993) to fit one polychotomous trait (calving ease), rather than binary, and several continuous traits (birth weight, gestation length, and pelvic size), rather than one continuous trait, with missing data and unequal models (i.e., different fixed effects).

The threshold methodology in a BLUP setting: A variety of approaches have been proposed to deal with ordered categorical responses in a BLUP setting. Several publications have translated categorical responses into quantitative responses by assigning K ordered numerical values to K categories (i.e., assigning a value to each category and then using the assigned values as observations). The analysis assumes the new discrete quantitative response follows a mixed linear model (Schaeffer and Wilton, 1976; Tong et al., 1976; Tong et al., 1977; Berger and Freeman, 1978). However, assumptions of additivity of effects and homogeneity of variances are much less reasonable and more likely to be violated in that approach (Gianola, 1982; Harville and Mee, 1984). Gianola (1980a) proposed a method based on the logistic distribution. Logarithmic transformations of counts are expressed as linear combinations of fixed effects and random variables whereas Quaas and Van Vleck (1980) proposed a procedure in which the probability of assignment to a particular category was assumed to be a random variable and the BLUP of the category frequencies of future progeny was obtained (Quaas and Van Vleck, 1980)

using that transformed data. The procedure proposed by Harville and Mee (1984) represented the threshold methodology applied to ordered categorical responses in a BLUP context. Authors described the procedure as “A mixed-model version of the threshold model in which it is assumed that the observed category is determined by the value of an underlying unobservable continuous response that follows a mixed linear model”.

The procedure of Harville and Mee (1984) represents the BLUP version of the threshold methodology and the procedure of Gianola and Foulley (1983) resembles the Bayesian methodology. Both are “best-described” and fit the discrete nature of ordered categorical traits. Both procedures are equivalent, despite the fact each used different approaches to derive the equations for estimation and prediction. Furthermore, both methods involve a system of nonlinear equations which must be solved iteratively; consequently, they are computationally expensive compared to the linear models of Henderson’s BLUP (Djemali et al., 1987).

Computational limitations of the threshold model: The computational demand of the threshold model analysis is about three to five times larger than the demand of the linear model (Misztal et al., 1989). The authors stated that solutions of the threshold model need to be obtained iteratively, and in each round a linear system of equations must be solved. The number of threshold computations is proportional to the number of thresholds and records (Misztal et al., 1989). Because it requires solving a system of nonlinear equations iteratively, the threshold methodology is computationally more demanding than the linear approach (Djemali et al., 1987) and could therefore be problematic for very large data. Another limitation arises when all observations in a given class or level of a fixed effect fall in the same category. This situation is called the extreme category problem (ECP) where solutions of those fixed effects tend toward ($\pm\infty$) (i.e., solutions for those classes would not converge). Further, denominators of some

formulae approach zero which cause division by zero errors. As a result, convergence rate becomes poor and eventually the system will be slow or not converge (Misztal et al., 1989). To avoid the ECP, Harville and Mee (1984) recommended treating fixed effects as random or removing the extreme observations causing the problem. However, discarding classes with observations in extreme categories may cause distorted inferences (i.e., data would not be representative “biased”) (Misztal et al., 1989). The authors proposed two methods to handle the ECP. First, to avoid division by zero, values that cause division by zero are restricted and should not drop below a specified value. Second, solutions, that are expected to approach plus or minus infinity, should be set to a large number (in absolute sense) which has normal integral close to 1 or 0 (this technique is called intercepting). This technique does not affect the overall system of equations because observations in such fixed effects do not contribute to the coefficient matrix.

Sorensen and Gianola (2002) illustrated the application of the threshold model in the genetic evaluation of categorical traits as single trait and with a bivariate analysis jointly with continuous traits. Below we present the sampling model which described the transformation of the observed ordered categorical trait to an underlying liability scale. The notations are the same as those used by Sorensen and Gianola (2002). Liabilities (l_i) were presented by a vector (l) where $l = \{l_i\}(i = 1, 2, \dots, n)$ and the i th observation is assumed to be

$$l_i = x_i' \beta + z_i' a + e_i \quad (2.1)$$

Where β were the fixed effects, a is a vector of additive effects, random residual $e_i \sim N(0, \sigma_e^2)$, x_i' and z_i' were incidence row vectors. The conditional distribution of vector (l) was:

$$(l | \beta, a, \sigma_e^2) \sim N(X\beta + Za, I\sigma_e^2) \quad (2.2)$$

The parameterization $\sigma_e^2 = 1$ was assumed. The vector y denoted the observed categorical data, where $y = \{y_i\}(i = 1, 2, \dots, n)$ and each y_i represents an assignment into one of (c) categories

which result from $c + 1$ hypothetical thresholds (t_i) in the underlying scale. Those thresholds were as follow $t_{\min} < t_1 < t_2 < \dots < t_{c-1} < t_{\max}$. The two extreme thresholds were set to be $t_{\min} = t_0$, $t_{\max} = t_c$, so the remaining $(c-1)$ thresholds can take any value that falls between t_{\min} and t_{\max} . In order to center the distribution, one of the thresholds must be fixed, typically t_1 was assigned to be zero. As a result of this setting, the conditional probability that y_i falls in category j ($j = 1, 2, \dots, c$), given $\boldsymbol{\beta}$, \mathbf{a} , and $\mathbf{t} = (t_{\min}, t_1, \dots, t_{c-1}, t_{\max})'$ is

$$\begin{aligned} \Pr(y_i = j | \boldsymbol{\beta}, \mathbf{a}, \mathbf{t}) &= \Pr(t_{j-1} < l_i < t_j | \boldsymbol{\beta}, \mathbf{a}, \mathbf{t}) \\ &= \Phi(t_j - x'_i \boldsymbol{\beta} - z'_i \mathbf{a}) - \Phi(t_{j-1} - x'_i \boldsymbol{\beta} - z'_i \mathbf{a}) = p(y_i | \boldsymbol{\beta}, \mathbf{a}, \mathbf{t}) \end{aligned} \quad (2.3)$$

where Φ is the standard cumulative distribution function of the normal distribution which gives the area under the normal curve up to and including the j th category.

Since the data were conditionally independent, given $\boldsymbol{\beta}$, \mathbf{a} , and \mathbf{t} . Therefore the sampling model can be written as

$$\begin{aligned} p(\mathbf{y} | \boldsymbol{\beta}, \mathbf{a}, \mathbf{t}) &= \prod_{i=1}^n \sum_{j=1}^c I(y_i = j) p(y_i | \boldsymbol{\beta}, \mathbf{a}, \mathbf{t}) \\ &= \prod_{i=1}^n \sum_{j=1}^c I(y_i = j) [\Phi(t_j - x'_i \boldsymbol{\beta} - z'_i \mathbf{a}) - \Phi(t_{j-1} - x'_i \boldsymbol{\beta} - z'_i \mathbf{a})] \end{aligned} \quad (2.4)$$

where $I(y_i = j)$ is an indicator that equals 1 if the observation falls in category j and 0 if not.

Reviewed literature in this section, theoretically, revealed the superiority of the threshold model over the linear model resulting in a better fit of the ordered categorical responses. However, advantages of the threshold model over the linear model, applied to field data and via means of simulation studies, will be discussed later in this chapter.

2.4. Markov Chain Monte Carlo and Gibbs sampler

Markov Chain Monte Carlo (MCMC) is a highly used Bayesian estimation methodology. The advantage of MCMC over other methods (*e.g.*, Restricted Maximum Likelihood (REML) that require analytical or numerical integration techniques) is its capability to allow inferences to be drawn from complex posterior distributions. The concept of MCMC is in general that a Markov chain is generated via iterative Monte Carlo simulation which has the desired posterior distribution as its equilibrium (Sorensen and Gianola, 2002). The work of Metropolis et al. (1953) and Hastings (1970) was the foundation of a general MCMC named after them as “the Metropolis-Hastings algorithm”. In a later work, Geman and Geman (1984) proposed the Gibbs sampler algorithm which is considered a special case of Metropolis-Hastings. For variance components estimation (random variables) using MCMC algorithms, the Markov chains are assumed to have a continuous state spaces which means they are normally distributed.

2.4.1. The Gibbs sampler

The Gibbs sampler is a very highly used MCMC algorithm, because of its simplicity, compared to other MCMC algorithms. It was first introduced by Geman and Geman (1984) who named it after Josiah Willard Gibbs, an American mathematical physicist who introduced the Gibbs distribution which was used in the paper of Geman and Geman (1984). The notation that will be used in this section are the standard ones found in the literature following the same notation used in Sorensen and Gianola (2002).

Suppose we have a joint distribution $p(\theta_1, \theta_2, \dots, \theta_p)$, where θ_s were the parameters of interest, and the posterior distribution is $p(\theta_1, \dots, \theta_{i-1}, \theta_i, \theta_{i+1}, \dots, \theta_p | y)$ where y was the response. Let the parameter vector with the i th parameter deleted be $\theta_{-i} = (\theta_1, \dots, \theta_{i-1}, \theta_{i+1}, \dots, \theta_p)$, then the fully conditional posterior distribution of θ_i was

$$\begin{aligned}
p(\theta_i | \theta_{-i}, y) &= \frac{p(\theta_1, \dots, \theta_{i-1}, \theta_i, \theta_{i+1}, \dots, \theta_p | y)}{\int p(\theta_1, \dots, \theta_{i-1}, \theta_i, \theta_{i+1}, \dots, \theta_p | y) d\theta_i} \\
&\propto p(\theta_1, \dots, \theta_{i-1}, \theta_i, \theta_{i+1}, \dots, \theta_p | y)
\end{aligned} \tag{2.5}$$

The parameter updates could be for one parameter at a time (single-site updating) or for several parameters (a block). The latter approach allows updating several parameters simultaneously, leading to a faster convergence rate (Liu et al., 1994).

2.4.2. The Gibbs sampling algorithm

Consider a model with vector of parameters $p(\theta_1, \theta_2, \theta_3, \dots, \theta_p)$ that have a posterior density $p(\theta_1, \theta_2, \theta_3, \dots, \theta_p | y)$. Let the starting values be $(\theta_1^{(0)}, \theta_2^{(0)}, \dots, \theta_p^{(0)})$, then sampling parameters from their prospective fully conditional distributions through the iterative process of the Gibbs sampler to convergence will be:

Sampling $\theta_1^{(1)}$ form $(\theta_1 | \theta_2^{(0)}, \dots, \theta_p^{(0)}, y)$,

Sampling $\theta_2^{(1)}$ form $(\theta_2 | \theta_1^{(1)}, \theta_3^{(0)}, \dots, \theta_p^{(0)}, y)$,

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Sampling $\theta_p^{(1)}$ form $(\theta_p | \theta_1^{(1)}, \theta_2^{(1)}, \theta_3^{(1)}, \dots, \theta_{p-1}^{(1)}, y)$,

Then the new round of iterations begins with $\theta_i^{(1)}$ attained from previous iteration and so forth.

Samples are dependent on the starting values for a period of time called the burn-in period for which results are usually discarded. Burn-in period is determined by the visual examination of what is known as trace plots “or history plots” which plots the parameter value as a function of sample number. The discarded burn-in samples are the initial samples obtained during the search for the marginal posterior distribution of parameters. These samples (rounds) reveal trend and

fluctuation before the parameters posterior distribution is reached. After the burn in period, the samples are drawn from the normal posterior distribution with density

$$\frac{p(\theta_1, \theta_2, \dots, \theta_p | y)}{\int p(\theta_1, \theta_2, \dots, \theta_p | y) d\theta_1 \dots \theta_p}$$

Samples of $\theta_j^{(i)}$ are regarded as draws from its marginal posterior distribution with density of

$$\frac{p(\theta_j | y)}{\int p(\theta_j | y) d\theta_j}$$

The joint distribution is uniquely determined by the fully conditional distributions, so Gibbs sampler draws samples from the joint distribution by sampling from all fully conditional distributions. If the model has converged, the trace plot will move up and down around the mode of the distribution. A clear sign of non-convergence occurs when we observe some trending in the trace plot.

2.5. Threshold model versus linear model

Problems associated with analyzing categorical traits using linear models were addressed by Gianola (1980a, 1980b, 1982). The author pointed out that fitting a linear model to categorical responses does not account for constraining the probability across all categories to unity. Further, he illustrated that additive genetic variance on the observed scale is not constant and depends on the incidence of the trait in subpopulations examined by the model.

One of the first comparisons between a linear model and threshold model was presented in a simulation study of sire evaluation for categorical data by Meijering and Gianola (1985). The authors found that fitting a threshold model for binary traits and unbalanced data outperformed the linear model when heritability of the trait was moderate (0.2) or high (0.5) and the incidence of trait used for categorizing the underlying liability was 1% or 5%. Efficiency of

selection under both models was the comparison criterion. Efficiency was estimated as the realized genetic progress as a percentage of maximum genetic progress. Maximum genetic progress was defined as the genetic selection differential occurring if the true transmitting abilities of sires were observable. Differences between efficiencies of the two models ranged from 3.9%, when $h^2 = 0.5$ and incidence = 5%, to 12.2%, when $h^2 = 0.2$ and the binary trait incidence equaled 1%. However, they found that threshold and linear models did not differ under three scenarios: a very low heritability (0.05), incidence of binary response was 25% or greater, and a situation where the trait was tetrachotomous. That means the more categories the trait had, the more normally distributed it became.

In another simulation study by Hoeschele (1988), Quasi Best Linear Unbiased Prediction (QBLUP) and Maximum A Posteriori Estimation (MAPE) were compared using two criteria: the correlation between true and estimated breeding values and the realized genetic response resulting from truncation selection. Results revealed that magnitude of the correlation between true and estimated breeding values was dependant on heritability, the differences in subpopulation averages, and the threshold locations on the underlying scale. MAPE outperformed QBLUP by 1-3% when the incidence of response was 93%, 6%, and 1%, and the heritability was either 0.2 or 0.5; however, there was no difference when heritability was 0.05. Correlation differences between MAPE and QBLUP, for binary data, decreased from 5-12% to 0-1% when incidence of response reduced from 99% to be 77% (became more normally distributed). Moreover, higher differences between subpopulation means (fixed effects) resulted in superiority of MAPE over QBLUP. The author reported that the loss in accuracy of selection, resulted from using the categorical phenotype instead of the underlying variate, depended on both the threshold location, which reflect the incidence of the trait, and the heritability. Higher

incidence rates of greater than 0.90 combined with low heritability lead to inefficient estimation using the binary observed phenotype. On the other hand, evaluation of binary trait, on the observed scale, with low incidence (<0.90) and moderate heritability (0.20) resulted in higher accuracy. Results obtained by Hoeschele (1988) were in agreement with those reported by Meijering and Gianola (1985).

In a simulation study by Wang et al. (2005), they evaluated calving ease and birth weight for simulated beef cattle population using a bivariate linear-linear (LL) and a linear-threshold (LT) sire-maternal grandsire model. Results revealed that both models performed the same with respect to accuracy (Pearson correlation) and Spearman rank correlation between true and predicted breeding values.

Abdel-Azim and Berger (1999) in a simulation study showed that the threshold model gave more accurate estimates of genetic parameters than the linear model. Given an expected heritability of 0.2, they found that estimated heritability using a threshold model was 0.22 compared to an estimate of 0.10 using linear model. Authors stated that accuracy was increased with higher number of categories, higher heritability, more balanced data, and increasing incidence of the trait (*i.e.*, more normally distributed).

For field data, evidence supporting the threshold model superiority was inconclusive. Several studies did not find differences between the methodologies. Renand et al. (1990), in a study using Charolais data reported, no differences between threshold and linear models fitted to calving score (unassisted, easy assistance, hard pull or caesarean) and dystocia score (easy or difficult). However, when data was reduced using only 20% of the progeny per sire, the threshold model showed a better efficiency (Rank correlation between sire evaluations). Harville and Mee (1984), in a study using Holslein bulls ($n = 85$), reported that dairy bulls ranked first

and last using a threshold model were also ranked the same under linear model. However, the re-ranking of some bulls ($n = 9$), by the two models, were more than 20 places. Similarly, ranking of dairy sires by a threshold model did not differ from those by BLUP (Clutter et al., 1989). Other studies by Jensen (1986), Djemali et al. (1987), Weller et al. (1988), Hagger and Hofer (1989), Ron et al. (1990), McGuirk et al. (1999), Andersen-Ranberg et al. (2005), Marcondes et al. (2005), and Guerra et al. (2006) reported very high correlations (>0.9) between sire solutions from threshold and linear models.

Most studies used the correlations between sire solutions from both threshold and linear models as a means of evaluating approaches. This method may give high correlations even if both models are inefficient. A study of dairy cattle by Hagger and Hofer (1989) was the first to apply data splitting methodology (i.e. cross validation, for models evaluating dystocia). The study by Olesen et al. (1994) on Norwegian sheep was one of the first studies to use the cross validation technique, which yielded correlations between estimated and predicted sire solutions (breeding values). The cross validation procedure was done by sampling 50% of data (sample 1) and the remaining data was used as sample 2. This technique examines the predictive ability of the model (i.e., the model's ability to repeatedly produce the same breeding values). The higher the correlation the better the model ranks sires. Even though results of this study showed that threshold and linear models were not different in their predictive ability and goodness of fit, it provided new means for models comparison. Another study of sheep by Matos et al. (1997) also did not find differences between threshold and linear models with respect to their goodness of fit and their predictive ability.

Most studies evaluated threshold model versus linear model only for categorical traits; however, studies by Varona et al. (1999b) and Ramirez-Valverde et al. (2001) incorporated

correlated continuous traits in the genetic evaluation of the discrete traits. Therefore, the model comparison expands to become threshold-linear versus linear-linear instead of merely threshold versus linear. In a study using Gelbvieh data, Varona et al. (1999b) compared univariate threshold animal models with linear animal models for calving ease and then also compared bivariate models which were threshold-linear animal model versus the linear-linear animal model for calving ease and birth weight. Authors then used two criteria to compare the predictive ability of models fitted to Gelbvieh data ($n = 26,006$) and also simulated data ($n = 6,200$). Those criteria were mean square error (MSE), for both field data and simulated data, and the correlation between simulated and predicted breeding values for simulated data. Results from the simulation study showed that the average MSE for linear, threshold, linear-linear, and threshold-linear were 0.39, 0.37, 0.32, and 0.29, respectively, with correlations between simulated and predicted breeding values of 0.45, 0.47, 0.51, and 0.52, respectively. For Gelbvieh data, the MSE was 0.40, 0.39, 0.33, and 0.31, respectively. These results revealed that the threshold methodology outperformed the linear method.

Ramirez-Valverde et al. (2001) in their study of calving difficulty and birth weight in Gelbvieh cattle, compared the predictive ability of threshold, linear, linear-linear, threshold-linear animal and sire-maternal grandsire models. The comparison criterion was the average correlation between five replicates of two complementary data subsets. The sampling procedure was done by randomly sampling 50% of data (sample 1) with the remaining records used as sample (2). Five replicates, each consisting of two complementary samples, were created by re-sampling from data. Correlation estimates between estimated and predicted calving difficulty breeding values for sires with progeny ($n \leq 50$) were 0.64, 0.68, 0.87, and 0.90 for linear, threshold, linear-linear, and threshold-linear animal models, respectively. For sires with progeny

($50 < n \leq 100$), correlations were 0.71, 0.70, 0.87, and 0.90, respectively. For sires with progeny ($n > 100$), correlations were 0.80, 0.81, 0.88, and 0.91, respectively. Correlation estimates from sire-maternal grandsire model, for sires with ($n \leq 50$), were 0.45, 0.42, 0.56, and 0.56 for their respective models. For sires with progeny ($50 < n \leq 100$), correlations were 0.70, 0.68, 0.86, and 0.86, respectively. For sires with progeny ($n > 100$), correlations were 0.80, 0.80, 0.87, and 0.88, respectively. Authors concluded that the threshold model outperformed the linear model when animal model was fitted. However, they did not find differences when the sire-maternal grandsire model was fitted. Authors suggested that the threshold-linear animal model is the model of choice for genetic prediction of both direct and maternal effects.

In a study of litter size and days to lambing in Ripollesa ewes, Casellas et al. (2007) used mean square error (MSE) and correlation between observed and predicted records as criteria for models comparison in terms of goodness of fit and predictive ability. Litter size was fitted as a binary trait. The threshold model appeared superior to linear model, furthermore, bivariate models showed a better accuracy, as expected, compared to univariate models. Authors concluded that the genetic evaluation of litter size using threshold-linear model was justified.

Data on clinical mastitis (CM), somatic cell score (SCS), 305-day milk (MY), and protein (PY) and fat yield (FY) in first-lactation Finnish Ayrshire cows were analyzed fitting the following models: threshold (TM), linear (LM), linear-linear (LLM), and threshold-linear (TLM) (Negussie et al., 2008). Clinical mastitis was either fitted as a discrete or a continuous trait. The correlation between estimated breeding values for CM from replicates of randomly split data sets was used to assess the predictive ability of models. Results from TLM, LLM, TM and LM indicated better performance of TLM compared to LLM. Superiority of bivariate models (i.e. higher correlations between estimated breeding values for CM from replicates of randomly split

data sets, was noted compared to univariate models for clinical mastitis). However, univariate models did not yield differences for correlations between EBV for CM, except for sires with low accuracy.

Gevrekci et al. (2011) evaluated dystocia in Holsteins using different models. They compared threshold sire model (TS), threshold sire-maternal grandsire (TS-MGS), and linear sire-maternal grandsire (L). Authors concluded that the threshold model was superior to the linear model in the genetic evaluation of dystocia with the sire-MGS being the best approach.

De Maturana et al. (2009) evaluated the predictive ability of threshold and linear models for calving difficulty (CD) and gestation length (GL) in US Holsteins. Four criteria were used to evaluate the predictive ability of the alternative models. Comparison criteria were mean squared error of the difference between observed and predicted CD scores, a Kullback-Leibler divergence measure between the observed and predicted distributions of CD scores, Pearson's correlation between observed and predicted CD scores, and ability to correctly classify bulls as above or below average for incidence of CD. Authors concluded that all the models had similar predictive ability, even though, the bivariate models showed slight improvement over univariate models with respect to model predictive ability. They justified the similar predictive ability of models by the number of categories (3 and 4 categories) used for calving difficulty which provides more information compared to a binary scoring approach.

In a study of Czech Charolais cattle, Vostrý et al. (2014) compared predictive ability of threshold and linear models for the genetic evaluation of birth weight and calving ease. Fitted models were linear-linear animal model (L-LM) with calving ease score, linear-linear animal model (SC-LM) in which calving ease scores transformed into Snell scores, bivariate threshold-linear animal model (T-LM) with calving ease scores. Correlations between split data sets for

calving ease fitting L-LM, SC-LM, and T-LM were 0.41, 0.63, and 0.75, respectively. The authors found that the threshold model was superior; however, because of its advantages in terms of computation time and practical considerations, they recommended the use of linear model with calving ease scores transformed to Snell scores.

In summary, results from literature related to the superiority of the threshold model vary. Several studies from reviewed literature suggest threshold model superiority, either from theoretical perspective or from using simulated and field data. However, there were many studies that showed no difference between threshold and linear models. The superiority of the threshold model depends basically on the data structure and the categorical trait of interest. A categorical trait is expected to be better evaluated using the threshold model methodology if it has the following characteristics: high incidence, small number of categories (i.e., a binary trait), large proportion of sires with few progeny, and large differences in subpopulations averages (i.e., herds) (Meijering and Gianola, 1985; Hoeschele, 1988; Abdel-Azim and Berger, 1999). Consequently, when data and trait of interest are lacking those characteristics, the threshold model is expected to produce genetic predictions close or similar to those produced by the linear model with no apparent superiority to the threshold model.

2.6. Phenotypic averages of calving ease, postweaning gain, and weights at birth, weaning, and yearling

The ultimate goal of the genetic improvement of farm animals is producing animals with the best genetic makeup for performance traits. However, information on animals is provided as phenotypic records which are used to predict animals genetic merit (i.e., EBV); therefore, the selection of animals that have the best genetic makeup relies on phenotypic information and will correspondingly results in producing animals with better phenotypes. Phenotype is a function

(i.e., heritability) of genotype and vice versa. Therefore, any change in the average breeding value of a trait, e.g. due to selection, is associated with a change in its phenotypic average. The phenotypic average is the simplest and easiest statistic to interpret when describing the phenotype of performance traits. Thus, estimates of phenotypic averages of studied traits were reviewed in this section.

Roughsedge et al. (2005) reported that the average observed calving ease score of Simmental was 1.18 on a 5 point scale. Other studies, on different beef cattle breeds, have reported average calving ease score ranged from 1.04 to 1.64 (Pribyl et al., 2003; Eriksson et al., 2004; Phocas and Laloe, 2004; Roughsedge et al., 2005; Gutierrez et al., 2007; Matilainen et al., 2009). However, the average observed score could be a misleading statistic because of the different scoring systems used in some studies. Changing the observed calving ease scores by merging different categories to be one category will result in a change in the average, even for the same data set. The percentage of unassisted calvings, regardless the number of other categories, may be a better way to represent calving ease scores. Percentage of unassisted calving of Simmental cattle reported by Bennett and Gregory (2001) and Brandt et al. (2010) and were 43% and 87.6%, respectively.

Koots et al. (1994b) reported a weighted average birth weight of 35.1 kg for beef cattle. Several studies reported average birth weight for different beef cattle breeds ranging from 34.58 to 47.3 kg (Lee, 2002; Pribyl et al., 2003; Eriksson et al., 2004; Phocas and Laloe, 2004; Iwaisaki et al., 2005b; Gutierrez et al., 2007; Matilainen et al., 2009; Mujibi and Crews, 2009; Brandt et al., 2010). For Simmental cattle, Brandt et al. (2010) reported an average birth weight of 44.3 kg. In the current study, the average birth weight of the Simmental beef cattle was 40.1 kg.

In his review paper, Koots et al. (1994b) estimated a weighted average weaning weight of 203 kg for beef cattle. For Simmental beef cattle, the average weaning weight estimated by Roughsedge et al. (2005) and Brandt et al. (2010) was 297 and 271 kg, respectively. A relatively low weaning weight average of 229.2 kg for Hereford cattle was reported by Meyer et al. (1994), but was estimated over a decade earlier than the other reports. Iwaisaki et al. (2005a) published average weaning weights of 271.9 and 246 kg for Gelbvieh and Limousin cattle, respectively.

Postweaning daily gain weighted average of 0.978 kg/d was estimated by Koots et al. (1994b). For Simmental cattle, postweaning average daily gain ranged from 0.43 to 1.46 kg/d (Benyshek and Little, 1982; Wright, 1987; Stålhammar and Philipsson, 1997; Eriksson et al., 2003). The 160-d postweaning gain for Simmental averaged from 71.8 to 200 kg (Benyshek and Little, 1982; Wright, 1987). Stålhammar and Philipsson (1997), in their study of Simmental cattle, reported total postweaning gain of 191 and 131 kg for males and females, respectively, and their respective average daily gain were 1.16 and 0.79 kg.

Average yearling weight of 12 breeds of beef cattle was 361.9 kg (Pribyl et al., 2003). Roughsedge et al. (2005) in their study of Simmental cattle, they reported an average of 534 kg at age of 400 days. Koots et al. (1994a) in their review of published genetic parameter estimates for beef production traits, estimated an average yearling weight of 345 kg. For Gelbvieh and Angus cattle, the average yearling weights were 432.3 and 410 kg, respectively, (Iwaisaki et al., 2005b; Costa et al., 2011).

2.7. Genetic and residual parameters

2.7.1. Heritability

Heritability is defined as “a measure of the strength of the relationship between performance (phenotypic values) and breeding values for a trait in a population” (Bourdon,

1999). Genetic improvement of beef cattle breeds is mainly driven by selection of best animals to be parents of the next generations. Response to selection depends on several factors that are summarized in what is known as the key equation. The rate of genetic change, based on the key equation, is affected by accuracy of selection, selection intensity, and genetic variability (Bourdon, 1999). The higher the genetic variation the higher the heritability, which leads to increased response to selection. In this section, heritability estimates from literature are summarized and reviewed.

2.7.1.1. Direct heritability

Heritability estimates of calving difficulty, on the underlying scale, for Charolais and Hereford first parity heifers were 0.22 and 0.23, respectively, (Eriksson et al., 2004). However, heritability estimates, on the observed scale, from the same study were 0.12 and 0.16, respectively. Estimated calving ease heritabilities, on the observed scale, for Canadian Simmental heifers were 0.06 and 0.07 (Kemp et al., 1988; Jamrozik and Miller, 2014), respectively. Several studies involving Simmental cattle, Burfening et al. (1978b), Burfening et al. (1981), Trus and Wilton (1988), and Dong et al. (1991) reported calving ease heritability estimates of 0.25, 0.2, 0.21, and 0.18, respectively. Matilainen et al. (2009) reported an estimate of 0.26, on the underlying scale, for heifer calving ease heritability in Limousin beef cattle. Roughsedge et al. (2005) estimated heritabilities of calving difficulty, on the observed scale, for Angus, Limousin, Simmental, and South Devon cattle to be 0.26, 0.12, 0.35, and 0.19, respectively. Estimated weighted average heritability of heifer calving ease was 0.13 (Koots et al., 1994a). Heritability for beef heifer (different breeds) calving difficulty was 0.18 (Splan et al., 1998). Carnier et al. (2000) and Albera et al. (2004) in their study of Piemontese cattle, estimated calving ease heritability for heifers of 0.19 and 0.16, respectively. Reviewed literature of calving

ease heritability revealed that, on the observed scale, calving ease has a low heritability; however, when heritability estimated on the underlying scale, it notably increased which was a reflection of the added information when calving ease was fitted as a threshold trait.

Because of abundance of birth weight data collected by the beef industry, genetic parameters for birth weight were some of the most estimated in literature. Heritability of birth weight is considered relatively high compared to other growth traits such as weaning and yearling weight. Birth weight heritability estimates for Charolais and Hereford first calving heifers were 0.50 and 0.51, respectively, (Eriksson et al., 2004). Koots et al. (1994a) reported, in their review of published genetic parameter estimates for beef production traits, a weighted average of 0.31 which is relatively low compared to most estimates in other citations. Similarly, Phocas and Laloe (2004) reported relatively low estimates for Charolais and Limousin cattle birth weight heritabilities (0.33 and 0.38, respectively). Heritability estimates for nine different beef cattle breeds ranged from 0.26 to 0.66 with an average heritability estimate of 0.47 (Bennett and Gregory, 1996) in another study. However, in a study of Simmental beef cattle by Brandt et al. (2010), a low heritability estimate of 0.23 which could be a result of their small data ($n = 568$) was reported. Similarly, estimated birth weight heritabilities for Canadian Simmental heifers were 0.19 and 0.23 (Kemp et al., 1988; Jamrozik and Miller, 2014), respectively. Several studies of Simmental cattle, Burfening et al. (1978b), Benyshek and Little (1982), Quaas et al. (1985), Elzo et al. (1987), Trus and Wilton (1988), Garrick et al. (1989), Dong et al. (1991), Redman and Brinks (1991), Woodward et al. (1992), Swalve (1993), Rust et al. (1998), and Eriksson et al. (2002 as cited in (Eriksson et al., 2004)), reported heritability estimates of 0.4, 0.18, 0.16, 0.14, 0.34, 0.44, 0.18, 0.52, 0.28, 0.33, 0.30, and 0.37, respectively. Iwaisaki et al. (2005b) in their study of Gelbvieh cattle reported birth weight heritability estimate of 0.52. Estimated heritability

for Charolais was 0.46 (Mujibi and Crews, 2009). Estimated birth weight heritability for Angus was 0.4 (Carter et al., 1990). In summary, estimates of birth weight heritability from literature were moderate to high which, along with the trait linearity, justify the incorporation of birth weight in the analysis of calving ease.

The weighted average of weaning weight heritability was estimated as 0.27 by Koots et al. (1994a) in their review of published genetic parameter estimates for beef production traits. Several studies of Simmental cattle, Burfening et al. (1978b), Benyshek and Little (1982), Elzo et al. (1987), Wright et al. (1987), Garrick et al. (1989), Mrode and Thompson (1990), Boldman et al. (1991), Redman and Brinks (1991), Woodward et al. (1992), Swalve (1993), Bennett and Gregory (1996), Lee and Pollak (1997), Lee et al. (1997), Rust et al. (1998), Dodenhoff et al. (1999), and Roughsedge et al. (2005), reported weaning weight heritability estimates of 0.28, 0.34, 0.14, 0.12, 0.36, 0.19, 0.17, 0.48, 0.34, 0.34, 0.24, 0.28, 0.21, 0.26, 0.22 and 0.26, respectively, with an overall average of 0.26. Estimates of weaning weight heritability for different beef cattle breeds ranged from 0.13 to 0.49 (Meyer et al., 1994; Bennett and Gregory, 1996; Phocas and Laloe, 2004; Iwaisaki et al., 2005a,b; Roughsedge et al., 2005). For Angus cattle, heritability estimate was 0.22 (Carter et al., 1990). Bertrand and Benyshek (1987) reported a heritability estimate of 0.28 for Brangus cattle. It is worth noting that most heritability estimates for beef cattle breeds fall within the range 0.2-0.4; however, weaning weight heritability estimate for Charolais have been relatively low (0.16 estimated by Bennett and Gregory (1996) and 0.13 Phocas and Laloe (2004). Reviewed literature revealed that weaning weight has a low to a moderate (0.2-0.4) heritability. For Simmental cattle, estimates ranged from 0.12 to 0.48 with an average of 0.26. Beef cattle breeds appear to have different weaning weight heritability estimates and weaning weight has a low heritability compared to birth weight.

Heritability estimates for post weaning gain of different beef cattle breeds averaged 0.31 in the review of Koots et al. (1994a). For Simmental cattle, several articles by Benyshek and Little (1982), Quaas et al. (1985), Wright (1987), Garrick et al. (1989), Woodward et al. (1992), and Eriksson et al. (2003) reported heritability estimates of 0.13, 0.2, 0.23, 0.26, 0.27 and 0.29, respectively, with an overall average of 0.23. Bennett and Gregory (1996), in a study of nine different beef cattle breeds, reported heritability estimates for post weaning gain (168 days) ranging from 0.39 to 0.51 with an average of 0.46 and heritability of postweaning gain for Simmental cattle was 0.5 (n = 1494). Stålhammar and Philipsson (1997) reported that heritability for Simmental males (0.19) was lower than that for females (0.22). Studies of Angus cattle reported postweaning gain heritability estimates of 0.26, 0.28 and 0.26 (Carter et al., 1990; Arthur et al., 2001; MacNeil et al., 2011), respectively. Researchers Koch et al. (1973), Mavrogenis et al. (1978), and Fan et al. (1995) in their studies of Hereford, reported postweaning gain heritabilities of 0.29, 0.23, and 0.16, respectively. Studies of Charolais cattle by Meyer (1993) and Eriksson et al. (2003) reported heritability estimates of 0.22 and 0.37, respectively. Generally, postweaning gain has a low heritability where the average postweaning gain of Simmental cattle was 0.23. Heritability of postweaning gain was the lowest compared to other growth-related traits. Clear differences were reported amongst beef cattle breeds. Further, different estimates were obtained for males and females.

Yearling weight heritability estimates for Simmental cattle were 0.33, 0.27, 0.27, 0.27, 0.37, 0.41, and 0.34 (Benyshek and Little, 1982; Elzo et al., 1987; Wright, 1987; Mrode and Thompson, 1990; Swalve, 1993; Bennett and Gregory, 1996; Roughsedge et al., 2005), respectively, with an overall average of 0.32. A weighted average estimated by Koots et al. (1994a) was 0.33 for different beef cattle breeds. However, yearling weight heritability for

Gelbvieh cattle estimated by Iwaisaki et al. (2005b) was higher (0.59). Yearling weight (400 days) heritability estimates for Angus, Limousin, Simmental, and South Devon were 0.36, 0.35, 0.34, and 0.29, respectively, (Roughsedge et al., 2005). Bennett and Gregory (1996), in a study of Angus, Braunvieh, Charolais, Gelbvieh, Hereford, Limousin, Pinzgauer, Red Poll, and Simmental, reported yearling weight (averaging 368 days) heritability estimates ranged from 0.27 to 0.62 with an average of 0.44. Yearling weight heritability estimates for Angus cattle, by Carter et al. (1990), Fan et al. (1995), and Arthur et al. (2001) were 0.36, 0.45, and 0.28, respectively. For Hereford, estimates by Mavrogenis et al. (1978) and Fan et al. (1995) were 0.49 and 0.43, respectively. Meyer (1993) in a study on Charolais reported an estimate of 0.32 for yearling weight heritability. Reviewed literature on yearling weight heritability revealed that yearling weight, as anticipated, has a higher heritability compared to its component traits (*i.e.*, weaning weight and postweaning gain). The Simmental beef cattle, on average, have a yearling weight heritability of 0.32. Heritability estimates for yearling weight were more diverse than other growth traits. This might be a result of the assumption of homogeneous residual variance which does not hold when yearling weight measured at different ages. When the homogeneity of residual variance is assumed, the residual variance estimates will be biased which results in biased heritability estimates (Olori et al., 1999).

2.7.1.2. Maternal heritability

A considerable amount of literature has been published on maternal heritability of calving ease. Estimates in Simmental cattle ranged from 0.05 to 0.28 (Burfening et al., 1981; Trus and Wilton, 1988; Dong et al., 1991; Bennett and Gregory, 2001; Jamrozik and Miller, 2014). Furthermore, Wright (1987) reported estimates of 0.10 and 0.05 for American and Canadian Simmental, respectively. Maternal heritability estimates for other beef cattle breeds range from

0.03 to 0.18 (Albera et al., 1999; Varona et al., 1999a; Carnier et al., 2000; Eriksson et al., 2003; Phocas and Laloe, 2003; Albera et al., 2004; Eriksson et al., 2004; Phocas and Laloe, 2004; Roughsedge et al., 2005). Reported maternal heritability estimates using threshold model approaches were 0.19, 0.09, 0.28, 0.048, and 0.14 (Dong et al., 1991; Varona et al., 1999a; Bennett and Gregory, 2001; Wiggans et al., 2003; Gevrekci et al., 2011), respectively. Generally, calving maternal heritabilities estimated using the threshold models were higher than those estimated using the linear model. The higher maternal heritability estimates under the threshold model were a result of fitting calving ease as a threshold trait (i.e., an underlying continuous liability).

Several studies of Simmental cattle by Quaas et al. (1985), Wright (1987), Trus and Wilton (1988), Garrick et al. (1989), Swalve (1993), Marques et al. (2000), and Jamrozik and Miller (2014) reported birth weight maternal heritability estimates of 0.057, 0.05, 0.2, 0.12, 0.07, 0.05, and 0.04, respectively. For other beef cattle breeds, estimates ranged from 0.03 to 0.18 (Bertrand and Benyshek, 1987; Waldron et al., 1993; Meyer, 1995; Snelling et al., 1996; Dodenhoff et al., 1998; Varona et al., 1999a; Eriksson et al., 2004; Meyer et al., 2004; Phocas and Laloe, 2004; Iwaisaki et al., 2005b; Brandt et al., 2010). Literature review revealed that the maternal effects on birth weight represent a small and important proportion of the total variance of the trait. Therefore, birth weight maternal effects should be accounted for in the genetic evaluation of birth weight.

Weaning weight maternal heritability for Simmental cattle ranged from 0.05 to 0.2 (Graser and Hammond, 1985; Quaas et al., 1985; Wright, 1987; Wright et al., 1987; Garrick et al., 1989; Boldman et al., 1991; Swalve, 1993; Lee and Pollak, 1997; Lee et al., 1997; Marques et al., 2000). Several studies of other beef cattle breeds reported estimates that ranged from 0.03

to 0.2 (Bertrand and Benyshek, 1987; Cantet et al., 1993; Meyer, 1993; Waldron et al., 1993; Meyer, 1995; Arthur et al., 2001; Meyer et al., 2004; MacNeil, 2005). These studies revealed that the weaning weight maternal effects should be fitted in the analysis of the trait. Here, the maternal component of weaning weight total variation is mainly due to the milk production of the dam; therefore, the weaning weight maternal breeding value is also known as the milk breeding value.

2.7.2. Direct genetic correlations

Historically, the high genetic correlation between calving ease and birth weight was, and is still used, as a tool to improve the ease of calving. Some studies reported correlations between birth weight and calving difficulty, but not calving ease, and as this relationship is discussed, those correlations are reported with negative signs in this section. Koots et al. (1994b) estimated a weighted average of -0.74 for the genetic correlation between calving ease and birth weight. Estimated genetic correlations between calving ease, on observed scale, and birth weight for Simmental cattle were -0.33, -0.76, and -0.85 (Burfening et al., 1978b; Burfening et al., 1981; Jamrozik and Miller, 2014), respectively. Genetic correlation between birth weight and calving ease estimated by Eriksson et al. (2004) as -0.62 and -0.72 for Charolais and Hereford cattle, respectively. Phocas and Laloe (2004) obtained estimates of -0.66, -0.4, -0.72, and -0.78 for Charolais, Limousin, Blonde d'Aquitaine, and Maine-Anjou, respectively. Lee (2002) in a study of Gelbvieh heifers estimated a higher correlation (-0.82). Calving ease for Charolais cattle has a correlation of -0.66 with birth weight, however, the estimate was lower (-0.4) for Limousin. Results obtained from reviewed literature on genetic correlation between calving ease and birth weight can be summarized as follow: The strong genetic correlation between the two traits justifies the use of birth weight as an indicator trait for calving ease and the inclusion of birth

weight as a linear trait in the genetic evaluation of calving ease which increases the accuracy of the genetic evaluation.

Calving ease has genetic correlation of -0.08 and -0.2 with weaning weight of Simmental beef cattle (Burfening et al., 1978b; Roughsedge et al., 2005), respectively. Similarly, in review of published genetic parameter estimates for beef production traits by Koots et al. (1994b) they estimated a weighted average of -0.21. Bennett and Gregory (2001) obtained a higher estimate (-0.41) between calving ease and 200-d WT. Estimates of genetic correlations between calving ease and weaning weight for different beef cattle breeds ranged from -0.12 to -0.44 (Phocas and Laloe, 2004; Roughsedge et al., 2005). The genetic correlation between calving ease and weaning weight was considerably lower than the correlation between birth and weaning weights. This supports the hypothesis: selection for high calving ease instead of selection for low birth weight could reduce the loss in the correlated response of weaning weight.

Koots et al. (1994b) in their review of genetic correlation estimates, reported a weighted average of -0.54 for genetic correlation between calving ease and post weaning gain while Bennett and Gregory (2001), in their study on several beef cattle breeds, obtained a weaker correlation of -0.36 between calving ease and postweaning gain. Gregory et al. (1995) estimated genetic correlation of -0.11 between calving ease and postweaning gain of male progeny of 2 year old heifers from different purebred and composite beef cattle.

The genetic correlation between calving ease and yearling weight as estimated by Roughsedge et al. (2005) for Angus, Limousin, Simmental, and South Devon cattle were -0.2, -0.33, -0.19, and -0.46, respectively. A weighted average (-0.29) reported by Koots et al. (1994b) falls within the range of estimates reported by Roughsedge et al. (2005). Calving ease has

correlation of -0.27 with 368-d WT for population of different beef cattle breeds (Gregory et al., 1995). From reviewed literature, calving ease, as oppose to birth weight, showed a weaker genetic correlation with yearling weight which supports the hypothesis that selection for calving ease would result in smaller changes in yearling weight.

Estimates from literature for different beef cattle breeds show a high genetic correlation between birth weight and weaning weight which ranged from 0.26 to 0.56 (Koch et al., 1973; Meyer, 1993; Bennett and Gregory, 1996, 2001; Phocas and Laloe, 2004; Iwaisaki et al., 2005b; Gutierrez et al., 2007). Koots et al. (1994b) estimated a weighted average of 0.5 for the genetic correlation between birth and weaning weights. In the literature, several reports involving Simmental cattle had estimated the genetic correlation between birth and weaning weights. These correlation estimates were 0.33, 0.29, 0.43, 0.43, 0.49, 0.33, and 0.58 (Burfening et al., 1978b; Benyshek and Little, 1982; Quaas et al., 1985; Elzo et al., 1987; Garrick et al., 1989; Woodward et al., 1992; Swalve, 1993), respectively. Further, Wright (1987), in his study of Simmental cattle, reported estimates of 0.43 and 0.64 for American and Canadian Simmental, respectively. The high genetic correlation between birth and weaning weight would cause great loss in weaning weight when downward selection on birth weight is applied. Conversely, the lower genetic correlation between calving ease and weaning weight is a promising means to improve calving ease by the direct selection for calving ease without major loss in yearling weight.

Birth weight has a weighted average genetic correlation of 0.32 with post weaning gain (Koots et al., 1994b) which is in line with Bennett and Gregory (1996) who reported the same estimate as an average for nine purebred beef cattle breeds. Carter et al. (1990) published an estimate of 0.16 for Angus beef cattle. For Simmental cattle, Benyshek and Little (1982), Quaas

et al. (1985), and Garrick et al. (1989) found that birth weight and postweaning gain have genetic correlations of 0.57, 0.36, and 0.32, respectively. Wright (1987) in another study of Simmental cattle reported estimates of 0.39 and 0.45 for the American and Canadian cattle, respectively. Results from reviewed literature showed that the genetic correlation between birth weight and postweaning gain for Simmental beef cattle ranged from 0.32 to 0.57 with an overall average of 0.41. Therefore, a moderate postweaning gain correlated response would be expected when selection for low birth weight is practiced.

Estimates of genetic correlation between birth and yearling weights for Simmental cattle by Benyshek and Little (1982), Elzo et al. (1987), and Swalve (1993), were 0.61, 0.47, and 0.4, respectively; while another study of Simmental cattle by Wright (1987) reported correlations of 0.47 and 0.6 for the American and Canadian cattle, respectively. Estimates of genetic correlation between birth weight and both weaning weight and postweaning gain in a study of Simmental by Garrick et al. (1989) resulted in a genetic correlation between birth weight and yearling weight was 0.47. Iwaisaki et al. (2005b) in a study of Gelbvieh, reported a genetic correlation of 0.5 between birth and yearling weights. Bennett and Gregory (1996) reported a genetic correlation of 0.47. However, Koots et al. (1994b) estimated a higher correlation (0.55) between birth weight and yearling weight. Correlations obtained by Carter et al. (1990) and Meyer (1993) were 0.59 (Angus) and 0.66 (Charolais), respectively. In summary, birth weight showed a moderate genetic correlation with yearling weight. This strong correlation was a result of the strong correlations between birth weight and the component traits of yearling weight (i.e., weaning weight and postweaning gain). Therefore, selection for low/high birth weight would cause a high correlated response in the subsequent growth traits.

A positive genetic correlation of 0.56 was estimated between weaning weight and post weaning gain (Bennett and Gregory, 1996) with Koots et al. (1994b) reporting similar genetic correlation of 0.44 with post weaning gain. Quaas et al. (1985), Wright (1987), and Garrick et al. (1989), in their studies of American Simmental cattle, found that weaning weight and postweaning gain have genetic correlation of 0.53, 0.52, and 0.51, respectively. Further, Wright (1987) obtained a relatively higher estimate of 0.66 for Canadian Simmental. However, Carter et al. (1990) obtained a lower genetic correlation (0.22) for Angus beef cattle. In summary, weaning weight and postweaning gain are moderately correlated traits. Thus, any genetic changes (positive or negative) in either one will be reflected on the other trait which eventually results in similar changes in yearling weight.

Genetic evaluation for yearling weight is usually done by evaluating its component traits, weaning weight and post weaning gain. Yearling weight genetic (co)variances are calculated as summation of those of weaning weight and post weaning gain. This approach is a result of the high genetic correlation between yearling weight and its component traits which make it hard to reach convergence when estimating variance components. Estimates from literature for genetic correlation between weaning and yearling weight ranged from 0.70 to 0.92 (Carter et al., 1990; Koots et al., 1994b; Gregory et al., 1995; Bennett and Gregory, 1996; Arthur et al., 2001; Roughsedge et al., 2005; Costa et al., 2011). For Simmental beef cattle, three different studies in Canada, Australia, and United Kingdom by Wright (1987), Swalve (1993), and Roughsedge et al. (2005), respectively, found that weaning weight and yearling weight have genetic correlations of 0.91, 0.83, and 0.87, respectively. Articles describing American Simmental by Benyshek and Little (1982), Elzo et al. (1987), and Wright (1987) reported estimates of 0.87, 0.83, and 0.84, respectively. Calculated genetic correlation between weaning weight and yearling weight for

Simmental cattle, given genetic (co)variances for weaning weight and postweaning gain, was 0.89 (Garrick et al., 1989). Reviewed literature showed a very high genetic correlation between weaning and yearling weights. Therefore, the upward/downward selection for either trait is expected to substantially change the other trait in same direction.

Wright (1987) in his study of Simmental cattle reported a correlation of 0.91 between postweaning gain and yearling weight. From (co)variance components between postweaning gain and weaning weight, Garrick et al. (1989) estimated a genetic correlation of 0.84 between postweaning gain and yearling weight. Correlation estimates reported by Koch et al. (1973), Mavrogenis et al. (1978), and Bennett and Gregory (1996) ranged from 0.71 to 0.92. The weighted average genetic correlation estimate of 0.81 by Koots et al. (1994b) in their review of published genetic parameters estimates for beef production traits was very similar. Generally, postweaning gain, as a component trait for yearling weight, has a strong positive genetic correlation with yearling weight. The positive and strong genetic correlations amongst growth traits are a useful means to improve weight gain in the beef industry; however, it should be used with caution because of the dystocia problems associated with heavier animals.

2.7.3. Direct-Maternal genetic correlations

Estimated direct-maternal correlations for calving ease, on the observed scale, were -0.023 and -0.008 for American and Canadian Simmental cattle (Wright, 1987). On the underlying scale, the correlation estimate for Simmental was -0.16 (Dong et al., 1991). However, Jamrozik and Miller (2014), fitting a univariate model, reported a lower correlation (-0.05) for Canadian Simmental. For other beef cattle breeds, estimates from literature using the threshold model methodology (*i.e.*, on the underlying scale) ranged from -0.087 to -0.28 (Varona et al., 1999a; Wiggans et al., 2003; Gevrekci et al., 2011).

Literature shows that direct-maternal genetic correlation estimates for Simmental cattle ranged from -0.04 to -0.43 (Quaas et al., 1985; Trus and Wilton, 1988; Garrick et al., 1989; Swalve, 1993; Marques et al., 2000; Eriksson et al., 2002). Several studies of Limousin, Brangus, Hereford, Gelbvieh, and composite beef cattle breeds reported direct-maternal correlations for birth weight that ranged from -0.05 to -0.35 (Bertrand and Benyshek, 1987; Snelling et al., 1996; Varona et al., 1999a; MacNeil, 2005). Snelling et al. (1996), in their study on Hereford, they obtained a correlation of -0.14.

Results from several studies of Simmental cattle found that direct-maternal genetic correlation for weaning weight has ranged between -0.01 and -0.39 (Quaas et al., 1985; Garrick et al., 1989; Boldman et al., 1991; Swalve, 1993; Lee and Pollak, 1997; Lee et al., 1997; Dodenhoff et al., 1999; Marques et al., 2000). Further, Wright (1987) obtained estimates of -0.023 and -0.008 for American and Canadian Simmental cattle, respectively. Estimates for Limousin, Brangus, and Angus cattle ranged from -0.17 to -0.31 (Bertrand and Benyshek, 1987; Cantet et al., 1993; Arthur et al., 2001). However, MacNeil (2005) reported a lower estimate of -0.06 for composite beef cattle (50% Red Angus, 25% Charolais, and 25% Tarentaise).

2.7.4. Residual correlations

Residual correlation estimate, on the observed scale, between calving ease and birth weight for Charolais and Hereford cattle in a study by Eriksson et al. (2004) were -0.25 and -0.27, respectively. Similarly, Koots et al. (1994b), in their review paper, estimated a weighted average residual correlation of -0.28. For American Simmental cattle, residual correlation between calving ease and birth weight was -0.29 (Burfening et al., 1978a). However, Varona et al. (1999a) and Bennett and Gregory (2001) estimated higher residual correlations (-0.5 and -

0.41, respectively). Given the high genetic correlation between calving ease and birth weight, the research to date has tended to focus on evaluation of calving ease with birth weight and marginalized other growth traits such as weaning weight, postweaning gain, and yearling weight. Consequently, there has been relatively few studies that published genetic and residual correlations between calving ease and postnatal growth traits.

Residual correlations between calving ease and weaning weight for American Simmental cattle was -0.02 (Burfening et al., 1978a). Similarly, Bennett and Gregory (2001), in a study of composite and parental populations of beef cattle, found that calving ease had a residual correlation of -0.02 with weaning weight (200-d WT). Those estimates show a very weak environmental association between calving ease and weaning weight which tends to be close to zero.

Estimates of residual correlation between calving ease and postweaning gain are expected to be very small and close to those for calving ease and weaning weight. Bennett and Gregory (2001) found that calving ease has a residual correlation of -0.03 with 168-d gain across several composite and parental beef cattle populations.

In the literature, several articles reported that the residual correlation between birth weight and weaning weight for Simmental beef cattle ranged from 0.18 to 0.51 (Burfening et al., 1978a; Benyshek and Little, 1982; Wright, 1987; Garrick et al., 1989; Woodward et al., 1992). Bennett and Gregory (1996) reported residual correlation of 0.29 between birth and weaning weights for nine beef cattle breeds. For Charolais cattle, Meyer (1993) reported residual correlation estimate of 0.19 which was near the lower limit of estimates described in literature.

The literature of American Simmental beef cattle reported that birth weight and postweaning gain have residual correlation estimates of 0.07 and 0.10 (Benyshek and Little, 1982; Garrick et al., 1989), respectively. Further, a study by Wright (1987) reported estimates of 0.10 and 0.03 for American and Canadian Simmental, respectively. Birth weight in purebred beef cattle has residual correlation of 0.12 with postweaning gain (Bennett and Gregory, 1996).

In a study of American Simmental cattle by Benyshek and Little (1982), the residual correlation between birth weight and yearling weight was 0.42. Similarly, estimates from Wright (1987) for American and Canadian Simmental were 0.31 and 0.39, respectively. However, calculated residual correlation between birth weight and yearling weight for American Simmental cattle, given (co)variance components for birth weight with both weaning weight and postweaning gain, was relatively lower (0.21; Garrick et al., 1989). The estimated residual correlation between birth weight and yearling weight of Gelbvieh and Charolais cattle were 0.14 and 0.12, respectively, (Meyer, 1993; Iwaisaki et al., 2005b). However, Bennett and Gregory (1996), in their study for nine beef cattle breeds, reported that birth weight has a higher residual correlation (0.28) with yearling weight.

Studies of American Simmental by Benyshek and Little (1982), Wright (1987), and Garrick et al. (1989) reported residual correlation estimates (-0.18, -0.10, and -0.17, respectively) between weaning weight and postweaning gain. For Canadian Simmental cattle, the correlation estimate was -0.15 (Wright, 1987) and for Angus, MacNeil et al. (2011) reported a correlation of -0.18 between weaning weight and postweaning BW gain. However, Bennett and Gregory (1996) estimated a positive residual correlation (0.08) between weaning weight and postweaning gain for nine beef cattle breeds.

Residual correlation between weaning weight and yearling weight for American Simmental cattle were 0.64 and 0.67 (Benyshek and Little, 1982; Wright, 1987), respectively. Additionally, the later study reported an estimate of 0.72 for Canadian Simmental cattle. Furthermore, calculated correlation from another study on American Simmental by Garrick et al. (1989) was 0.57. Residual correlation estimates from articles on different beef cattle breeds ranged from 0.55 to 0.75 (Meyer, 1993; Bennett and Gregory, 1996; Iwaisaki et al., 2005b; Costa et al., 2011).

In Studies of American Simmental cattle by Benyshek and Little (1982) and Wright (1987), residual correlation estimates between postweaning gain and yearling weight were 0.57 and 0.68, respectively. The latter study also reported a correlation estimate of 0.58 for Canadian Simmental cattle. Using (co)variance estimates from Garrick et al. (1989) between weaning weight and postweaning gain, a calculated residual correlation between postweaning gain and yearling weight for American Simmental was 0.7. The estimate of residual correlation between postweaning gain and yearling weight reported by Bennett and Gregory (1996) was 0.72.

Review of literature on direct genetic, maternal genetic, and residual parameters for calving ease, birth weight, weaning weight, postweaning gain, and yearling weight can be summarized as follow: 1) Birth weight has the highest heritability among all traits. 2) Heritability estimates for other growth traits were moderate. 3) For calving ease, estimates of heritability on the underlying scale were higher than those on the observed scale which means capturing more variation on liability scale. 4) There is a high negative genetic correlation between calving ease and birth weight. 5) The continuous distribution of birth weight justifies the importance of incorporating birth weight in the genetic evaluation of calving ease. 6) Moderate positive genetic correlations between birth weight and subsequent growth traits unveil the antagonistic

relationship between calving ease and postnatal growth traits when selection for birth weight is applied. 7) The importance of incorporating maternal effects in the genetic evaluations of calving ease, birth weight, and weaning weight.

2.8. Selection index

Candidate animals for selection should be evaluated on overall genetic merit. Hence, genetic evaluation should involve multiple traits on animals selected to produce progeny in the next generation. Selection index is a widely used and a powerful tool to achieve optimal genetic gain that ultimately maximizes profitability through selection of animals with best genetic makeup to be parents. Selection index is a linear combination of phenotypic information and weighting factors that is used for genetic prediction of net merit. Selection index was first introduced by Hazel and Lush (1942) and Hazel (1943). For the selection index of Hazel (Eq. 2.6), the index value is calculated for one trait based on (n) different phenotypic sources of information (X_i), (e.g., animal's own record, ancestors, progeny, half-sibs, and full-sibs), and weighting coefficients (b_i) for those sources of information. However, instead of selection index for one trait, multiple traits can be combined into one selection index which represents the aggregate genotype.

$$I = b_1X_1 + b_2X_2 + \dots + b_nX_n \quad (2.6)$$

However, after Henderson (1973, 1975) introduced BLUP methodology, which has become the standard procedure of the genetic evaluation, the classical economic selection index of Hazel was replaced with the economic selection index that uses BLUP solutions. The economic selection index is defined as combination of weighting factors or “economic weights” and genetic information on more than one trait (Bourdon, 1999). The optimal properties of BLUP solutions allow adjustment for fixed effects and account for inbreeding making it the

preferred method of genetic prediction. Yet, use of these predictions in the economic selection index gives a measure of the aggregate genetic merit of an animal for multiple traits in the selection objective and/or their indicator traits. The same formula as that used for the classic selection index is also used for the economic selection index. Nonetheless, phenotypic sources of information are replaced with the genetic predictions from BLUP (*e.g.*, estimated breeding values “EBV” or expected progeny differences “EPD”) weighting coefficients are replaced with relative economic values in the “new” selection index.

Considerations in selection index implementation: Level of production, goals of production, and production resources such as labor, management, etc., may vary by enterprise. Consequently, the relative economic value will vary amongst production systems. Therefore, industry-wide selection indexes are not suggested but rather indexes should be specific for each enterprise or production unit (MacNeil et al., 1997). Given the nonlinear relationships between profit and performance or any other changes in economic circumstances, selection indices should be subject to periodic recalculation (Hazel et al., 1994). In the case of a generation interval of 5 years, relative economic values should be calculated using average prices over the past 10 to 15 years (MacNeil et al., 1997).

A widely used example of selection index is that described by Dickerson et al. (1974) who published a selection index for efficient beef production (Eq. 2.7). This index was expected to increase economic efficiency of beef production by 6% higher than the single trait selection for yearling weight. This increase was due to decreasing mature cow size and thus feed requirements, reducing calf birth weight and thus calving difficulty and associated mortality relative to selection on yearling weight. However, calf weights at weaning and yearling would be expected to decrease by only approximately 10%. Dickerson’s selection index was adopted by

MacNeil (2003) to improve efficiency of beef production. Results showed that, despite the genetic antagonism that commute selection response for lower birth weight and increased postnatal weights, the index yielded positive correlated responses for direct genetic effects on weight traits at all ages.

$$I = YWT - 3.2 BWT \quad (2.7)$$

In summary, selection index is a powerful method that helps animal breeders make selection decisions to improve profitability of their enterprises through maximizing economic response of multiple trait selection programs. This is a result of its unique capabilities to combine genetic information on multiple traits weighted by their economic weights into one value of the aggregate merit of the animal. The importance of each trait in the selection index is determined by its contribution to profitability either by its effect on cost of production (i.e., negative weight) or its effect on profit (i.e., positive weight).

2.9. Genetic trends

Genetic change in a trait, over time (per year or per generation), is primarily driven by the genetic variability, accuracy of selection, generation interval, and selection intensity and, in multiple trait selection programs, by genetic correlations with other traits of interest. Here, genetic trend of a trait can be expressed in the trait's actual units or in standard deviation units. In selection programs, selection goals vary and tools to achieve those goals vary accordingly. Therefore, selection could be applied via means of single trait selection or multiple traits selection in which selection indexes are preferred, but independent culling levels used as well. In this section, beef cattle selection trials and their different selection approaches are reviewed.

Simmental beef cattle: Elzo et al. (1985) estimated direct and maternal genetic trends for Simmental cattle during the 1972-1983 time period. Difference in means between 1983 and 1972 of direct birth weight, weaning weight, yearling weight were -0.6, 0.6, and 11.1 kg, respectively. For maternal genetic effects, mean differences for maternal birth and weaning weights were -0.2 and 1.1 kg, respectively. Despite the positive genetic correlations between birth weight and postnatal growth traits, a negative genetic trend for birth weight was achieved. Elzo et al. (1987) also estimated genetic trends of Simmental sires (1973-1984) for first-parity calving ease, birth weight, weaning weight, and yearling weight. Direct genetic trends for calving ease, weaning and yearling weights were positive while that for birth weight was negative. Maternal genetic trends for first-parity calving ease and birth weight were positive and that for weaning weight did not show significant change. Wright (1987) estimated genetic trends (1973-1985) for growth traits and calving ease of Canadian Simmental cattle. The author concluded that breeders were mainly selecting for weaning and yearling weight which resulted in heavier calves at birth. In their study on different beef cattle breeds, Sullivan et al. (1999) reported estimates of genetic trends for Simmental. They found that regression lines for birth and weaning weights were broken (i.e., two different regression lines). As a result, genetic trend estimates were reported for two periods: 1985-1990 and 1990-1995. Corresponding genetic trends for birth weight were 0.125 and 0.048 kg/yr and those for weaning gain were 0.87 and 0.72 kg/yr. However, the genetic trend (1985-1995) for yearling gain was 1.46 kg/yr.

Single trait selection experiments (selection for high growth traits): In a study involving Hereford cattle, two lines were selected for high weaning weight (WWL) and high yearling weight (YWL) (Frahm et al., 1985a,b). Estimated genetic gains in standard deviation units per generation of the two lines, respectively, were 0.29, 0.26 for birth weight; 0.22, 0.19 for weaning

weight; -0.02, 0.04 for postweaning average daily gain; 0.08, 0.14 for yearling weight. Hough et al. (1985), in a selection study of Hereford cattle, estimated the difference in response to selection for high yearling weight versus control. Difference in selection response between the two lines for calving difficulty, birth weight, 205-d weight, postweaning average daily gain and yearling weight were 0.05 score/yr, 0.27 kg/yr, 5 kg/yr, 0.009 kg/d per yr, and 6.2 kg/yr, respectively. Irgang et al. (1985a, 1985b, 1985c) developed three Hereford lines selected for increased weaning weight (WWL), postweaning gain (PGL), and a control line (CTL). Results revealed that selection for either increased weaning weight or postweaning gain improved yearling weight; however, selection for increased postweaning gain produced higher correlated responses in all other growth traits. Birth weight increased in PGL, but it did not show correlated response in WWL. Aaron et al. (1986a, 1986b) established four lines of Angus cattle which were selected for increased weaning weight (WWL), increased yearling weight (YWL), increased combination of animal and its progeny weaning weight (PTL), (i.e., five bulls were selected on the basis of individual 205-d weaning weight and then two bulls were subsequently selected on the basis of progeny weaning weight), and a control line (CL). Estimated genetic responses in standard deviation units per generation in WWL, YWL and PTL, respectively, were: birth weight, 0.24, .47, .42; weaning weight, 0.28, 0.30, 0.51; postweaning gain, 0.12, 0.36, 0.16; yearling weight, 0.26, 0.44, 0.41. Results revealed that selection for yearling weight produced heavier animals at all ages; consequently, incidence of calving difficulty is expected to be high. Mrode et al. (1990a, 1990b) established two selected lines and a control line of Hereford beef cattle. Animals were selected for lean growth rate (LGR) from birth to 400 days of age and lean food conversion ratio (LFCR) from 200 to 400 days of age. Corresponding correlated responses

for birth weight were 0.127 and 0.105 kg/yr. Corresponding correlated responses for first-parity calving difficulty score were -0.018 and 0.018.

Single trait selection experiments (selection for high calving ease): Bennett (2008) used selection (1993-1999) to create two lines: select and control lines within 4 purebred (Charolais, Gelbvieh, Hereford, and Angus) and 3 composite cattle (MARC I, II, and III) populations. Selection was for lower 2-yr-old heifer calving difficulty score EBV in the select lines and animals in the control lines were selected for average birth weight EBV. The difference in average EBV between select and control lines for calving difficulty and birth weight across populations were -1.06 and -3.5 kg, respectively. However, both lines did not show differences in maternal calving difficulty, maternal birth weight, weaning weight and postweaning gain. Results revealed that selection for lower calving difficulty reduced birth weight and the incidence of calving difficulty and did not affect growth at later ages.

Selection index experiments: Three Hereford lines resulted from selection for weaning weight (WWL), yearling weight (YWL), and an index of yearling weight and muscling score (IXL) (Buchanan et al., 1982a,b). Response to selection in standard deviation units per generation for birth weight were 0.26, 0.27, 0.29; for weaning weight were 0.24, 0.24, 0.21; for postweaning gain were 0.21, 0.4, 0.33; and for yearling weight were 0.29, 0.39, 0.34, for their respective selection lines. Dickerson's selection index was adopted by Doornbos et al. (1994) who estimated genetic trends for birth, weaning, and yearling weights of Hereford beef cattle. Rates of genetic change for weights at birth, weaning, and yearling were 0.011, 1.17, and 1.97 kg/yr, respectively. Results showed that weaning and yearling weight can be improved with little change in birth weight. Koch et al. (1994) practiced selection in three lines of Hereford cattle. They selected for increased weaning weight (WWL), yearling weight (YWL), and an index of

yearling weight and muscle score (IXL). For WWL, YWL, and IXL, reported annual genetic responses were: birth weight, 0.22, 0.24, 0.27 kg; weaning weight, 0.98, 0.63, 1.26 kg; and yearling weight, 2.43, 2.64, 3.44 kg, respectively. Respective responses to selection in standard deviation units were: birth weight, 0.22, 0.23, 0.27; weaning weight, 0.20, 0.12, 0.22; yearling weight, 0.31, 0.32, 0.40. In all three lines, the traits showed positive trends and responses from IXL which were the highest. In a simulation study, Gould (1996) simulated four selected lines. Two of those were selected for increased yearling weight (GT) and Dickerson's selection index (ET). Corresponding genetic trends were, for first-parity direct calving ease, 0.001 and 0.011 SD/yr; for birth weight, 0.08 and -0.005 kg/yr; for direct weaning weight, 2.14 and 2.13 kg/yr; for maternal weaning weight, 0.009 and -0.01 kg/yr; for yearling weight, 4.77 and 4.65 kg/yr. For both selected lines, trends for direct weaning and yearling weights were significantly different from zero. However, in the ET line, calving ease was significantly improved and birth weight did not show a trend. Conversely, selection for increased yearling weight increased birth weight and did not affect calving ease. MacNeil et al. (1998) created two selected lines via independent culling levels for below-average birth weight and high yearling weight (YB) and a single-trait mass selection for high yearling weight (YW) in the inbred population of Line 1 Hereford cattle. Corresponding estimated genetic trends for birth weight were -0.014 and 0.105 kg/yr. For yearling weight, corresponding genetic trends were 0.91 and 1.5 kg/yr. However, maternal genetic trends were similar for both selection lines. First-parity calving difficulty was less frequent in YB line. However, in order to improve calving ease, authors suggested that direct selection for the trait should be applied.

MacNeil et al. (2000) used the same lines in MacNeil et al. (1998) to characterize genetic changes in age-weight relationships of females resulting from these selection lines. They

reported genetic gain of females per generation of 8 and 10.1 kg for BY and YW lines, respectively. Corresponding intercepts of growth curves (i.e., birth weight) were -0.00134 and -0.00116 kg. MacNeil (2003) implemented Dickerson's selection index to improve efficiency of beef production for a stabilized composite population (CGC): $\frac{1}{2}$ Red Angus, $\frac{1}{4}$ Charolais, and $\frac{1}{4}$ Tarentaise. A control line without selection was also established. For the selected line, estimates of direct genetic changes for the index, birth weight, 200-d weight, 365-d weight, and cow weight were 6.0, 0.45, 3.42, and 7.74 kg/generation, respectively. Enns and Nicoll (2008) evaluated genetic trends of New Zealand Angus which selected (1976-1993) using an economically based, multi-trait breeding objective. Traits were slaughter weight and dressing percentage of harvest progeny and cull cows, and the number of calves weaned in the lifetime of each cow. Correlated responses for genetic changes for weaning weight direct and maternal breeding value were 0.43 and 0.03 kg/yr, respectively. Corresponding genetic trends for postweaning gain and yearling weight were 0.29 and 0.72 kg/yr, respectively.

Generally, selection for increased postnatal growth traits resulted in heavier births which are expected to raise the incidence of calving difficulty. However, selection for low birth weight and high postnatal growth traits reduced birth weight, but not necessarily calving difficulty. Selection for increased postnatal growth traits and calving ease should be considered as means of effectively reducing calving difficulty and increases growth at later ages.

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CHAPTER III.

PERFORMANCE LOSSES DUE TO SELECTION FOR LOW BIRTH WEIGHT VERSUS HIGH CALVING EASE: A SIMULATION STUDY IN BEEF CATTLE

3.1. Introduction

The economic importance of calving difficulty is well documented (Wiltbank et al., 1961; Laster et al., 1973; Meijering, 1984; Dematawewa and Berger, 1997). Costs associated with extreme dystocia (i.e., animals with score of 3, 4, and 5) in primiparous Holsteins cows were estimated to be \$96.48, \$159.82, and \$379.61, respectively, (Dematawewa and Berger, 1997). These costs were estimated from losses in milk yield, fat yield, protein yield, days open, number of services, and calf deaths. However, the total cost associated with dystocia (i. e., sum of costs associated with dystocia scores weighted by the probability of occurrence) was \$28.53 for an average heifer and about \$10.00 for an average older cow. Amongst genetic and environmental factors that affect the incidence of calving difficulty, birth weight is considered most important (Bellows, 1993). Incidence of dystocia increases by 2.3-13% when birth weight increases by 1 kg (Laster et al., 1973; Johanson and Berger, 2003). Therefore, historically genetic improvement of calving ease relied heavily on selection of animals with low birth weight. Such a strategy could potentially reduce beef cattle efficiency in two different ways. First, given the fact that the genetic correlation between calving ease and birth weight is not one, selection for low birth weight does not necessarily improve the ease of calving. Second, selection for low birth weight can reduce growth at later ages given the unfavorable genetic relationship with those traits. Several researchers reported that selection for low birth weight did not improve calving ease and

they suggested that direct selection for calving ease would be more effective (Burfening et al., 1978b; MacNeil et al., 1998). Compared to selection for lower birth weight, we hypothesize that direct selection for high calving ease would result in animals with lower incidence of calving difficulty and higher growth rates at later ages. Therefore, the first objective of this study was to determine the consequences of alternative selection criteria for either low birth weight or high calving ease.

Although calving ease is recorded as an ordered categorical trait (i.e., discrete), it is a quantitative trait with a hypothetical underlying continuous “liability” scale which has the characteristic of normally distributed variables. Gianola (1980a, 1980b, 1982) reported that assumptions of linear methodologies were violated when used for the analysis of ordered categorical responses (i.e., observed scores were treated as a linear variable). Gianola and Foulley (1983) suggested a nonlinear method, called the threshold methodology, to analyze ordered categorical traits which are also known as threshold traits. For such traits, polygenic inheritance and large number of loci must be evident to justify the assumption of the underlying normal distribution, which is essential for the evaluation of such traits using the threshold methodology (Foulley et al., 1990). Results from reports of superiority of the threshold model over the linear model with respect to their goodness of fit and their predictive ability have varied. Several researchers have supported the hypothesis that the threshold model is a better fit to categorical traits (Varona et al., 1999b; Ramirez-Valverde et al., 2001; Casellas et al., 2007; Gevrekci et al., 2011). However, other studies found that the two methodologies performed similarly (Renand et al., 1990; Olesen et al., 1994; Wang et al., 2005). Therefore, the second objective of the present study was to compare the threshold model with the linear model in terms of their predictive ability of calving ease EPD using the cross validation technique.

3.2. Materials and Methods

Studied traits were calving ease (CE), birth weight (BWT), weaning weight (WWT), postweaning gain (PWG), and yearling weight (YWT). Two selection scenarios were simulated to compare rates of genetic change resulting from selection for high calving ease (HCE) versus selection for low birth weight (LBW). Weighted means for phenotypic averages and genetic and residual (co)variances of studied traits were required to create data for the two selection scenarios. Furthermore, genetic and residual parameters of studied traits were estimated, using a multivariate threshold-linear animal model with Gibbs sampling algorithm, to predict EPD for those traits. For both selection scenarios, genetic trends of studied traits EPD by birth year were estimated. Threshold animal model and linear animal models were compared in terms of their predictive ability. Models were compared in terms of linearity “threshold vs. linear” with calving ease fitted either as a binary or polychotomous trait. The criteria used to compare the predictive ability of models were Spearman’s rank correlation and Pearson’s correlation between observed and predicted EPD from two complementary subsets in which 50% of the data was used.

3.2.1. Estimation of weighted means of (co)variances and phenotypic averages from literature

One of the aims of the current study is to generate data that mimic real field situations, as such weighted averages of (co)variance components from literature were estimated. Weighted means of trait averages required to create data sets for the two selection scenarios were estimated as shown in Eq. (3.1).

$$\bar{x}_w = \frac{\sum_{i=1}^k n_i \bar{x}_i}{\sum_{i=1}^k n_i} \quad (3.1)$$

where \bar{x}_w was the weighted mean, n_i was the number of records in the i th study, and k was the number of studies.

(Co)variance component estimation is a very crucial step in genetic evaluation procedures. Genetic predictions acquired from BLUP procedures (e.g., breeding values “EBV” or expected progeny differences “EPD”) require (co)variance components to be known. The latter are the dispersion parameters that describe the random blocks (i.e., genetic and residual effects) of Henderson’s mixed models equations. In particular, genetic (co)variances describe the genetic variation within (i.e., direct or maternal variance) and between traits (i.e., genetic correlations amongst traits in multi-trait genetic evaluations). Furthermore, residual (co)variances describe environmental variation within and between traits. Hence, we need to estimate both genetic and residual (co)variances, which are the elements of two respective matrices known as \mathbf{G} and \mathbf{R} . In simulation studies, (co)variance components depend on the objective of the simulation. First, if the objective of the simulation study was for example to test the effect of a theoretical incremental change in a heritability of a trait on correlated response of another trait, genetic (co)variances would take arbitrarily assumed values (i.e., incremental values). Second, if the objective of the simulation requires data that mimics field data, (co)variance components used to create such data should be either estimates of a specific field data or weighted averages from literature. Since the aim of the current study required mimicking field data, weighted averages of (co)variance components from literature were estimated.

Estimates from literature included direct genetic and phenotypic variances, heritabilities, direct genetic and residual correlations for calving ease, birth weight, weaning weight, and postweaning gain. These values were compiled and weighted averages and their respective standard errors (Table 3.1) were estimated. Weighted means were estimated for direct heritability, direct genetic variance, and genetic and residual correlations. However, weighted means for phenotypic and residual variances were calculated given the weighted mean estimates

of direct heritabilities and direct genetic variances. Residual covariances were directly calculated from their respective residual correlations and residual variances.

Published heritability estimates were averaged (Eq. 3.2; Koots et al. 1994a) using the inverse of the sampling variance for each estimate (Eq. 3.3; Koots et al. 1994a) as a weighting factor. Standard errors for heritability weighted means (SE_w) were estimated by taking the square root of the summation of weighting factors (Eq. 3.4; Koots et al. 1994a).

$$h_w^2 = \frac{\sum_{i=1}^n h_i^2 / (SE_{h_i^2})^2}{\sum_{i=1}^n 1 / (SE_{h_i^2})^2} \quad (3.2)$$

where h_w^2 is the weighted mean for heritability, h_i^2 is the heritability estimate from the i th cited source, and $SE_{h_i^2}$ is the corresponding estimated standard error.

$$\text{weight of } h_i^2 = \frac{1}{(SE_{h_i^2})^2} \quad (3.3)$$

$$SE_w = \sqrt{\sum_{i=1}^n 1 / (SE_{h_i^2})^2} \quad (3.4)$$

To remove the dependency of the variance on the estimate, genetic and residual correlations and direct genetic variances were transformed to an approximate normal scale using Fisher's Z transformation (Steel and Torrie, 1960) as shown in Eq. (3.5). Next, weighted means of the Z transformed correlations were calculated using Eq. (3.2). Then, resulted weighted means were back transformed using Eq. (3.6).

$$Z = 0.5 * \log \left[\frac{1+r}{1-r} \right] \quad (3.5)$$

where Z was the transformed correlation and r was untransformed correlation from literature.

$$r_w = \frac{e^{2z} - 1}{e^{2z} + 1} \quad (3.6)$$

where r_w was the weighted mean correlation (phenotypic or genetic) and z was the weighted mean for the Z transformed correlations.

Table 3.1: Number of literature estimates (n) and estimated weighted mean (Es.) with standard error (S.E. X100) in parenthesis for direct genetic variance (bold faced on diagonal), genetic correlation (above diagonal), residual correlation (below diagonal), and heritability (h^2) for calving ease (CE), birth weight (BWT), weaning weight (WWT), and postweaning gain (PWG) with source cited.

Trait	CE			BWT			WWT			PWG		
	Source ^a	n	Es. (S.E.)	Source ^a	n	Es. (S.E.)	Source ^a	n	Es. (S.E.)	Source ^a	n	Es. (S.E.)
CE	-	-	0.24^b	7,9,13,14,18	10	0.73 (1)	9,13,18,19	9	0.22 (0.5)	2, 8	2	0.21 (6)
BWT	7	1	0.25 (3)	1,9,11,17	4	9.67 (39)	1,9,11,13,18	6	0.5 (0.5)	1,13	2	0.32
WWT	2,4	2	0.02	1	1	0.29 (0.8)	1,5,9,10,11,16,18,19,	16	221 (262)	1,13	2	0.47 (0.4)
PWG	2	1	0.03	1	1	0.12 (0.8)	1	1	0.08 (0.8)	1	1	216.9
h^2	6,7	3	0.19 (0.9)	3,7,9,11,12,15,17,18	16	0.32 (0.2)	1,9,10,11,16,18,19	28	0.29 (1)	1	10	0.45 (0.4)

^a1 = Bennett and Gregory (1996), 2 = Bennett and Gregory (2001), 3 = Brandt et al. (2010), 4 = Burfening et al. (1978a), 5 = Costa et al. (2011), 6 = Dong et al. (1991), 7 = Eriksson et al. (2004), 8 = Gregory et al. (1995), 9 = Gutierrez et al. (2007), 10 = Iwaisaki et al. (2005a), 11 = Iwaisaki et al. (2005b), 12 = Koots et al. (1994a), 13 = Koots et al. (1994b), 14 = Lee (2002), 15 = Matilainen et al. (2009), 16 = Meyer et al. (1994), 17 = Mujibi and Crews (2009), 18 = Phocas and Laloe (2004), 19 = Roughsedge et al. (2005)

^bDirect genetic variance of calving ease was calculated given the weighted average of heritability (0.19) and residual variance of one.

3.2.2. Simulated data

Two data sets were simulated using weighted means of genetic and residual (co)variances (Table 3.1) and phenotypic averages for calving ease (CE), birth weight (BWT), weaning weight (WWT), and postweaning gain (PWG). Schematic representation of the data simulation process is presented in Fig. 3.1. The base population consisted of 1,200 sires randomly mated to 36,000 dams (30 dams/sire) to produce 36,000 F₁ progeny. Animals were then partitioned into 120 herds of 300 cows/herd. Two populations were selected for three generations under two selection scenarios: 1) selection for high calving ease (HCE) 2) selection for low birth weight (LBW). For

each selection scenario, the selection criteria was the true breeding values (TBV) for either calving ease on the underlying scale or birth weight where top 5% ($TBV \leq \text{male average TBV} - 1.65SD$) males across the generations were selected and randomly mated to the top 80% ($TBV \leq \text{female average TBV} + 0.85 SD$) females (i.e., 2 year old) from previous generation (Fig. 3.2).

In order to create observations, year and season of birth effects were assumed to be constant; however, sex and herd effects were used to create observations. Based on R code written by Larry Schaeffer (<http://www.aps.uoguelph.ca/~lrs/Summer2012Full/MTiter.R>), observations for studied traits were created, using R program (R Core Team, 2014), as a linear function of trait average, sex, herd, TBV, and residual error (Eq. 3.7). For details about simulated data see appendix B.

$$y_{ijkl} = \mu_j + s_k + h_l + tbv_{ij} + e_{ijkl} \quad (3.7)$$

where y_{ijkl} was the observation for the j th trait on the i th animal, μ_j was the average of the j th trait, s_k was the sex effect, h_l was the herd effect, tbv_{ij} was the true breeding value, and e_{ijkl} was residual. Resulted observations for calving ease on the continuous underlying scale were transformed to an observed categorical scale of four categories using fixed thresholds 0, 1, and 1.4 SD.

Elements of G and R matrices represent the weighted means of genetic and residual (co)variances from literature and were used to create observations for CE, BWT, WWT, and PWG, respectively. Summary statistics and data structure of simulated data sets resulted from selection for high calving ease and selection for low birth weight are presented in Table 3.2.

$$G = \begin{bmatrix} 0.24 & 1.11 & 1.60 & 1.51 \\ 1.11 & 9.67 & 23.11 & 14.65 \\ 1.60 & 23.11 & 221 & 103 \\ 1.51 & 14.65 & 103 & 217 \end{bmatrix}, \quad R = \begin{bmatrix} 1 & 1.13 & 0.46 & 0.48 \\ 1.13 & 20.5 & 30.37 & 8.78 \\ 0.46 & 30.37 & 534 & 29.87 \\ 0.48 & 8.78 & 29.87 & 261 \end{bmatrix}$$

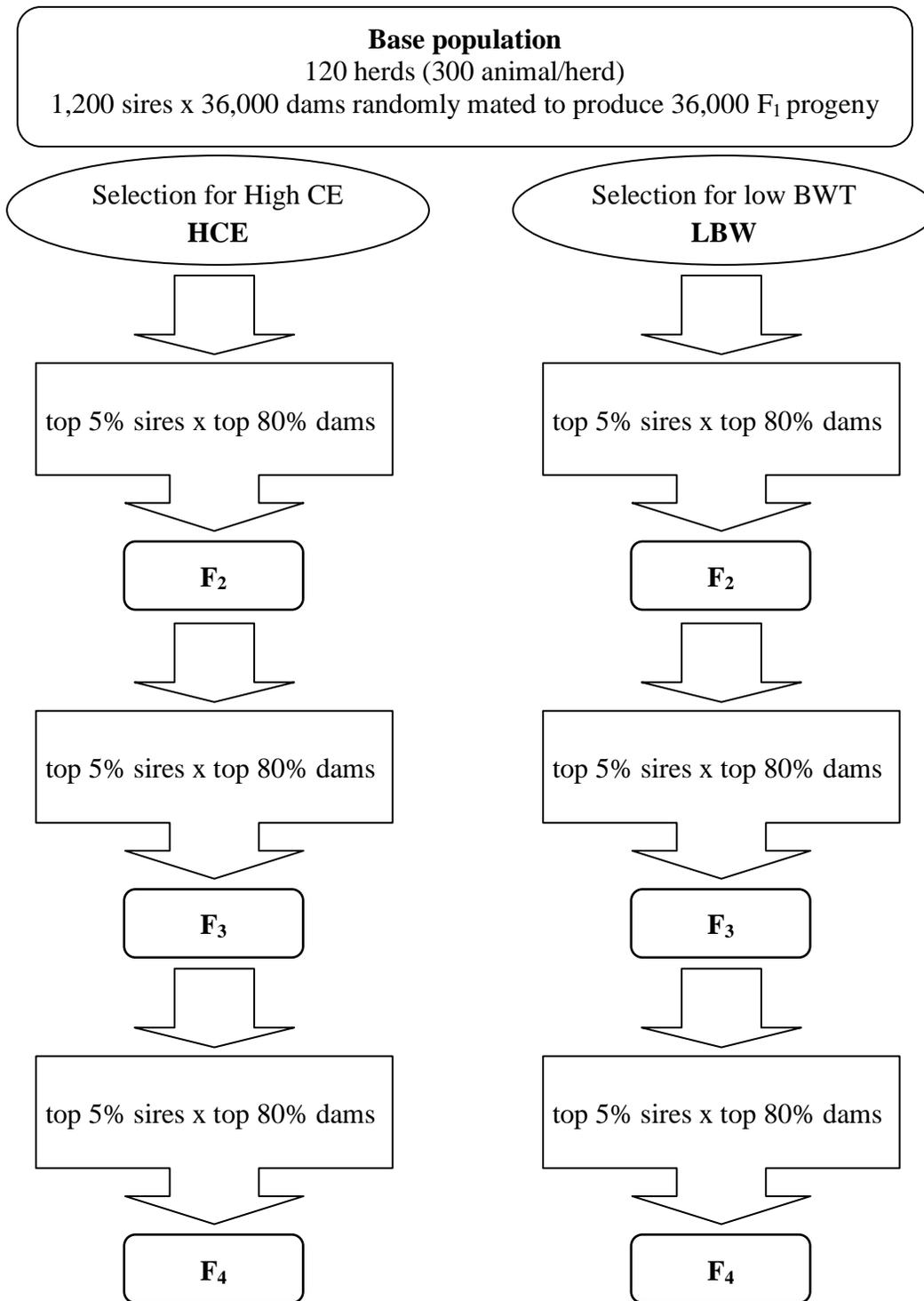


Figure 3.1: Schematic representation of two simulated data sets for two selection scenarios: High calving ease (HCE) and Low birth weight (LBW)

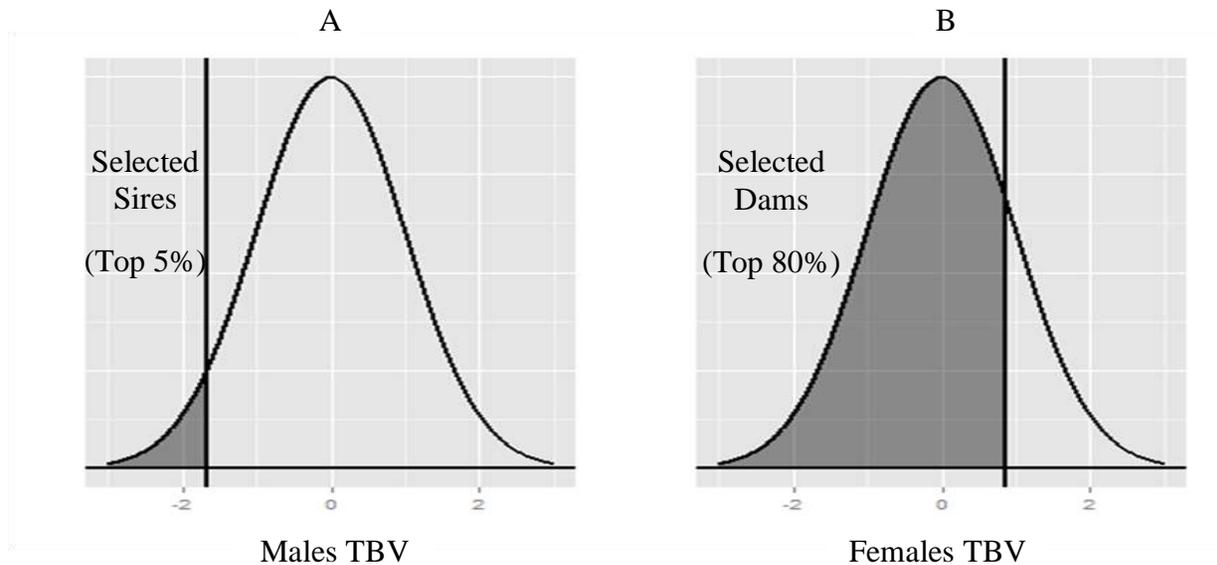


Figure 3.2: Selected sires (top 5%: $TBV \leq \text{male average TBV} - 1.65SD$) across generations (A) and selected 2 yrs old dams (top 80%: $TBV \leq \text{female average TBV} + 0.85 SD$) from previous generation (B) for high calving ease (HCE) and low birth

Table 3.2: Data structure of simulated beef cattle populations.

Item	Selection scenario ¹	
	HCE	LBW
No. of animals in pedigree	105,950	105,830
No. of animals with records	68,853	68,733
No. of dams	68,853	68,733
No. of sires	3,794	3,808
No. of dams/sire	18.14	18.04
No. of herds	120	120
Herd size	573.7	572.7
Calving Ease	Mean (SD)	1.66 (0.76)
BWT, Kg	Mean (SD)	35.8 (6.94)
WWT, Kg	Mean (SD)	242 (31)
PWG, Kg/day	Mean (SD)	0.97 (0.023)

¹HCE: Selection for high calving ease; LBW: Selection for low birth weight.

3.2.3. (Co) variance components estimation

For both selection scenarios, (co)variance components for calving ease, birth weight, weaning weight, and postweaning gain were estimated with Bayesian inference via means of Gibbs sampling algorithm with a threshold-linear animal model (Eq. 3.8). Here, calving ease was modeled as a threshold trait with four categories (Eq. 3.9) which were: 1 = unassisted calving, 2 = minor assistance, 3 = major assistance and 4 = caesarean. Frequencies (in percentage) of calving ease scores in HCE data were 1 = 52, 2 = 30.2, 3 = 9.8, and 4 = 8%; while calving ease frequencies in the LBW were 1 = 51, 2 = 30, 3 = 9, and 4 = 10%. However, because of convergence problems, categories 3 and 4 were subsequently merged. The program THRGIBBS1F90 from the BLUPF90 family of programs by Misztal et al. (2002) was employed to estimate (co)variance components and breeding values of studied traits. The THRGIBBS1F90 program uses the probit link function to transform observed incidence to liability. Yearling weight breeding values were estimated as the summation of breeding values of WWT and PWG. For both data sets, the analysis was carried out with a single chain of 120,000 iterations with a burn in period of 20,000 samples. Out of the remaining 100,000 samples, only 10,000 samples (i.e., every 10th sample) were used to obtain posterior means of (co)variance components and their respective posterior standard deviations. The multiple trait model equation used in the analysis is presented below.

$$\begin{bmatrix} L_{ce} \\ Y_{bwt} \\ Y_{wwt} \\ Y_{pww} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{wwt}\beta_{wwt} \\ X_{pww}\beta_{pww} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \\ Z_{wwt}u_{wwt} \\ Z_{pww}u_{pww} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{wwt} \\ e_{pww} \end{bmatrix}, \quad (3.8)$$

In the above equation, β were effects associated with sex of calf and herd subclasses; u were direct breeding values; e were the residuals; and X and Z were incidence matrices that link data with fixed effects and random effects, respectively. Y was vector of observations for respective

trait. An underlying distribution (L) of the calving ease was assumed, where calving ease was modeled with the following distribution:

$$f(y|L) = \prod_{i=1}^n f(y_i|L_i) = \prod_{i=1}^n [I(L_i < t_1)I(y_i = 1) + I(t_1 < L_i < t_2)I(y_i = 2) + I(t_2 < L_i < t_3)I(y_i = 3) + I(t_3 < L_i)I(y_i = 4)] \quad (3.9)$$

where t_1 , t_2 , and t_3 were thresholds that defined the four categories of CE. However, prior to (co)variance components estimation, calving ease observations (3 and 4) were merged.

The (co)variance structure of random effects was defined as: $\text{var} \begin{bmatrix} u \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 \\ 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$

where \mathbf{G} = a 4×4 additive genetic (co)variance matrix, \mathbf{A} = additive genetic relationship matrix, \mathbf{R} = a 4×4 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations, and \otimes =Kronecker product.

3.2.4. Comparison of models: Threshold versus Linear

Data of high calving ease selection scenario (HCE) was used to compare the predictive ability of the threshold animal model versus the linear animal model with calving ease fitted either as a binary or polychotomous (3 categories) trait. A total of 12 different models were fitted to calving ease and growth traits (Table 3.3). Based on the complexity of models, there were three general categories: univariate, bivariate, and multivariate animal models. Here, four different models within each category are result of calving ease being fitted either as a threshold trait (with 2 or 3 categories) or as a linear trait (with 2 or 3 categories).

(Co)variance components (Table 3.4) and solutions (breeding values) for all models were estimated via Gibbs sampling using THRGIBBS1F90 program by Misztal et al. (2002).

Table 3.3: Models fitted to calving ease and growth traits from the high calving ease data (HCE) to compare them in terms of their predictive ability of EPD.

Model ¹	CE ²	Fitted traits ³	Model representation ⁴
Univariate			
L-UAM-CE2	L+B	CE	$Y_{ce} = X_{ce}\beta_{ce} + Z_{ce}u_{ce} + e_{ce}$
L-UAM-CE3	L+P	CE	$Y_{ce} = X_{ce}\beta_{ce} + Z_{ce}u_{ce} + e_{ce}$
T-UAM-CE2	T+B	CE	$L_{ce} = X_{ce}\beta_{ce} + Z_{ce}u_{ce} + e_{ce}$
T-UAM-CE3	T+P	CE	$L_{ce} = X_{ce}\beta_{ce} + Z_{ce}u_{ce} + e_{ce}$
Bivariate			
LL-BAM-CE2	L+B	CE + BWT	$\begin{bmatrix} Y_{ce} \\ Y_{bwt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \end{bmatrix}$
LL-BAM-CE3	L+P	CE + BWT	$\begin{bmatrix} Y_{ce} \\ Y_{bwt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \end{bmatrix}$
TL-BAM-CE2	T+B	CE + BWT	$\begin{bmatrix} L_{ce} \\ Y_{bwt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \end{bmatrix}$
TL-BAM-CE3	T+P	CE + BWT	$\begin{bmatrix} L_{ce} \\ Y_{bwt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \end{bmatrix}$
Multivariate			
LL-MAM-CE2	L+B	CE + BWT + WWT + PWG	$\begin{bmatrix} Y_{ce} \\ Y_{bwt} \\ Y_{wwt} \\ Y_{pwg} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{wwt}\beta_{wwt} \\ X_{pwg}\beta_{pwg} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \\ Z_{wwt}u_{wwt} \\ Z_{pwg}u_{pwg} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{wwt} \\ e_{pwg} \end{bmatrix}$
LL-MAM-CE3	L+P	CE + BWT + WWT + PWG	$\begin{bmatrix} Y_{ce} \\ Y_{bwt} \\ Y_{wwt} \\ Y_{pwg} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{wwt}\beta_{wwt} \\ X_{pwg}\beta_{pwg} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \\ Z_{wwt}u_{wwt} \\ Z_{pwg}u_{pwg} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{wwt} \\ e_{pwg} \end{bmatrix}$
TL-MAM-CE2	T+B	CE + BWT + WWT + PWG	$\begin{bmatrix} L_{ce} \\ Y_{bwt} \\ Y_{wwt} \\ Y_{pwg} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{wwt}\beta_{wwt} \\ X_{pwg}\beta_{pwg} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \\ Z_{wwt}u_{wwt} \\ Z_{pwg}u_{pwg} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{wwt} \\ e_{pwg} \end{bmatrix}$
TL-MAM-CE3	T+P	CE + BWT + WWT + PWG	$\begin{bmatrix} L_{ce} \\ Y_{bwt} \\ Y_{wwt} \\ Y_{pwg} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{wwt}\beta_{wwt} \\ X_{pwg}\beta_{pwg} \end{bmatrix} + \begin{bmatrix} Z_{ce}u_{ce} \\ Z_{bwt}u_{bwt} \\ Z_{wwt}u_{wwt} \\ Z_{pwg}u_{pwg} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{wwt} \\ e_{pwg} \end{bmatrix}$

¹L = linear; T = threshold; UAM = univariate animal model; BAM = bivariate animal model; MAM = multivariate animal model; CE2 = 2 categories; CE3 = 3 categories.

²L = linear; T = threshold; B = binary; P = polychotomous.

³CE = calving ease; BWT = birth weight; WWT = weaning weight; PWG = postweaning gain.

⁴Models terms are illustrated in Equations 3.8 and 3.9, except for Y_{ce} which was a vector of calving ease scores (2 or 3) on the observed scale.

Table 3.4 : Posterior mean and posterior standard deviation (in parentheses) for (co)variance components¹ of calving ease (CE), birth weight (BWT), weaning weight (WWT), and post weaning gain (PWG) for the high calving data (HCE) under different models.

Model ²	Effect ³	Trait	CE ⁴				BWT	WWT	PWG
			L-CE2	L-CE3	T-CE2	T-CE3			
Univar.									
	Dir.								
		CE	0.02(0.001)	0.06(0.003)	0.16(0.01)	0.18(0.01)			
	Resid.								
		CE	0.22(0.001)	0.51(0.004)	1(0.007)	1.13(0.01)			
Bivar.									
	Dir.								
		CE	0.015(0.001)	0.044(0.003)	0.10(0.009)	0.13(0.009)			
		BWT	0.38(0.013)	0.61(0.022)	1.02(0.038)	1.08(0.039)	21.55(0.31)		
	Resid.								
		CE	0.23(0.001)	0.52(0.004)	1(0.007)	1.17(0.016)			
		BWT	0.44(0.013)	0.74(0.021)	1.18(0.034)	1.30(0.037)	16.17(0.20)		
Multivar.									
	Dir.								
		CE	0.015(0.001)	0.045(0.003)	0.11(0.008)	0.13(0.01)			
		BWT	0.38(0.014)	0.62(0.022)	1.02(0.036)	1.08(0.03)	21.51(0.30)		
		WWT	0.66(0.067)	1.14(0.110)	1.76(0.180)	1.98(0.18)	48.27(1.11)	305.9(7.25)	
		PWG	0.35(0.062)	0.60(0.010)	0.93(0.170)	1.04(0.17)	22.64(0.91)	133.7(4.65)	256.8(5.43)
	Resid.								
		CE	0.23(0.001)	0.53(0.003)	1(0.007)	1.17(0.01)			
		BWT	0.44(0.013)	0.74(0.021)	1.18(0.034)	1.29(0.03)	16.20(0.20)		
		WWT	0.73(0.070)	1.15(0.108)	1.97(0.184)	2.02(0.18)	23.69(0.80)	544.2(5.90)	
		PWG	0.62(0.057)	1(0.090)	1.67(0.155)	1.75(0.15)	7.57(0.64)	37.98(3.44)	292.6(3.89)

¹variances (bold faced) and covariances (below diagonal of effect block).

²Univar. = univariate animal model; Bivar. = bivariate animal model; and Multivar. = multivariate animal model.

³Dir. = direct genetic effect; and Resid. = residual effect.

⁴L-CE2 = calving ease was fitted as a linear binary trait; L-CE3 = calving ease was fitted as a linear trait with 3 categories; T-CE2 = calving ease was fitted as a threshold binary trait; and T-CE3 = calving ease was fitted as a threshold trait with 3 categories.

Models were compared in terms of their predictive ability using cross validation procedure (i.e., data splitting technique). This procedure was performed by duplicating the HCE data (selection for high calving ease), which results in two identical data sets. In one of these data, 50% of calving ease observations were randomly set to be missing. Further, the remaining calving ease observations in this data were discarded in the other data. This splitting technique results in two complementary data sets in which one half of animals have calving ease observations and the same animals do not have calving ease observations in the other data. For each model, solutions were obtained for both complementary data sets and correlations between solutions (EBV were transformed to EPD) from were calculated to evaluate the predictive ability of models. Here, Pearson's and Spearman's (Rank correlation) correlation coefficients were calculated between predicted EPD from two complementary data sets.

3.2.5. Genetic trends

For both selection scenarios, solutions (EPD) for calving ease (% unassisted calving) and growth traits (kg) obtained from a threshold-linear multivariate model were regressed on year of birth. Since selection was applied to produce F_2 , F_3 , and F_4 generations, year of birth for F_1 generation, which is produced by random mating of founders, was considered year zero. Under the constraint of allowing only the 2 year old dams to produce the next generation, a period of 2 years was assumed to take measurements on the following generation; therefore, average EPD for all traits were calculated for every other year. Genetic trends (slope of regression line) of studied traits were estimated as rates of change in average EPD per year.

3.3. Results and Discussion

Estimates of posterior mean and posterior standard deviation of (co)variance components obtained using Bayesian inference via means of a Gibbs sampling algorithm with a threshold-

linear animal model (Eq. 3.8), for both selection scenarios; high calving ease (HCE) and low birth weight (LBW), are presented in Tables 3.5 and 3.6, respectively. These values were used to estimate direct genetic effects (i.e., EPD) from which genetic trends were calculated.

Table 3.5: Posterior means (from 10,000 Gibbs samples) and posterior standard deviations (in parentheses) for (co)variance components¹ from the threshold-linear multivariate animal model using Gibbs sampling analysis of calving ease (CE, liability²), birth weight (BWT, kg²), weaning weight (WWT, kg²), and post weaning gain (PWG, kg²/d²) for high calving ease selection scenario (HCE).

Effect	Trait	CE	BWT	WWT	PWG
Direct genetic					
	CE	0.13(0.01)			
	BWT	1.08(0.03)	21.51(0.30)		
	WWT	1.98(0.18)	48.27(1.11)	305.9(7.25)	
	PWG	1.04(0.17)	22.64(0.91)	133.7(4.65)	256.8(5.43)
Residual					
	CE	1.17(0.01)			
	BWT	1.29(0.03)	16.20(0.20)		
	WWT	2.02(0.18)	23.69(0.80)	544.2(5.90)	
	PWG	1.75(0.15)	7.57(0.64)	37.98(3.44)	292.6(3.89)

¹variances (on diagonal) and covariances (below diagonal).

Table 3.6: Posterior means (from 10,000 Gibbs samples) and posterior standard deviations (in parentheses) for co-variance components¹ from the threshold-linear multivariate animal model using Gibbs sampling analysis of calving ease (CE, liability²), birth weight (BWT, kg²), weaning weight (WWT, kg²), and post weaning gain (PWG, kg²/d²) for low birth weight selection scenario (LBW).

Effect	Trait	CE	BWT	WWT	PWG
Direct genetic					
	CE	0.21(0.01)			
	BWT	0.98(0.04)	25.54(0.31)		
	WWT	1.15(0.19)	67.75(1.12)	366.9(6.85)	
	PWG	1.02(0.18)	29.87(0.90)	159.4(4.51)	260.7(5.27)
Residual					
	CE	1.11(0.01)			
	BWT	1.33(0.03)	14.91(0.20)		
	WWT	2.37(0.18)	15.79(0.77)	526.6(5.55)	
	PWG	1.59(0.16)	5.26(0.62)	30.03(3.36)	294.5(3.84)

¹variances (on diagonal) and covariances (below diagonal).

Average EPD for calving ease and growth traits corresponding to four generations of selection are presented in Table 3.7 and depicted in Fig. 3.3. Both selection scenarios showed increases in calving ease average EPD. However, Table 3.8 shows that rate of genetic change of calving ease (% unassisted calving/yr) from HCE selection scenario (1.56 ± 0.05) was higher ($P < 0.001$) than that from LBW selection scenario (1.20 ± 0.07). Average EPD for birth weight from both selection scenarios showed decreases (Figure 3.3). Nevertheless, the decrease from LBW selection scenario was ($P < 0.001$) more severe (-1.17 ± 0.03 kg/yr) compared to (-0.86 ± 0.02 kg/yr) HCE. These results were in agreement with Bennett (2008) who reported that selection for higher calving ease reduced birth weight and the incidence of calving difficulty and did not affect growth at later ages. For weaning weight, average EPD showed a decrease in both selection populations; however, the rate of genetic change of WWT EPD in the LBW selection scenario experienced ($P < 0.001$) a steeper decline, -3.55 ± 0.10 kg/yr, compared to the -1.90 ± 0.09 kg/yr for HCE selection scenario. Similarly, postweaning gain average EPD from the LBW selection scenario had ($P < 0.001$) a faster rate of decrease at -0.25 ± 0.01 kg/yr compared to a -0.13 ± 0.01 kg/yr for PWG from HCE selection scenario. Even though both selection scenarios yielded decreasing rates for yearling weight average EPD, the difference between the two scenarios was more pronounced ($P < 0.001$) where smaller losses in yearling weight average EPD were found in HCE selection scenario versus LBW selection scenario.

Compared to selection for low birth weight, selection for high calving ease increased ($P < 0.001$) the annual genetic gain for the studied traits. These increases in the rate genetic change, (i.e., slope differences between HCE and LBW), were 0.37%, 1.65 kg, and 1.77 kg for CE, WWT, and YWT, respectively, which correspond to 30.83, 46.47, and 46.45% annual increase for these traits. Therefore, selection for the economically relevant trait (CE) instead of its

indicator trait (BWT) reduced losses by producing animals with a lower incidence of dystocia and heavier weights at marketing age. Conversely, in both selection scenarios, all growth-related traits showed negative genetic trends. These negative trends were a result of the single trait selection procedure applied. Such a procedure is not typically used as means for genetic improvement; but rather, multiple trait selection programs are the preferred method to achieve selection goals. Nonetheless, the use of single trait selection in the current study is justified by the need to exclusively quantify response to selection attributed to selection for high calving ease as opposed to low birth weight.

In conclusion, it appears that selection for high calving ease (HCE) produces cattle with improved calving ease EPD and higher growth rates at later ages compared to selection for low birth weight (LBW); therefore, we accept the hypothesis that direct selection for high calving ease would results in animals with lower incidence of calving difficulty and higher growth rate. However, both selection scenarios resulted in negative genetic trends for growth-related traits. These results were expected because of applying single trait selection schemes and the genetic correlations amongst the traits. Incorporating economically relevant traits, (e.g., weaning and yearling weights), with calving ease in a multitrait selection program would produce cattle with low incidence of dystocia and higher growth rates.

Table 3.7: Average EPD for calving ease (% unassisted calving) and growth traits (kg) under two selection scenarios¹.

Trait ²	HCE				LBW			
	Year of birth				Year of birth			
	0	2	4	6	0	2	4	6
CE	0.04	3.84	6.63	8.75	0.03	2.64	5.00	6.87
BWT	-0.03	-2.20	-3.69	-4.74	-0.05	-2.93	-5.02	-6.54
WWT	-0.09	-5.12	-8.23	-10.26	-0.17	-8.95	-15.28	-19.65
PWG	-0.008	-0.33	-0.58	-0.76	-0.01	-0.60	-1.08	-1.44
YWT	-0.10	-5.45	-8.82	-11.03	-0.18	-9.56	-16.37	-21.09

¹HCE = selection for high calving ease; LBW = selection for low birth weight

²CE = calving ease; BWT = birth weight; WWT = weaning weight; PWG = postweaning gain; YWT=yearling weight.

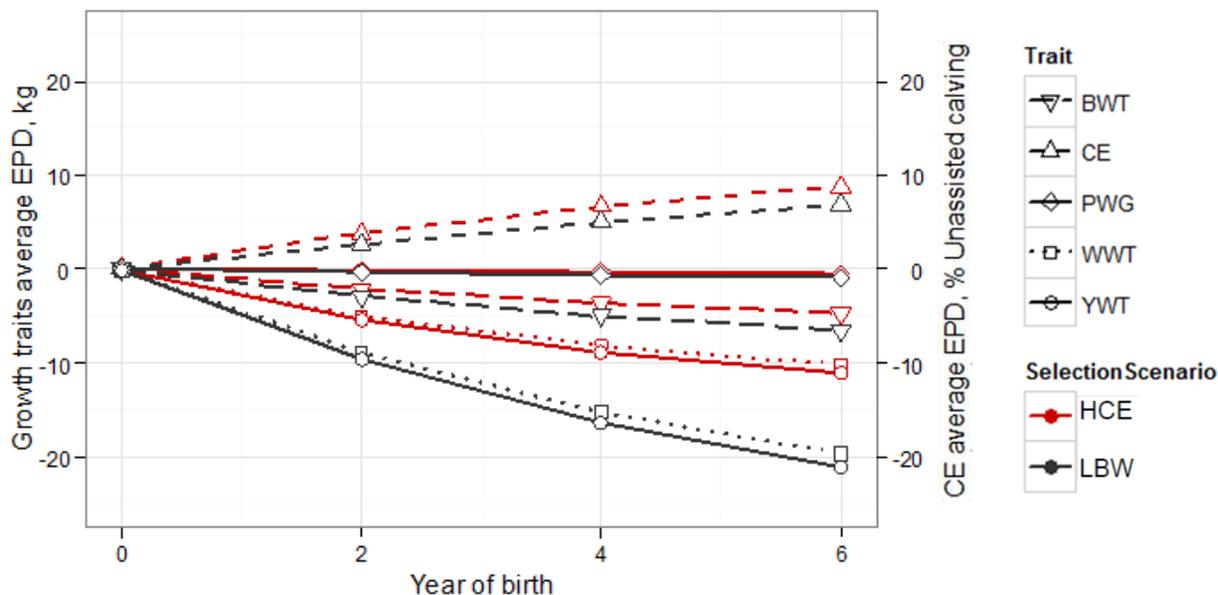


Figure 3.3: Genetic trends (average EPD) of calving ease (CE), birth weight (BWT), weaning weight (WWT), postweaning gain (PWG), and yearling weight (YWT) under two selection scenarios: selection for high calving ease (HCE) versus selection for low birth weight (LBW).

Table 3.8: Rate of genetic change¹ (EPD/yr) for calving ease (% unassisted calving) and growth traits (kg) under two selection scenarios².

Trait ³	HCE		LBW		Slope Difference
	Intercept	Slope	Intercept	Slope	
CE	-1.42 ± 0.15	1.56 ± 0.05	0.06 ± 0.14	1.20 ± 0.07	0.37 ± 0.09
BWT	0.76 ± 0.06	-0.86 ± 0.02	-0.13 ± 0.05	-1.17 ± 0.03	0.31 ± 0.03
WWT	1.63 ± 0.20	-1.9 ± 0.09	-0.42 ± 0.21	-3.55 ± 0.10	1.65 ± 0.13
PWG	-0.01 ± 0.03	-0.13 ± 0.01	-0.02 ± 0.03	-0.25 ± 0.01	0.12 ± 0.02
YWT	1.75 ± 0.27	-2.04 ± 0.10	-0.44 ± 0.22	-3.81 ± 0.11	1.77 ± 0.15

¹All estimates were different from zero ($P < 0.001$)

²HCE= selection for high calving ease; LBW = selection for low birth weight

³CE = calving ease; BWT = birth weight; WWT = weaning weight; PWG = postweaning gain; YWT = yearling weight.

Table 3.9 shows correlations (Spearman's and Pearson's) between predicted EPD from two complementary data sets (*i.e.*, animal with a calving ease record in one data and has no calving ease observation in the other data) under different animal models. Here, the different models were 1) Calving ease fitted as a linear or a threshold trait with either of two approaches (*i.e.*, as a binary), or three categories (*i.e.*, as polychotomous trait), 2) Univariate and multivariate which considers fitting: calving ease as "univariate", calving ease and birth weight as "bivariate", and calving ease with all growth traits as "multivariate". For the univariate animal models, fitting calving ease as a threshold or linear did not affect model predictive ability (0.27 vs.0.27 and 0.28 vs. 0.28 rank correlations for binary and polychotomous calving ease, respectively); however, fitting calving ease with three categories improved the model predictive ability by 6.25% (0.32 vs. 0.34 rank correlation) and 9.4% (0.32 vs. 0.35 correlation) for sires with more than 20 progeny. Increasing the number of categories increases the amount of information obtained from the observed scores. These results were in agreement with those found in a simulation study by Meijering and Gianola (1985) who found that increasing the number of categories causes the categorical trait to become more normally distributed. Further, Abdel-Azim and Berger (1999), in a simulation study, reported that the accuracy of prediction increased when the number of categories increased. In a study of US Holsteins, De Maturana et al. (2009) justified the similar predictive ability of the threshold model versus the linear model by the number of categories (3 and 4 categories) used for calving difficulty which provide more information compared to a binary scoring approach. Neither linearity (threshold vs. linear) nor the number of categories affected the predictive ability of the bivariate models. Similar results were obtained by Wang et al. (2005) in a simulation study where they found that a linear-linear (LL) and a linear-threshold (LT) sire-maternal grandsire model performed the same with respect

to accuracy (Pearson correlation) and Spearman rank correlation between true and predicted breeding values. It is worth noting that adding a highly correlated continuous trait (*e.g.*, birth weight) to the genetic evaluation of a categorical trait such as calving ease greatly improves the accuracy of genetic prediction. For all sires, the predictive ability of the univariate models, compared to birth weight added as correlated continuous trait, was poorer, but with the addition of the second trait the predictive ability improved by 210% (rank correlation) and 163% (correlation). This supported the results obtained by Foulley et al. (1983) and Janss and Foulley (1993) who showed the advantages of using a bivariate analysis for the genetic evaluation of calving ease, by incorporating birth weight as a correlated trait. Furthermore, for discrete traits, superiority of bivariate models over univariate models was also reported by Casellas et al. (2007) and Negussie et al. (2008). In the multivariate models, there were no differences between the different models. Furthermore, estimates of correlations did not differ from those obtained from the bivariate analysis. These results suggested that adding more correlated continuous traits (*e.g.*, weaning weight and postweaning gain) to the genetic evaluation of calving ease did not or only slightly improved the accuracy of prediction. This could be explained by the strong genetic correlation between calving ease and birth weight, which indicates the incorporation of birth weight provides sufficient information to achieve high accuracy and adding more traits has a little effect on the genetic evaluation of calving ease.

Generally, superiority of the threshold model over the linear model was not evident in this study. Data in the current study was balanced (all animals had BWT, WWT, and PWG records) with large size herds ($n=573$) and number of records per sire was 18.4. Such data are not characteristic of field data that more likely to indicate the superiority of the threshold model over the linear approach. The threshold methodology typically outperforms the linear method when

data is highly unbalanced, high incidence of one category of the trait, and for a trait has few categories, i.e., binary (Meijering and Gianola, 1985; Hoeschele, 1988; Abdel-Azim and Berger, 1999). The advantage of threshold models comes when dealing with unbalanced data with different incidence rates across levels of fixed effects; however, it may only offer a slight advantage in well designed progeny testing programs in which there are a large number of records per sire (McGuirk et al., 1999). The advantages of the threshold methodology over the linear methods would be more pronounced in beef cattle field data which is usually unbalanced with high incidence of calving ease and where sires have a relatively small number of progeny.

Table 3.9: Estimates of Spearman’s (Rank) and Pearson’s (r) correlation coefficients between predicted EPD from complementary data sets under different models.

Model ¹	All sires		Sires with progeny > 20		Sires with progeny < 20	
	Rank	r	Rank	r	Rank	r
Univariate						
L-UAM-CE2	0.27	0.31	0.32	0.32	0.25	0.30
T-UAM-CE2	0.27	0.31	0.32	0.32	0.25	0.30
L-UAM-CE3	0.28	0.33	0.34	0.35	0.25	0.32
T-UAM-CE3	0.28	0.33	0.34	0.35	0.25	0.32
Bivariate						
LL-BAM-CE2	0.87	0.87	0.89	0.90	0.82	0.82
TL-BAM-CE2	0.87	0.87	0.89	0.90	0.82	0.82
LL-BAM-CE3	0.87	0.88	0.88	0.87	0.81	0.80
TL-BAM-CE3	0.87	0.88	0.89	0.90	0.82	0.81
Multivariate						
LL-MAM-CE2	0.87	0.87	0.89	0.90	0.82	0.83
TL-MAM-CE2	0.87	0.87	0.89	0.90	0.82	0.83
LL-MAM-CE3	0.87	0.87	0.89	0.90	0.81	0.82
TL-MAM-CE3	0.87	0.88	0.89	0.89	0.82	0.83

¹L = linear; T = threshold; UAM = univariate animal model; BAM = bivariate animal model; MAM = multivariate animal model; CE2 = 2 categories; CE3 = 3 categories.

3.4. Summary

Despite being an indicator trait, downward selection on birth weight is widely used as a tool to improve calving ease. However, the positive genetic correlation between birth weight and subsequent growth traits could lead to loss in performance at later age. The objectives of this study were 1) to assess performance losses under two scenarios in which selection for high calving ease (HCE) and selection for low birth weight (LBW) will be applied and 2) to compare the threshold model versus the linear model. Under the two selection scenarios (HCE and LBW), two populations with observations on calving ease (CE), birth weight (BWT), weaning weight (WWT), and postweaning gain (PWG) were simulated. Each population consisted of a base generation of 1,200 sires and 36,000 dams. The first generation was produced by random mating of founders (1,200 sires and 36,000 dams). Each of the three subsequent generations were produced by selecting the top 5% and 80% sires and dams, respectively, from previous generations. Simulation was carried out using a multivariate threshold-linear model with Gibbs sampling algorithm to estimate variance components. Fixed effects were herd ($n = 120$) and sex. Models predictive ability “threshold vs. linear” were compared using a cross validation procedure (i.e., data-splitting technique). The procedure was performed by duplicating the HCE data which resulted in two identical data sets. In one of those data, one half of calving ease observations was randomly set to be missing. The remaining calving ease observations in this data were discarded in the other data set. The procedure produced two complementary (for calving ease records) data sets. The criteria used to compare models predictive ability were Pearson’s and Spearman’s correlations between predicted calving ease EPD obtained from complementary data sets. Results showed that the rate of genetic change of CE (% unassisted calving/yr) from HCE selection scenario (1.56 ± 0.05) was higher ($P < 0.001$) than that from

LBW (1.20 ± 0.07). For yearling weight, the difference between the two scenarios was more pronounced ($P < 0.001$) where less losses in YWT average EPD were found in HCE selection scenario (-2.04 ± 0.10 kg/yr) versus (-3.81 ± 0.11 kg/yr) for LBW. Slope difference between both scenarios was significant ($P < 0.001$) for all traits. For HCE compared to LBW, the annual differences in CE, WWT, and YWT were 0.37%, 1.65 kg, and 1.77 kg, respectively. In conclusion, we accept the hypothesis that direct selection for high calving ease would result in animals with lower incidence of calving difficulty and higher growth rate at later ages. The predictive ability of the threshold model and the linear model were the same. A substantial increase in the accuracy of prediction for calving ease, when birth weight was incorporated as a correlated trait, was indicated. However, with birth weight already in the model, the addition of weaning weight and postweaning gain did not improve model's predictive ability. In conclusion, both selection scenarios (HCE and LBW) increased calving ease average EPD and decreased the EPD for growth traits. However, selection for high calving ease produced animals with better calving ease EPD and have higher growth rates at later ages compared to those produced by selection for low birth weight. The similar predictive ability of the threshold and linear models might be a result of the highly balanced data used in current study. The use of unbalanced data with high incidence of calving ease, different incidences across levels of fixed effects, and small numbers of records per sire would be more appropriate to investigate the superiority of the threshold model over the linear model.

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CHAPTER IV.

PERFORMANCE LOSSES UNDER DIFFERENT SELECTION SCENARIOS FOR LOW BIRTH WEIGHT VERSUS HIGH CALVING EASE IN AMERICAN SIMMENTAL BEEF CATTLE

4.1. Introduction

Profitability of beef cattle enterprises are directly affected by costs associated with calving difficulty. Attempts to reduce such costs historically have focused on another trait, birth weight, which has no direct economic importance. Nonetheless, birth weight is routinely used as an indicator trait for dystocia. The high genetic correlation with calving difficulty, a continuous measure (as opposed to categorical), and ease of measure are characteristics that have made birth weight the trait of choice for the genetic improvement of calving difficulty. To improve the efficiency of beef production, Dickerson et al. (1974) proposed a selection index in which birth and yearling weights were included as component traits with the purpose of incorporating birth weight to reduce the incidence of dystocia, yet a selection strategy that would improve growth through selection for higher yearling weight. However, the downward selection for birth weight would not certainly improve the ease of calving (Burfening et al., 1978b; MacNeil et al., 1998) as rapidly. Furthermore, given the high genetic correlation between birth weight and growth traits at later ages, selection for lower weight at birth might result in sacrificing growth at the marketing age. Therefore, we hypothesize that, instead of selection for low birth weight, direct selection for the trait of economic importance (*i.e.*, calving ease) should be used as means to reduce both the incidence of calving difficulty and losses in performance of growth-related traits.

The objective of the current study was to quantify the performance losses in the American Simmental beef cattle under different selection scenarios for low birth weight as opposed to selection for high calving ease.

4.2. Materials and Methods

Data used in this study was provided by the American Simmental Association (ASA). In this section, we will be presenting the methodologies including: preparation of raw data for subsequent analysis; description of final data and models used for estimation of (co)variance components and calculation of direct and maternal genetic effects (EPD) for calving ease (CE), birth weight (BWT), 205-*d* weight, 160-*d* gain, and 365-*d* weight for Simmental beef cattle. Using these EPD we estimated genetic trends under different selection scenarios for high calving ease versus low birth weight and follow that with a comparison of predictive ability of “threshold vs. linear” models.

4.2.1. Description of data:

The ASA provided data and pedigree files of calving ease and growth traits for Simmental beef cattle. That data consisted of 11,640,735 records. Each record contained a unique animal ID, sire’s animal ID, dam’s animal ID, maternal grandsire ID, sex, multiple birth code, breeder, herd, calving ease score, birth weight, birth date, weaning weight, weaning date, weaning management code, weaning pasture unit, yearling weight, yearling date, and yearling feed unit. The pedigree and breed composition file consisted of 9,250,633 animals. Fields of the pedigree file were animal ID, sire ID, birth year, with the remaining fields representing proportions of 19 different breeds.

To avoid the effects heterosis, data were edited so that only animals with $\geq 87.5\%$ Simmental composition were used. Since heifers have a higher incidence of dystocia than older

cows, only records of progeny of 2-yr old heifers were used. The former two steps markedly reduced the number of animals included in this study due to the high use of crossbreeding by Simmental breeders and the small number of progeny produced by first-calf heifers. In the ASA standard coding system, the multiple birth code ranges from 1 to 9 where single birth is coded as “1”. Therefore, records of animals with other multiple birth codes were removed from the data. The ASA added 2 additional categories to the primary coding system recommended by the BIF guidelines (1= unassisted calving to 5 = malpresentation). The additional two categories were scores 6 and 7 representing animals dead on arrival and premature calving, respectively. Calving ease scores from malpresentation (5), dead on arrival (6), and premature calving (7) were eliminated for the purposes of this study.

Adjusted 205-d and 365-d weights and adjusted 160-d postweaning gain: Weaning and yearling weights, and consequently postweaning gain, were adjusted to constant age endpoints of 205-d and 365-d, respectively. Adjusted weights were calculated and sifted as follows: 1) ages at weaning and yearling were calculated, 2) Records that did not fall within weaning and yearling age limits of 160 to 250 d and 320 to 410 d, respectively, were eliminated, 3) Weaning and yearling weights observations within ± 3 SD limits were used, 4) Weights were then regressed on their respective ages, 5) Regression coefficients were used to adjust weaning and yearling weights observations to constant age of 205-d and 365-d, respectively. Next, 160-d gain was obtained by subtracting the 205-d weight from the 365-d weight. Finally, weight measurement units were transformed from lb to kg.

Forming fixed effects (contemporary groups) and herd-year-season: Sex was fitted as a fixed effect (contemporary group) for both calving ease and birth weight. Weaning contemporary groups were constructed by combining sex, weaning management code, and weaning pasture

unit. Yearling contemporary groups for 160-*d* gain were formed using weaning contemporary group with the yearling feed unit code added. Since herds were coded within breeders, the two codes were combined to obtain a unique code for each herd. In other words, the breeder×herd code used in the ASA coding system were combined to form the herd code. Two birth seasons were formed as follow: animals born in the period from January to June were considered season 1 while animals born between July and December were in season 2. For all studied traits, the herd-year-season effect was formed and fitted as a random effect in all models for variance components estimation and calculation of EPD (*i.e.*, direct and maternal EPD).

Estimation of (co)variance components for calving ease, birth weight, 205-d weight, and 160-d gain: Preliminary analyses were performed using an animal model with Gibbs sampling algorithm to estimate (co)variance components of studied traits. The program THRGIBBS1F90 from the BLUPF90 family of programs by Misztal et al. (2002) was used to estimate (co)variance components. The THRGIBBS1F90 program uses the probit link function to transform observed incidence to a liability scale. Examination of Gibbs samples from their conditional distribution, using the animal model, showed that samples of parameters were not stable. Therefore, the estimated parameters from the animal model were not considered reliable. The inadequacy of the threshold animal model for the estimation of genetic parameters was reported by Moreno et al. (1997). Thus, the sire model was chosen to estimate (co)variance components for studied traits. For all analyses in the current study, a four-generation pedigree was used beginning with animals with at least one observation (*i.e.*, animals in the data file).

The dependence of 160-*d* gain observations on existence of observations for both 205-*d* weight and 365-*d* weight resulted in a smaller number of 160-*d* gain records (Table 4.1) compared to other traits. The absence of weaning weight observation, weaning date, yearling

weight observation, and yearling date, resulted in a missing 160-*d* gain observation. A multivariate sire model was fitted to all traits; however, the 160-*d* gain (co)variance components, especially the residual covariances with calving ease and birth weight and with other traits in the model did not converge. Here, Gibbs samples of these covariances fluctuated close to zero. The small residual correlations between 160-*d* gain and these two traits and the sparse 160-*d* gain data, which represented only 28.9, 30.7, and 40.5% of calving ease, birth weight, and 205-*d* weight observations, respectively, likely caused the instability in the system. Hence, a series of bivariate analyses were performed to estimate covariances between 160-*d* gain and the three other traits. Maternal grandsire variance and sire-maternal grandsire covariance for calving ease, birth weight, and 205-*d* weight were estimated using a univariate sire-maternal grandsire model.

For all data sets, analyses were performed with a single chain of 120,000 iterations. The initial number of samples obtained via the Gibbs sampler algorithm, usually show fluctuation due to Gibbs samples not reaching their stationary distribution. This period is called the burn-in period and samples obtained during this period should be discarded. Therefore, for this study the initial 20,000 iterations from all analyses were discarded. Another characteristic of this approach is that the adjacent samples have high autocorrelations. Thus, samples were thinned by selecting every 10th sample out of the remaining 100,000 samples. This thinning procedure yielded 10,000 samples which were subsequently used to obtain the posterior means of (co)variance components and their respective posterior standard deviations. Post-Gibbs analyses to examine the convergence of parameters and obtain the posterior means and standard deviations were performed using the program POSTGIBBSF90 from the BLUPF90 family of programs by Misztal et al. (2002). Parameters were then plotted as a function of the final 10,000 samples. In case of convergence, the plot will fluctuate around the mode of the distribution where samples

seem to be stable. However, when non-convergence occurs, the parameter value will show a clear trend.

Models used for (co)variance components estimation for Simmental data: Three sire models were fitted to estimate (co)variance components required to build the fully structured G and R matrices required for subsequent to estimate direct genetic and maternal additive genetic solutions. The (co)variance components estimated by sire and sire-maternal grandsire models were the sire (co)variance components and the maternal grandsire (co)variance components, respectively. These were then transformed to direct and maternal genetic (co)variance components. The estimated (co)variance components, after transformation, included: Direct genetic and residual (co)variances for all traits and maternal genetic and direct-maternal covariance for calving ease, birth weight, and 205- d weight. Calving ease was fitted as a threshold trait with categories 3 and 4 merged. Models used to estimate (co)variance components for calving ease, birth weight, 205- d weight, and 160- d gain for Simmental beef cattle were: 1) A multivariate threshold-linear sire model was used to estimate sire and residual (co)variances between calving ease, birth weight, and 205- d weight. 2) A series of three bivariate sire models to estimate sire and residual covariances between 160- d gain and traits from the previous model. 3) A series of three univariate sire-maternal grandsire models to estimate maternal grandsire variance and sire-maternal grandsire covariance for traits in the first model.

Description of different models used in the analyses is presented below:

- 1. A multivariate threshold-linear sire model used to estimate sire and residual (co)variances between calving ease, birth weight, and 205- d weight:*

A summary of data and pedigree information used for this analysis is presented in Table 4.1. Calving ease was fitted as a threshold trait with 3 categories. The fixed effect for both CE and

BWT was sex. For 205-d weight, the fixed was weaning contemporary group (sex, weaning management code, and weaning pasture unit). The equation of the multivariate threshold-linear sire model used in this analysis is presented below.

$$\begin{bmatrix} L_{ce} \\ Y_{bwt} \\ Y_{205wt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{205wt}\beta_{205wt} \end{bmatrix} + \begin{bmatrix} Z_1s_{ce} \\ Z_1s_{bwt} \\ Z_1s_{205wt} \end{bmatrix} + \begin{bmatrix} Z_2h_{ce} \\ Z_2h_{bwt} \\ Z_2h_{205wt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{205wt} \end{bmatrix}, \quad (4.1)$$

In the above equation, β were effects associated with sex, and weaning contemporary group subclasses; s and h were sire and herd-year-season random effects, respectively; e were the residuals; and X , Z_1 , and Z_2 were incidence matrices that link data with fixed effects, sire random effects, and herd-year-season random effects, respectively. Y was vector of observations for birth weight and weaning weight. Calving ease was assumed to follow an underlying continuous distribution (L) which is presented below:

$$\begin{aligned} f(y|L) = \prod_{i=1}^n f(y_i|L_i) = \prod_{i=1}^n [& I(L_i < t_1)I(y_i = 1) + I(t_1 < L_i < t_2)I(y_i = 2) \\ & + I(t_2 < L_i < t_3)I(y_i = 3) + I(t_3 < L_i)I(y_i = 4)] \end{aligned} \quad (4.2)$$

In the above equation, t_1 , t_2 , and t_3 were thresholds that defined the four categories of calving ease.

The (co)variance structure of random effects was defined as: $\text{var} \begin{bmatrix} s \\ h \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{S} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{H} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$

where \mathbf{S} = a 3×3 additive genetic (co)variance matrix for sires, \mathbf{A} = additive genetic relationship matrix, \mathbf{H} = a 3×3 diagonal matrix for herd-year-season random effects, \mathbf{R} = a 3×3 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations, and \otimes =Kronecker product.

Table 4.1: Summary statistics of Simmental data used in a multivariate threshold-linear sire model to estimate (co)variance components for CE, BWT, and 205-*d* weight.

Item ¹	N	Calving difficulty score				Mean	SD	Min.	Max.
		1	2	3	4				
<i>Data file:</i>									
Sire	12,199								
MGS	14,123								
CE	95,791	56,442	28,071	8,255	3,023	1.56	0.78	1	4
Males	45,256	23,897	14,313	4,787	2,259	1.67	0.85	1	4
Females	50,535	32,545	13,758	3,468	764	1.45	0.69	1	4
BWT, kg	90,157					40.80	5.15	24.09	55.45
Males	42,836					42.18	5.10	24.09	55.45
Females	47,321					39.55	4.88	24.09	55.45
205- <i>d</i> WT, kg	68,305					267.47	45.80	92.00	436.15
Males	31,623					282.22	48.16	92.00	436.15
Females	36,682					254.75	39.45	94.52	410.70
160- <i>d</i> gain, kg	27,695					174.24	54.70	-29.06	387.84
Males	14,986					208.07	45.27	30.91	387.83
Females	12,709					134.34	34.13	-29.06	294.57
WCG	7,524								
YCG	3,800								
HYS	14,533								
<i>Pedigree:</i>									
Sire	26,696								
Sire of sire	6,167								
MGS	5,367								

¹CE = Calving ease; BWT = Birth weight; 205-*d* WT = 205 days adjusted weight; 160-*d* gain = 160 days adjusted total postweaning gain; WCG = Weaning contemporary groups; YCG = yearling contemporary groups; HYS = Herd-Year-Season; MGS = Maternal grandsire.

2. *Bivariate sire models to estimate sire and residual covariances between 160-*d* gain and each of CE, BWT, and 205-*d* weight:*

Sire and residual covariances between 160-*d* gain and other traits, using the complete data presented in Table 4.1, did not converge using a full model that included all studied traits. This might be caused by: 1) the weak residual correlations between 160-*d* gain and both CE and BWT 2) the sparse 160-*d* gain data, relative to the other traits where missing observations are associated with 71.1, 69.3, and 59.5% of calving ease, birth weight, and 205-*d* weight

observations, respectively, (Table 4.1). As a result, three bivariate analyses were performed using two models: *a*) A bivariate threshold-linear sire model to estimate sire genetic and residual (co)variances between 160-*d* gain and calving ease; *b*) A bivariate linear-linear sire model used to perform the two other analyses to estimate sire and residual (co)variances for 160-*d* gain with birth weight and 205-*d* weight. Each of the models are described in more details as follows:

- a*) The data for the bivariate threshold-linear sire model used to estimate sire and residual (co)variances between 160-*d* gain and calving ease are summarized in Table 4.2. Calving ease was fitted as a threshold trait with observed 3 categories transformed to an underlying continuous liability presented in Eq. 4.2. The fixed effects for CE and 160-*d* gain were sex and yearling contemporary group (sex, weaning management code, weaning pasture unit, and yearling feed unit), respectively. The bivariate threshold-linear sire model equation used in this analysis is presented as

$$\begin{bmatrix} L_{ce} \\ Y_{160gain} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{160gain}\beta_{160gain} \end{bmatrix} + \begin{bmatrix} Z_1s_{ce} \\ Z_1s_{160gain} \end{bmatrix} + \begin{bmatrix} Z_2h_{ce} \\ Z_2h_{160gain} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{160gain} \end{bmatrix}, \quad (4.3)$$

In the above equation, β were effects associated with sex, and yearling contemporary group subclasses; s and h were sire and herd-year-season random effects, respectively; e were the residuals; and X , Z_1 , and Z_2 were incidence matrices that link data with fixed effects, sire random effects, and herd-year-season random effects, respectively. Y was vector of observations for respective trait. L was the underlying continuous liability.

The (co)variance structure of random effects was:
$$\text{var} \begin{bmatrix} s \\ h \\ e \end{bmatrix} = \begin{bmatrix} \mathbf{S} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{H} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

where \mathbf{S} = a 2×2 additive genetic (co)variance matrix for sires, \mathbf{A} = additive genetic relationship matrix, \mathbf{H} = a 2×2 diagonal matrix for herd-year-season random effects, \mathbf{R} = a 2×2 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations.

Using bivariate linear-linear sire model to estimate sire and residual (co)variances for 160-*d* gain with birth weight and 205-*d* weight,

b) Two bivariate analyses were performed to estimate (co)variance components for 160-*d* gain with BWT and 205-*d* weight. Here, the same model was used for both analyses with the appropriate changes in fixed effects that correspond to either BWT or 205-*d* weight. The fixed effects for BWT, 205-*d* weight, and 160-*d* gain were sex, weaning and yearling contemporary groups. Structure of data sets and pedigree information used in these analyses are presented in Table 4.2. Data sets used in these analyses (Table 4.2) were balanced data and showed a substantial increase in the number of records compared to the 160-*d* gain data presented in Table 4.1. The bivariate linear-linear sire model equation used in the two analyses is presented as follows:

$$\begin{bmatrix} Y_{wt} \\ Y_{160gain} \end{bmatrix} = \begin{bmatrix} X_{wt}\beta_{wt} \\ X_{160gain}\beta_{160gain} \end{bmatrix} + \begin{bmatrix} Z_1s_{wt} \\ Z_1s_{160gain} \end{bmatrix} + \begin{bmatrix} Z_2h_{wt} \\ Z_2h_{160gain} \end{bmatrix} + \begin{bmatrix} e_{wt} \\ e_{160gain} \end{bmatrix}, \quad (4.4)$$

In the above equation \mathbf{Y} was vector of observations for respective trait; \mathbf{wt} is either BWT or 205-*d* WT; $\boldsymbol{\beta}$ were effects associated with sex, weaning and yearling contemporary group subclasses; \mathbf{s} and \mathbf{h} were sire and herd-year-season random effects, respectively; \mathbf{e} were the residuals; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 were incidence matrices that link data with fixed effects, sire random effects, and herd-year-season random effects, respectively.

The (co)variance structure of random effects was defined as: $\text{var} \begin{bmatrix} \mathbf{s} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{S} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{H} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$

where \mathbf{S} = a 2×2 additive genetic (co)variance matrix for sires, \mathbf{A} = additive genetic relationship matrix, \mathbf{H} = a 2×2 diagonal matrix for herd-year-season random effects, \mathbf{R} = a 2×2 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations, and \otimes =Kronecker product.

Table 4.2: Summary statistics of three data sets used in bivariate sire models to estimate sire (co)variance components of 160-d gain with CE, BWT, and 205-d weight.

Item ¹	N	Calving difficulty score				Mean	SD	Min.	Max.
		1	2	3	4				
CE and 160-d gain									
<i>Data file:</i> Sire & MGS	4,714 & 5,869								
CE	24,488	13,508	7,833	2,213	934	1.61	0.80	1	4
Males	13,414	6,742	4,569	1,364	739	1.70	0.86	1	4
Females	11,074	6,766	3,264	849	195	1.50	0.71	1	4
160-d gain, kg	24,488	13,508	7,833	2,213	934	174.73	54.62	-29.06	387.84
Males	13,414	6,742	4,569	1,364	739	208	46.52	30.91	387.84
Females	11,074	6,766	3,264	849	195	134.34	35.12	-29.06	294.57
YCG	3,349								
HYS	4,875								
<i>Pedigree:</i> Sire	13,811								
Sire of sire	3,555								
MGS	3,015								
BWT and 160-d gain									
<i>Data file:</i> Sire & MGS	7,636 & 9,107								
BWT, kg	41,219					40.78	5.00	24.09	55.45
Males	21,313					41.90	5.00	24.09	55.45
Females	19,906					39.57	4.70	24.09	55.45
160-d gain, kg	41,219					171.68	55.44	-29.06	423.81
Males	21,313					206	46.85	8.95	423.81
Females	19,906					134	35.67	-29.06	324.60
YCG	6,392								
HYS	9,836								
<i>Pedigree:</i> Sire	19,539								
Sire of sire	4,674								
MGS	3,971								
205-d WT and 160-d gain									
<i>Data file:</i> Sire & MGS	8,358 & 9,827								
205-d WT, kg	45,520					276.80	45.50	94.25	440.96
Males						291.25	47.17	109.65	425
Females						261.29	37.94	94.25	440.96
160-d gain, kg	45,520					171	55.41	-29.06	423.81
Males						205.78	47.22	30.91	423.81
Females						133.70	35.82	-29.06	324.60
WCG	6,782								
YCG	7,032								
HYS	10,986								
<i>Pedigree:</i> Sire	20,535								
Sire of sire	4,858								
MGS	4,097								

¹CE = Calving ease; BWT = Birth weight; 205-d WT = 205 days adjusted weight; 160-d gain = 160 days adjusted total postweaning gain; WCG = Weaning contemporary groups; YCG = yearling contemporary groups; HYS = Herd-Year-Season; MGS = Maternal grandsire.

1. *Univariate sire-maternal grandsire models used to estimate maternal grandsire variance and sire-maternal grandsire covariance for CE, BWT, and 205-d WT:*

The maternal grandsire (co)variance components for calving ease, birth weight, and 205-d weight, obtained from more complex models did not converge; therefore, univariate analyses were carried out to estimate the maternal grandsire (co)variance components for these traits. These univariate analyses were performed using two different (threshold and linear) univariate models. Calving ease was analyzed using the threshold model while birth and 205-d weight were analyzed using the linear model.

The equations of models are described below.

- a) The threshold sire-maternal grandsire model used for calving ease maternal grandsire (co)variance components estimation:

Calving ease was modeled as a threshold trait (*i.e.*, underlying continuous liability was assumed) with 3 observed categories. Description of the data and pedigree used in this analysis is presented in Table 4.3. The threshold sire-maternal grandsire model is described below.

$$\mathbf{L} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_1\mathbf{s} + \mathbf{Z}_2\mathbf{mgs} + \mathbf{Z}_3\mathbf{h} + \mathbf{e}, \quad (4.5)$$

where \mathbf{L} was the underlying liability; $\boldsymbol{\beta}$ were fixed effects associated with sex; \mathbf{s} , \mathbf{mgs} , and \mathbf{h} were the random effects of sire, maternal grandsire, and herd-year-season, respectively; \mathbf{e} were the residual effects; and \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 were incidence matrices that link data with fixed effects, sire, maternal grandsire, and herd-year-season random effects, respectively.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} \mathbf{s} \\ \mathbf{mgs} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \sigma_s^2 \mathbf{A} & \sigma_{s,\text{mgs}} \mathbf{A} & 0 & 0 \\ \sigma_{s,\text{mgs}} \mathbf{A} & \sigma_{\text{mgs}}^2 \mathbf{A} & 0 & 0 \\ 0 & 0 & \sigma_h^2 & 0 \\ 0 & 0 & 0 & \sigma_e^2 \end{bmatrix}$$

with σ_s^2 , σ_{mgs}^2 , σ_h^2 , and σ_e^2 denoting variances of sire, maternal grandsire, herd-year-season, and residual random effects, $\sigma_{s,mgs}$ was covariance between sire and maternal grandsire effects, \mathbf{A} was the additive genetic relationship matrix.

b) The linear sire-maternal grandsire model used to estimate maternal grandsire (co)variance components for birth weight and 205-*d* weight:

The model was fitted in two separate univariate analyses to estimate maternal grandsire (co)variance components for birth and 205-*d* weights. The data and pedigrees used in both analyses are summarized in Table 4.3. The linear sire-maternal grandsire model is:

$$Y_i = X_i\beta_i + Z_{1i}s_i + Z_{2i}mgs_i + Z_{3i}h_i + e_i, \quad (4.6)$$

Where \mathbf{Y}_i were vectors of observations with subscript \mathbf{i} denoting either birth weight or 205-*d* weight; $\boldsymbol{\beta}$ were fixed effects associated with their respective trait; \mathbf{s} , \mathbf{mgs} , and \mathbf{h} were the random effects of sire, maternal grandsire, and herd-year-season, respectively; \mathbf{e} were the residual effects; and \mathbf{X} , \mathbf{Z}_1 , \mathbf{Z}_2 , and \mathbf{Z}_3 were incidence matrices that link data with fixed effects, sire, maternal grandsire, and herd-year-season random effects, respectively.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} s_i \\ mgs_i \\ h_i \\ e_i \end{bmatrix} = \begin{bmatrix} \sigma_{s_i}^2 \mathbf{A}_i & \sigma_{s_i, mgs_i} \mathbf{A}_i & 0 & 0 \\ \sigma_{s_i, mgs_i} \mathbf{A}_i & \sigma_{mgs_i}^2 \mathbf{A}_i & 0 & 0 \\ 0 & 0 & \sigma_{h_i}^2 & 0 \\ 0 & 0 & 0 & \sigma_{e_i}^2 \end{bmatrix}$$

with subscript \mathbf{i} denoting either birth weight or 205-*d* weight; $\sigma_{s_i}^2$, $\sigma_{mgs_i}^2$, $\sigma_{h_i}^2$, and $\sigma_{e_i}^2$ denoting variances of sire, maternal grandsire, herd-year-season, and residual random effects, σ_{s_i, mgs_i} was covariance between sire and maternal grandsire effects, \mathbf{A} was the additive genetic relationship matrix.

Table 4.3: Summary statistics of three data sets used in univariate sire-maternal grandsire models to estimate sire and maternal grandsire (co)variance components for calving ease, birth weight, and 205-*d* weight.

Item ¹	N	Calving difficulty score				Mean	SD	Min.	Max.
		1	2	3	4				
CE									
<i>Data file:</i>									
CE	97,375	57,357	28,468	8,436	3,114	1.56	0.78	1	4
Sire	12,388								
MGS	14,261								
Sex	2								
HYS	14,778								
<i>Pedigree:</i>									
Sire	26,907								
Sire of sire	6,196								
MGS	5,400								
BWT									
<i>Data file:</i>									
BWT, kg	141,132					40.12	5.16	24.09	55.45
Sire	18,078								
MGS	19,585								
Sex	2								
HYS	26,378								
<i>Pedigree:</i>									
Sire	34,995								
Sire of sire	7,646								
MGS	6,610								
205-<i>d</i> WT									
<i>Data file:</i>									
205- <i>d</i> WT, kg	81,451					267.53	45	92	433.15
Sire	10,762								
MGS	12,414								
WCG	3,015								
HYS	12,510								
<i>Pedigree:</i>									
Sire	23,217								
Sire of sire	5,357								
MGS	4,663								

¹CE = Calving ease; BWT = Birth weight; 205-*d* WT = 205 days adjusted weight; WCG = Weaning contemporary groups; HYS = Herd-Year-Season; MGS = Maternal grandsire.

4.2.2. Estimation of EPD for calving ease, birth weight, 205-d weight, 365-d weight, and 160-d gain in American Simmental beef cattle:

A multivariate threshold-linear maternal animal model was used to estimate direct and maternal EPD for CE, BWT, and 205-*d* weight and direct EPD for 160-*d* gain and 365-*d* weight. Direct and maternal genetic (co)variance components used in the model were obtained by the conversion of the formerly estimated sire and maternal grandsire (co)variance components using Equation (4.7) which is based on equating estimates of (co)variance components to their genetic expectation suggested by Kriese et al. (1991). The data and pedigree used in this analysis are summarized in Table 4.4. Calving ease was modeled as a threshold trait (*i.e.*, underlying continuous liability was assumed; Eq. 4.2), with 3 observed categories. Observed categories were 1 = unassisted, 2 =minor assistance, 3 = (categories 3and 4 merged). The 365-*d* weight was not included in the model; however, its direct EPD were calculated as the summation of the estimated EPD for 205-*d* weight and 160-*d* gain. For obtained calving ease EPD, the underlying liabilities of calving ease were multiplied by -1 to represent calving ease instead of calving difficulty.

$$\begin{bmatrix} \sigma_D^2 \\ \sigma_{DM} \\ \sigma_M^2 \end{bmatrix} = \begin{bmatrix} 4 & 0 & 0 \\ -2 & 4 & 0 \\ 1 & -4 & 4 \end{bmatrix} \begin{bmatrix} \sigma_S^2 \\ \sigma_{SMGS} \\ \sigma_{MGS}^2 \end{bmatrix}, \quad (4.7)$$

The equation of the multivariate threshold-linear maternal animal model used in the analysis is presented as follow:

$$\begin{bmatrix} L_{ce} \\ Y_{bwt} \\ Y_{205wt} \\ Y_{160gain} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{205wt}\beta_{205wt} \\ X_{160gain}\beta_{160gain} \end{bmatrix} + \begin{bmatrix} Z_1u_{ce} \\ Z_1u_{bwt} \\ Z_1u_{205wt} \\ Z_1u_{160gain} \end{bmatrix} + \begin{bmatrix} Z_2m_{ce} \\ Z_2m_{bwt} \\ Z_2m_{205wt} \\ 0 \end{bmatrix} + \begin{bmatrix} Z_3h_{ce} \\ Z_3h_{bwt} \\ Z_3h_{205wt} \\ Z_3h_{160gain} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{205wt} \\ e_{160gain} \end{bmatrix}, \quad (4.8)$$

Table 4.4: Summary of Simmental cattle data and pedigree used in a multivariate threshold-linear maternal animal model to estimate direct and maternal EPD for calving ease, birth weight, and 205-*d* weight, and direct EPD for 160-*d* gain.

Item ¹	N	Calving difficulty score ²				Mean	SD	Min.	Max.
		1	2	3	4				
<i>Data file:</i>									
Animal	155,898								
Dam	155,877								
CE	97,492	57,414	28,507	8,450	3,121	1.56	0.78	1	4
Males	45,978	24,271	14,486	4,897	2,324	1.68	0.85	1	4
Females	51,514	33,143	14,021	3,553	797	1.45	0.69	1	4
BWT, kg	141,271	39.38(4.7)	42.10(4.8)	44.15(5.1)	45.60(5.2)	40.1	5.16	24.09	55.45
205- <i>d</i> WT, kg	126,722	265.6(44.8)	271.4(46.9)	264.5(46.5)	273(48.9)	266	45.5	86.33	440.96
160- <i>d</i> gain, kg	45,545	170.1(54.3)	178.4(54.4)	178.6(55.1)	194.8(54.3)	171	55.4	-29.06	423.81
365- <i>d</i> WT ³ , kg	45,563	446.4(79.9)	460(82.4)	452.2(78.6)	477.8(81.4)	447	81.1	190.8	699.77
WCG	15,833								
YCG	7,040								
HYS	29,393								
<i>Pedigree:</i>									
Animal	465,710								
Sire	35,981								
Dam	302,432								

¹CE = Calving ease; BWT = Birth weight; 205-*d* WT = 205 days adjusted weight; 160-*d* gain = 160 days adjusted total postweaning gain; 365-*d* WT = 365 days adjusted weight; WCG = Weaning contemporary groups; YCG = yearling contemporary groups; HYS = Herd-year-Season.

²Growth traits were averaged (with SD in parenthesis) within calving ease score.

³365-*d* WT was not included in the model rather its EPD were calculated by the summation of 205-*d* WT and 160-*d* gain EPD.

4.2.3. Genetic trends for calving ease, birth weight, 205-d weight, 160-d gain, and 365-d weight in American Simmental beef cattle and the selection scenarios for high calving ease versus low birth weight

Since the four-generation pedigree ($n = 465,710$) used for EPD estimation included dams with age > 2 year old (Table 4.4), a subpopulation of 2 year old (first-calf) Simmental heifers ($n = 277,897$) was extracted by including only progeny of first-calf heifers for all analysis. This subpopulation was used for estimating genetic trends of Simmental and was also used as selection pool for various selection scenarios that will be described later. Therefore, this first-calf heifer Simmental population was treated as a control scenario for all selection scenarios. The estimated EPD for studied traits were used to produce genetic trends (EPD/yr) for the first-calf heifer American Simmental population (from 1969 “ ≤ 1969 ” to 2010). The rate of the genetic change for each of the studied traits was estimated by the regressing trait EPD on birth year.

To quantify the performance losses resulted from selection for low birth weight instead of selection for calving ease, six artificial selection scenarios were derived from the first-calf heifers American Simmental population (the control scenario). The selection scenarios included selection for: 1) high calving ease (**HCE**), 2) low birth weight(**LBWT**), 3) the Selection index of Dickerson et al. (1974), $\mathbf{DSI} = YWT - 3.2 BWT$, 4) The all-purpose selection index of ASA, (Lauren Hyde, the American Simmental Association, personal communication), $\mathbf{API} = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT$, in addition to two sub-selection indexes that we derived from the API, which were 5) $\mathbf{API}_1 = 1.3 CE + 0.20 YWT$, and 6) $\mathbf{API}_2 = -1.8 BWT + 0.20 YWT$. In the above selection scenarios, *CE*, *BWT*, *WWT*, and *YWT* were EBV for calving ease, and birth, weaning (205-d WT), and yearling (365-d WT) weights, respectively.

Starting with animals born in 1970, selection was applied within each birth year. Animals born before 1970 ($n = 1517$) were considered a base population (selection pool) for animals born in 1970. The selection criteria, in these selection scenarios, were the estimated EBV for the respective trait. EBV estimates for growth traits were standardized by their respective genetic standard deviation. For direct and maternal calving ease, the estimated underlying liabilities (multiplied by -1 to represent calving ease instead of calving difficulty) were standardized by their respective genetic standard deviation and centered based on the average liability of animals born before 1970. Using the first-calf heifer data (the control), data for each selection scenario was created by selecting sires, within each year of birth, with $EBV \geq$ the average for the 6 different methods of selection (either EBV or the index value), and then the top 75% of dams with progeny within selected sires were selected. This means selection was first applied to sires and then followed by selecting from the remaining dams after the culling of unselected sires along with their mates and progeny. The resulting data sets for all selection scenarios contained animals born in 1969 “ ≤ 1969 ” to 2004. In all selection scenarios, animals born after 2004 were discarded because of their small numbers.

For all selection scenario data sets, the obtained EPD for all traits were calculated as a deviation from their respective average EPD from the control data. Graphs of genetic trends were produced by plotting the standardized average EPD deviation versus the year of birth. Further, the standardized EPD were regressed on the birth year to estimate the rate of genetic change per year (SD/yr). For each trait across selection scenarios, the significance of differences between slopes and between intercepts was also tested.

Estimation of net profit for various selection scenarios using the API: The economic selection indexes measure the cumulative effect of the animal’s overall genetic merit on profit. Therefore,

selection strategies that using this methodology, produce cattle have the genetic makeup (i.e., economically relevant traits EPD) to increase profit. Shafer (2008) reported that the ASA published, in 2005, two economic selection indexes (terminal index “TI” and all-purpose index “API” which are presented in the equations below). These indexes were developed in collaboration with USDA research scientist, Dr. Mike MacNeil. The creation of these indexes was based on outcomes from a computer simulation program that mimics beef cattle production (i.e., cows conceive, gestate, calve, lactate, calves are weaned, heifers are retained and cull heifers and steers are placed on feed and eventually harvested). A simulated base herd was generated using: 1. Phenotypic averages of ERT in the index, 2. Salvage price, costs of feed (e.g., hay and pasture), and fixed costs, 3. Carcass prices (e.g., carcass, USDA beef grade, and yield grade). The average performance levels assumed in the creation of the ASA indexes can be found in Shafer (2008). The prices and cost data used were the averages over the last 5 years as reported by Cattle Fax at the time the indexes were created. Traits used in this simulation were weaning weight, feedlot gain, feedlot intake, cow size, milk production, pregnancy rate, incidence of dystocia, calf survival rate, harvest weight, dressing, carcass weight, marbling score, and yield grade. Economic weights for each ERT were estimated by changing each trait one unit while holding all others constant and comparing that with the base herd. Therefore, these weighting factors (i.e., economic weights), estimated based on the impact of the trait on profit, and were subsequently used to calculate the ASA economic indexes presented below.

$$API = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT + 2 STAY + 55 MRB - 6 YG$$

$$TI = -1.2 BWT + 0.9 CE + 0.50 WWT + 0.07 YWT + 25 MRB - 5 YG + 0.10 MLK$$

where: BWT = birth weight, CE = calving ease, WWT = weaning weight, YWT = yearling weight, STAY = stayability, MRB = marbling, YG = yield grade, MLK = milk

The API evaluates sires being used on the entire cowherd (bred to both Angus first-calf heifers and mature cows) with a portion of their daughters being retained for breeding and the steers and remaining heifers being put on feed and sold on a grade and yield basis (Shafer, 2015). The API puts emphasis on stayability and calving ease. This is because calving ease is strongly associated with calf survivability and, to a lesser degree, female longevity. In the current study, we used a subset of the API considering only calving ease and growth-related traits (i.e., stayability, marbling, and yield grade were not included in the API). Another perspective from which to look at this, is that all other traits were held constant in the index. The API value can be interpreted as the estimated differences between bulls in net profit per cow exposed (Shafer, 2015). For example, a bull with an API value of \$10, as opposed to a bull with value of \$0, is expected to worth extra \$10 per cow exposed. The TI was designed for evaluating sire's economic merit in situations where they are bred to mature Angus cows and all offspring are placed in the feedlot and sold on a grade and yield basis. Therefore, maternal traits such as milk, stayability and calving ease are not considered in the index.

In this study, the net profit resulting from selection for low birth weight as opposed to selection for high calving ease was investigated. The net profit for each animal, from various selection scenarios, was calculated using the All-purpose selection index used by ASA. To estimate the API value in dollars, EPD of trait in the API were measured in their actual units (i.e., growth traits in "kg" and calving ease liabilities of calving ease were converted to probabilities of an unassisted calving). For each selection scenario, estimates of net profit were regressed on birth year to estimate its rate of change per year. Differences between various regression lines (i.e., differences between intercepts and differences between slopes) were also tested.

4.3. Results and Discussion

4.3.1. (Co)variance components and genetic parameters estimation for calving ease and growth-related traits in American Simmental beef cattle:

The estimation of (co)variance components is an essential step in genetic evaluation. Known (co)variance components are needed to predict the genetic (i.e., prediction of EBV or EPD) makeup of animals for these traits.

Sire and maternal grandsire (co)variance components were estimated using sire and sire-maternal grandsire models with a Gibbs sampling algorithm. Estimated posterior mean and posterior standard deviations of sire and maternal grandsire variance components for calving ease, birth weight, 205-*d* weight, and 160-*d* postweaning gain using the American Simmental Association beef cattle database are presented in Table 4.5. Fitting a sire-maternal grandsire model to predict EPD for studied traits will produce EPD for sires only. However, estimation of direct and maternal EPD for all animals in the pedigree requires fitting a direct-maternal animal model which requires the direct and maternal (co)variance components to be known; therefore, sire and maternal grandsire (co)variance components were transformed to their respective direct and maternal (co)variance components using Eq. (4.7). Posterior mean and posterior standard deviation of direct and maternal (co)variance components for calving ease, birth weight, 205-*d* weight, 160-*d* postweaning gain, and 365-*d* weight in American Simmental beef cattle are shown in Table 4.6. It is worth noting that (co)variance components of 365-*d* weight were calculated the summation of (co)variance components of 205-*d* weight and 160-*d* gain. Estimates of direct and maternal (co)variance components were used to estimate direct and maternal genetic effects of studied traits (i.e., EPD) from which genetic trends were calculated. Furthermore, posterior

means and their respective standard deviations of direct genetic, maternal genetic, and residual parameters (Table 4.7) were calculated from their corresponding direct and maternal (co)variance components.

The heritabilities, genetic and residual correlations for calving ease and birth weight, 205-*d* weight, 160-*d* postweaning gain, and 365-*d* weight in the American Simmental beef cattle are presented in Table 4.7.

Direct heritability: The estimated posterior mean of calving ease direct heritability, on the underlying scale, (0.23) was within the limits of estimates of previous reports, which ranges from 0.18 to 0.26 as reported by Dong et al. (1991), Eriksson et al. (2004), and Matilainen et al. (2009). The relatively high birth weight direct heritability of 0.52 was in the upper limit of the breed heritability estimates previously reported (0.28 to 0.52; Burfening et al., 1978b; Trus and Wilton, 1988; Garrick et al., 1989; Redman and Brinks, 1991; Woodward et al., 1992). A moderate posterior mean for 205-*d* WT direct heritability, 0.28, was similar to the Simmental estimates reported by Burfening et al. (1978b) and Lee and Pollak (1997). For 160-*d* postweaning gain, direct heritability was estimated to be 0.21 which falls within the previous reports range of 0.20 to 0.26 (Quaas et al., 1985; Wright, 1987; Garrick et al., 1989). Direct heritability of 365-*d* WT was 0.33 which is a similar estimate to what reported in a study of Simmental by Benyshek and Little (1982) and within the range (0.27 to 0.37) of the Simmental yearling weight heritability estimates reported in the literature (Elzo et al., 1987; Wright, 1987; Mrode and Thompson, 1990; Swalve, 1993). Generally, estimates of direct heritability obtained in the current study were in agreement with reported heritabilities of the Simmental breed in the literature.

Table 4.5: Posterior mean and posterior standard deviation (in parentheses) of sire and maternal grandsire variance components¹ for calving ease and growth-related traits in American Simmental beef cattle.

Trait ²	CEs	BWTs	205-d WT _s	160-d gains	CE _{mgs}	BWT _{mgs}	205-d WT _{mgs}
CEs	0.069 (0.01)	1.883 (0.02)	0.992 (0.13)	1.731 (0.25)			
BWTs	0.320 (0.02)	3.303 (0.13)	26.63 (0.46)	11.74 (0.68)			
205-d WT _s	0.721 (0.11)	9.425 (0.67)	73.97 (5.29)	-18.52 (3.7)			
160-d gains	0.230 (0.21)	4.968 (0.92)	32.42 (5.03)	55.01 (6.86)			
CE _{mgs}	0.030 (0.01)				0.058 (0.01)		
BWT _{mgs}		1.524 (0.05)				1.007 (0.06)	
205-d WT _{mgs}			35.30 (2.73)				31.35 (2.78)
HYS ³	0.075	3.8	304	360			

¹sire and maternal grandsire variances are on the diagonal (bold faced); sire and sire-maternal grandsire covariances are below the diagonal; residual covariances are above the diagonal

²CEs = sire (co)variance component for calving ease; BWTs = sire (co)variance component for birth weight; 205-d WT_s = sire (co)variance component for 205-d weight; 160-d gains = sire (co)variance component for 160-d postweaning gain; CE_{mgs} = maternal grandsire (co)variance component for calving ease; BWT_{mgs} = maternal grandsire (co)variance component for birth weight; 205-d WT_{mgs} = maternal grandsire (co)variance component for 205-d weight.

³HYS = variance of herd-year-season

Table 4.6: Posterior mean and posterior standard deviation (in parentheses) of direct and maternal (co)variance components¹ for calving ease and growth-related traits in American Simmental beef cattle.

Trait ²	<i>CEd</i>	<i>BWTd</i>	205-d <i>WTd</i>	160-d <i>gaind</i>	365-d <i>WTd</i>	<i>CEm</i>	<i>BWTm</i>	205-d <i>WTm</i>
<i>CEd</i>	0.397 (.03)	1.31 (0.03)	0.81 (0.10)	1.50 (0.21)	2.31 (0.24)			
<i>BWTd</i>	1.53 (0.10)	13.2 (0.54)	15 (0.53)	6.96 (0.47)	22 (0.78)			
205-d <i>WTd</i>	3.45 (0.57)	37.7 (2.68)	296 (21.1)	-12.9 (2.66)	395.5 (14)			
160-d <i>gaind</i>	1.10 (1.01)	19.87 (3.7)	129.7 (20)	220 (27.44)	441 (21.38)			
365-d <i>WTd</i>	4.55 (1.14)	57.5 (4.64)	425.6 (30)	349.7 (34)	775.3 (54)			
<i>CEm</i>	-0.022(.02)					0.255 (.01)		
<i>BWTm</i>		-0.51(0.34)					1.23 (0.34)	
205-d <i>WTm</i>			-6.76 (5.27)					58.2 (16.3)
HYS ³	0.1072	3.8	304	360				

¹Direct and maternal genetic variances are on the diagonal (bold faced); direct genetic and direct-maternal genetic covariances are below the diagonal; residual covariances are above the diagonal

²*CEd* = direct calving ease; *BWTd* = direct birth weight; 205-d *WTd* = direct 205-d weight; 160-d *gaind* = direct 160-d postweaning gain; 365-d *WTd* = direct 365-d weight; *CEm* = maternal calving ease; *BWTm* = maternal birth weight; 205-d *WTm* = maternal 205-d weight.

³HYS = variance of herd-year-season

Table 4.7: Posterior mean and posterior standard deviation (in parentheses) of direct, maternal, and residual parameters¹ for calving ease and growth-related traits in American Simmental beef cattle.

Trait ²	<i>CEd</i>	<i>BWTd</i>	205-d <i>WTd</i>	160-d gain	365-d WT	<i>CEm</i>	<i>BWTm</i>	205-d <i>WTm</i>
<i>CEd</i>	0.23 (0.01)	0.48 (0.01)	0.04 (0.01)	0.07 (0.01)	0.08 (0.01)			
<i>BWTd</i>	0.67 (0.02)	0.52 (0.02)	0.27 (0.01)	0.12 (0.01)	0.28 (0.01)			
205-d <i>WTd</i>	0.32 (0.05)	0.60 (0.03)	0.28 (0.02)	-0.03(0.01)	0.67 (0.01)			
160-d gain	0.12 (0.11)	0.37 (0.06)	0.51 (0.08)	0.21 (0.02)	0.71 (0.01)			
365-d WT	0.26 (0.06)	0.57 (0.04)	0.89 (0.02)	0.84 (0.03)	0.33 (0.02)			
<i>CEm</i>	-0.064(0.03)					0.14 (0.02)		
<i>BWTm</i>		-0.12 (0.07)					0.049 (0.01)	
205-d <i>WTm</i>			-0.04 (0.01)					0.055 (0.01)

¹Direct and maternal heritability estimates are on the diagonal (bold faced); direct genetic and direct-maternal genetic correlation estimates are below the diagonal; residual correlation estimates are above the diagonal

²*CEd* = direct calving ease; *BWTd* = direct birth weight; 205-d *WTd* = direct 205-d weight; 160-d gain_d = direct 160-d postweaning gain; 365-d *WTd* = direct 365-d weight *CEm* = maternal calving ease; *BWTm* = maternal birth weight; 205-d *WTm* = maternal 205-d weight.

³HYS = variance of herd-year-season

Maternal heritability: Calving ease, birth and 205-*d* weights have a maternal component influencing expression of the trait. The posterior mean of calving ease maternal heritability was 0.14 (Table 4.7). Reported maternal heritability estimates using the threshold model approach ranged from 0.048 to 0.19 in previous reports (Dong et al., 1991; Varona et al., 1999a; Wiggans et al., 2003; Gevrekci et al., 2011). For birth weight, our estimate of maternal heritability was 0.05. Similar estimates from studies of Simmental were reported (Quaas et al., 1985; Wright, 1987; Jamrozik and Miller, 2014) and ranged from 0.05 to 0.057. The estimated posterior mean of 205-*d* weight maternal heritability was, 0.055, in the lower limit of reported weaning weight maternal heritability (0.05 to 0.2) for the Simmental breed (Quaas et al., 1985; Wright, 1987; Wright et al., 1987; Boldman et al., 1991; Marques et al., 2000).

Direct-Maternal genetic correlation: Direct and maternal genetic effects within CE, BWT, and 205-*d* WT had weak negative correlations (Table 4.7). For calving ease, the estimated direct-maternal genetic correlation was, -0.064, within the range (-0.05 to -0.16) of the breed reported estimates on the underlying scale (Dong et al., 1991; Jamrozik and Miller, 2014). Posterior mean of birth weight direct-maternal genetic correlation was, -0.12, within the wide range (-0.04 to -0.43) of the Simmental reported estimates (Quaas et al., 1985; Swalve, 1993; Marques et al., 2000; Eriksson et al., 2002). A weak negative direct-maternal genetic correlation was obtained (-0.04) for the Simmental 205-*d* weight. However, the estimate from the current study was similar to the correlation reported by Quaas et al. (1985) for the American Simmental beef cattle breed. Results from several studies of Simmental cattle have shown that direct-maternal genetic correlation for weaning weight has widely ranged between -0.01 and -0.32 (Garrick et al., 1989; Boldman et al., 1991; Lee et al., 1997; Doderhoff et al., 1999).

Direct genetic correlation: Since the scoring system of calving ease in the current study is actually a measure of calving difficulty rather than ease of calving, by definition, the positive correlations between calving ease and growth traits presented in Table 4.7 are in fact negative. From Table 4.7, calving ease had a strong negative genetic correlation (-0.67) with birth weight; nonetheless, direct correlations with subsequent growth traits have ranged between weak (-0.12 with 160-d gain) and moderate (-0.32 and -0.26 with 205-d WT and 365-d WT, respectively) relationships. The estimated correlation between calving ease and birth weight was in agreement with the findings of Burfening et al. (1978b) and Burfening et al. (1981) in their studies of Simmental cattle where they reported estimates of -0.33 and -0.76, respectively. However, calving ease direct correlation (-0.32) with 205-d WT was stronger than that reported by Burfening et al. (1978b; -0.08). Conversely, estimated calving ease direct correlations with 160-d gain and 365-d WT, in the present study, were less than those estimated by Koots et al. (1994b) and Roughsedge et al. (2005), respectively.

Birth weight had strong positive direct genetic correlations of 0.60 and 0.57 with 205-d WT and 365-dWT, respectively. However, with 160-d gain, the genetic correlation was moderate (0.37). Given those moderate positive correlations between birth weight and subsequent growth traits and the strong negative genetic correlation with calving ease, indicates the antagonistic genetic relationship between calving ease and both weaning and yearling weights, which might have consequences for selection for low birth weight. Genetic correlation estimates of BWT with 160-d gain and 365-d WT, from the current study, were in agreement with the breed estimates from the literature (Benyshek and Little, 1982; Quaas et al., 1985; Elzo et al., 1987; Wright, 1987; Garrick et al., 1989; Swalve, 1993). Nonetheless, the direct genetic correlation between BWT and 205-d WT estimated here (0.60) was slightly higher than reported estimates (ranged

from 0.29 to 0.58) for the Simmental breed (Burfening et al., 1978b; Benyshek and Little, 1982; Quaas et al., 1985; Elzo et al., 1987; Garrick et al., 1989; Woodward et al., 1992; Swalve, 1993).

The 205-*d* WT direct genetic correlation with 160-*d* gain was a strong positive correlation (0.51). Moreover, the genetic correlation with the 365-*d* WT was even higher with a posterior mean of 0.89. This strong genetic correlation is probably occurred because 205-*d* WT is a component trait of 365-*d* WT. Several studies of American Simmental cattle described similar estimates of the direct genetic correlation between weaning weight and postweaning gain (Quaas et al., 1985; Wright, 1987; Garrick et al., 1989). However, the direct genetic correlation between 205-*d* WT and 365-*d* WT was slightly higher than the estimates from other studies in this breed (Benyshek and Little, 1982; Elzo et al., 1987; Wright, 1987) which have ranged from 0.84 to 0.87.

Table 4.7 showed that 160-*d* gain had a strong positive direct genetic correlation of 0.84 with 365-*d* WT. This was expected since the 365-*d* WT is a function (summation) of both 205-*d* WT and 160-*d* gain. The estimated correlation from the present study was within the range of estimates obtained by Wright (1987) and Koots et al. (1994b) who reported correlations of 0.91 and 0.81, respectively.

Residual correlation: Calving ease, on the underlying scale, had a strong residual correlation with birth weight (-0.48); however, the residual correlations of -0.04, -0.07, and -0.08 with 205-*d* WT, 160-*d* gain, and, 365-*d* WT, respectively, were markedly weak. The estimated residual correlation between CE and BWT was in agreement with the reported estimates in the literature which ranged from -0.28 to -0.50 (Burfening et al., 1978a; Koots et al., 1994b; Varona et al.,

1999a). Calving ease residual correlations with 205-*d* WT and 160-*d* gain were higher than those obtained by Burfening et al. (1978a) and Bennett and Gregory (2001).

Birth weight had moderate residual correlations, 0.27 and 0.28, with 205-*d* WT and 365-*d* WT, respectively. Conversely, the residual correlation with 160-*d* gain was weak (0.12). The estimated residual correlation between birth weight and weaning weight (205-*d* WT) was within the estimates range (0.18 to 0.51) of the breed (Burfening et al., 1978a; Benyshek and Little, 1982; Wright, 1987; Garrick et al., 1989; Woodward et al., 1992). Nonetheless, the residual correlation with 160-*d* gain (0.12) was slightly higher than the breed estimates (0.07 to 0.10) reported by Benyshek and Little (1982), Wright (1987), and Garrick et al. (1989). The posterior mean of the residual correlation (0.28) between BWT and 365-*d* WT was less than the correlations obtained by Benyshek and Little (1982) and Wright (1987), in their studies on the American Simmental, who reported estimates of 0.42 and 0.31, respectively.

The posterior means of 205-*d* weight residual correlations with 160-*d* gain and 365-*d* weight were -0.03 and 0.67, respectively, (Table 4.7). The 205-*d* weight residual correlation with 160-*d* gain was less than the American Simmental estimates (-0.10 to -0.18) reported in previous reports (Benyshek and Little, 1982; Wright, 1987; Garrick et al., 1989). Estimated residual correlation between 205-*d* weight and 365-*d* weight was in agreement with the breed estimates reported by Benyshek and Little (1982) and Wright (1987).

The 160-*d* postweaning gain showed a strong positive residual correlation of 0.71 with 365-*d* weight (Table 4.7). This correlation was slightly higher than the American Simmental estimates obtained by Benyshek and Little (1982) and Wright (1987) who reported residual correlations of 0.57 and 0.68, respectively.

Generally, results of the direct genetic, maternal genetic, and residual parameters for calving ease, birth weight, weaning weight, postweaning gain, and yearling weight showed that: 1) Birth weight has the highest heritability among all traits while other traits showed moderate heritability. 2) The high negative genetic correlation between calving ease and birth weight, high heritability of birth weight, and its linearity justify the importance of incorporating birth weight in the genetic evaluation of calving ease. 3) High positive genetic correlations between birth weight and subsequent growth traits expose the genetic antagonistic relationship between calving ease and postnatal growth traits.

4.3.2. Genetic trends for calving ease, birth weight, 205-*d* weight, 160-*d* gain, and 365-*d* weight in American Simmental first-calf heifer and selection scenarios for high calving ease versus low birth weight

*Genetic trends for calving ease, birth weight, 205-*d* weight, 160-*d* gain, and 365-*d* weight in American Simmental first-calf heifer:* The average EPD, expressed in units of genetic standard deviations, of 277,897 calves born to first-calf Simmental heifers from 1969 (≤ 1969) to 2010 were used to assess additive genetic trends for calving ease direct (CE d), birth weight direct (BWT d), 205-*d* weight direct (205-*d* WT d), 160-*d* postweaning gain direct (160-*d* gain), and 365-*d* weight direct (365-*d* WT). Maternal genetic trends were also obtained for calving ease (CE m), birth weight (BWT m), and 205-*d* weight (205-*d* WT m). Genetic trends for calving ease and growth traits in the first-calf Simmental heifer are depicted in Figure 4.1. Further, the standardized EPD of studied traits were regressed on the year of birth to estimate the annual genetic change (SD/yr) (Table 4.8). Intercepts and slopes for all traits (Table 4.8) were

significantly different ($P < 0.001$) from zero. In subsequent analyses, different selection scenarios were derived from this population as this was considered the control scenario.

Trends of direct effects (SD/yr) for growth-related traits increased from 1969 to 2010, whereas maternal effects showed decreased trends and remained relatively flat throughout the period of study (Fig. 4.1). In contrast, the direct effects for calving ease showed a decreased trend while the maternal effects increased (Fig. 4.1). The standardized calving ease direct EPD showed a negative trend of -0.0032 SD/yr; on the other hand, the maternal EPD were increased with genetic change of 0.0131 SD/yr (Table 4.8). In contrast, Elzo et al. (1987), in a study on Simmental sires (1973-1984), reported a positive genetic trend for first-parity direct calving ease and a negative trend for maternal calving ease. Unlike the current study where we used data from purebred animals (87.5% Simmental), data used in Elzo et al. (1987) consisted of 23 base breeds represented in the base dam population which was upgraded using Simmental sires. Therefore, heterosis effects may have clouded reported results by Elzo et al. (1987).

For growth traits, direct genetic EPD consistently increased with rates of 0.0160 , 0.0255 , 0.0192 , and 0.0447 SD/yr for birth weight, 205-*d* weaning weight, 160-*d* postweaning gain, and 365-*d* yearling weight, respectively. These findings, with respect to weaning and yearling weights, were in agreement with those of Elzo et al. (1985) and Elzo et al. (1987) in their studies of the American Simmental in the 1980s. Furthermore, Sullivan et al. (1999) reported estimates of positive genetic trends for birth weight, weaning weight, and yearling weight in Canadian Simmental cattle. Compared to the direct EPD, the maternal EPD of birth and weaning weights were also increased with lower rates of genetic change (0.0023 and 0.0057 , respectively). Elzo et al. (1985) estimated the maternal genetic trends, expressed as the difference in means between 1983 and 1972, for birth weight (-0.2 kg) and weaning weight (1.1 kg) of the Simmental breed.

The positive trend of the maternal 205-d WT estimated in the current study agreed with the positive trend reported by Elzo et al. (1985); in contrast, the positive genetic change of maternal birth weight, in the present study, contradicts that reported by Elzo et al. (1985). While results from this study for maternal additive effects on birth weight were similar to those reported by Elzo et al. (1987). Results have shown that the direct genetic components of growth-related traits in the American Simmental first-calf heifer increased during the period of 1969-2010 while the maternal genetic component for birth and weaning weights also increased, but only slightly.

Table 4.8: Regression coefficients estimates¹ (in SD units) with SE for calving ease and growth-related traits EPD of first-calf Simmental heifers²

Trait ³	intercept	SE ($\times 10^3$)	Slope	SE ($\times 10^3$)
<i>CEd</i>	-0.0640	0.83	-0.0032	0.04
<i>BWTd</i>	-0.1066	1.19	0.0160	0.06
205-d <i>WTd</i>	-0.1800	1.00	0.0255	0.05
160-d <i>gaind</i>	-0.1404	0.84	0.0192	0.04
365-d <i>WTd</i>	-0.3201	1.73	0.0447	0.09
<i>CEm</i>	0.0118	0.85	0.0131	0.04
<i>BWTm</i>	-0.0450	0.80	0.0023	0.04
205-d <i>WTm</i>	-0.1513	0.70	0.0057	0.04

¹EPD were regressed on birth year; all regression coefficients were significantly different from zero ($P < 0.001$)

²first-calf Simmental heifers is considered the control selection scenario

³*CEd* = direct calving ease; *BWTd* = direct birth weight; 205-d *WTd* = direct 205-d weight; 160-d *gaind* = direct 160-d postweaning gain; 365-d *WTd* = direct 365-d weight; *CEm* = maternal calving ease; *BWTm* = maternal birth weight; 205-d *WTm* = maternal 205-d weight.

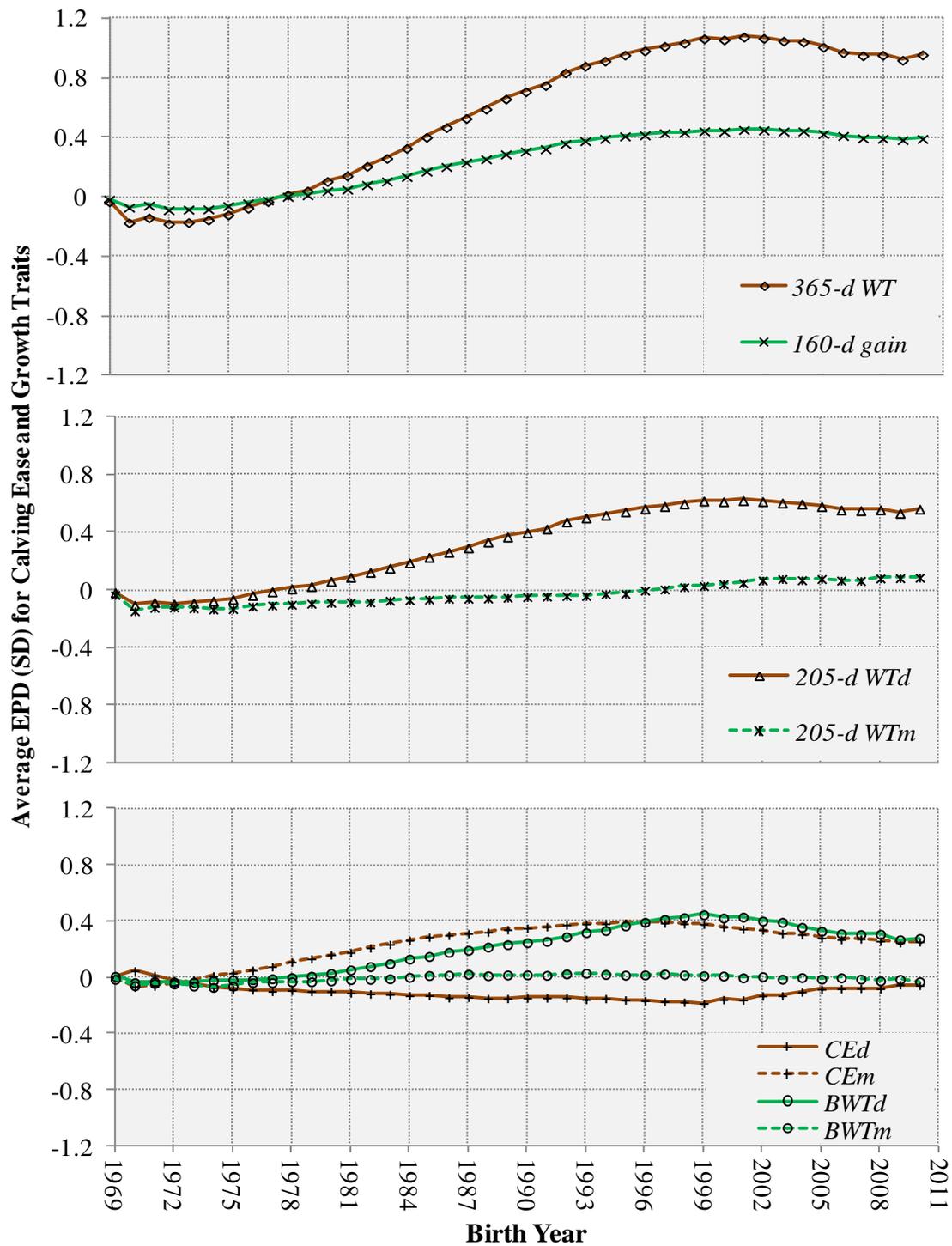


Figure 4.1: Genetic trend (1969-2010) of standardized average EPD for direct calving ease (*CEd*), direct birth weight (*BWTd*), direct 205-d weight (*205-d WTd*), direct 160-d postweaning gain (*160-d gain*), 365-d weight (*365-d WT*), maternal calving ease (*CEm*), maternal birth weight (*BWTm*), and maternal 205-d weight (*205-d WTm*) for first-calf Simmental heifers

Selection scenarios for high calving ease versus low birth weight in American Simmental first-calf heifers: Six artificial selection scenarios were derived from the first-calf heifers in the American Simmental population, depicted in Fig. 4.1, (the control scenario). Our goal was to quantify the performance losses resulting from selection for low birth weight instead of selection for calving ease. The scenarios investigated include selection for:

1) High calving ease (**HCE**), 2) low birth weight (**LBWT**), 3) the Selection index of Dickerson et al. (1974), $DSI = YWT - 3.2 BWT$, 4) The all-purpose selection index of the ASA, $API = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT$, and two sub-selection indexes derived from the API: 5) $API_1 = 1.3 CE + 0.20 YWT$, and 6) $API_2 = -1.8 BWT + 0.20 YWT$. Here, *CE*, *BWT*, *WWT*, and *YWT* were calving ease, and birth, weaning, and yearling weights, respectively. The first-calf American Simmental heifers (Fig. 4.1) were used as a selection pool “control scenario” for the six selection scenarios. Starting with animals born in 1970, selection was applied within each birth year. For example, animals born before 1970 ($n = 1517$) were considered a base population (selection pool) for animals born in 1970. Sires with $EBV \geq$ the average (either *EBV* in the single trait selection or the index value in the multiple trait selection) were selected, then the top 75% of dams with progeny within selected sires were selected. This procedure was repeated for each birth year. The selection criteria, in these selection scenarios, were the standardized *EBV* for the respective trait. For direct and maternal calving ease, the estimated underlying liabilities were standardized by their respective genetic standard deviation and centered on the average liability of animals born before 1970. The resulting data for all selection scenarios contained animals born in 1969 “ ≤ 1969 ” to 2004. In all selection scenarios, animals born after 2004 were discarded because of their limited numbers. *EBV* were transformed to *EPD* then expressed as a deviation from their birth year average *EPD* of the control scenario.

Regression coefficients of studied traits standardized EPD, expressed as a deviation from the respective average EPD in the control population, regressed on birth year under the different selection scenarios are presented in Table 4.9. Differences between slopes (genetic trends in SD units) and between intercepts of the direct EPD of each studied trait under all selection scenarios are shown in Table 4.10. Differences between slopes and between intercepts of the maternal EPD of CE, BWT, and 205-d WT under all selection scenarios are shown in Table 4.11.

Table 4.9: Regression coefficients^{1,2} of standardized EPD (expressed as a deviation from their respective average EPD of the control population) for traits of interest regressed on birth year estimated from different selection scenarios in first-calf Simmental heifers.

Trait ³		Selection Scenario ⁴					
		HCE	LBWT	DSI	API	API ₁	API ₂
CEd	<i>b</i> ₀	0.1199	0.0760	0.0616	0.1048	0.0985	0.0789
	<i>b</i> ₁	0.0025	0.0036	0.0038	0.0029	0.0027	0.0035
BWT	<i>b</i> ₀	-0.1063	-0.1135	-0.0725	-0.1178	-0.0682	-0.1111
	<i>b</i> ₁	-0.0049	-0.0068	-0.0071	-0.0059	-0.0047	-0.0066
205-d WTd	<i>b</i> ₀	-0.0612	-0.0790	-0.0081	-0.0621	-0.0130	-0.0601
	<i>b</i> ₁	-0.0020	-0.0032	-0.0033	-0.0027	-0.0018	-0.0032
160-d gain	<i>b</i> ₀	-0.0090	-0.0405	0.0260	-0.0136	0.0352	-0.0206
	<i>b</i> ₁	-0.0021	-0.0025	-0.0026	-0.0024	-0.0019	-0.0025
365-d WT	<i>b</i> ₀	-0.0702	-0.1195	0.0179	-0.0757	0.0222	-0.0807
	<i>b</i> ₁	-0.0041	-0.0057	-0.0058	-0.0051	-0.0037	-0.0057
CEm	<i>b</i> ₀	-0.0192	-0.0483	-0.0006 ^{NS}	-0.0308	0.0067	-0.0395
	<i>b</i> ₁	0.0005	0.0005	-0.0004	0.0004	0.0001 ^{NS}	0.0003
BWTm	<i>b</i> ₀	-0.0022 ^{NS}	-0.0049**	0.0103	-0.0019 ^{NS}	0.0210	-0.0018 ^{NS}
	<i>b</i> ₁	-0.0011	-0.0009	-0.0009	-0.0008	-0.0015	-0.0008
205-d WTm	<i>b</i> ₀	0.0195	-0.0168	0.0237	0.0086	0.0402	-0.0061
	<i>b</i> ₁	-0.0004	0.0010	-0.0002	0.0002*	-0.0011	0.0008

¹ *b*₀ = intercept; *b*₁ = Slope “rate of genetic change” expressed in standard deviation units per year

² NS = estimate is not significantly different ($P > 0.05$) from the control population; * = $P < 0.05$; ** = $P < 0.01$; estimate with no superscript is significantly different ($P > 0.001$) from the control population.

³ CEd = calving ease standardized direct EPD; BWTd = birth weight standardized direct EPD; 205-d WTd = 205-d weight standardized direct EPD; 160-d gain = 160-d postweaning gain standardized direct EPD; 365-d WT = 365-d weight standardized direct EPD; CEm = calving ease standardized maternal EPD; BWTm = birth weight standardized maternal EPD; 205-d WTm = 205-d weight standardized maternal EPD

⁴ HCE = high calving ease selection scenario; LBWT = low birth weight selection scenario; DSI = Dickerson’s selection index; API = All-purpose index; API₁ = 0.2 YWT + 1.3 CE; API₂ = 0.2 YWT – 1.8 BWT

Table 4.10: Difference (X100) between regression coefficients^{1,2} (intercept above the diagonal, slope below the diagonal) of studied traits standardized *direct* EPD regressed on birth year estimated from different selection scenarios in first-calf Simmental heifers.

Trait ³	Selection scenario ⁴	HCE	LBWT	DSI	API	API ₁	API ₂
<i>CEd</i>	HCE		4.39	5.83	1.51	2.14	4.10
	LBWT	-0.11		1.44	-2.88	-2.25	-0.29
	DSI	-0.13	-0.02 ^{NS}		-4.32	-3.69	-1.73
	API	-0.04	0.07	0.09		0.63*	2.59
	API ₁	-0.02 ^{NS}	0.09	0.11	0.02 ^{NS}		1.96
	API ₂	-0.10	0.02 ^{NS}	0.03**	-0.06	-0.08	
<i>BWTd</i>	HCE		0.72 ^{NS}	-3.38	1.15	-3.81	0.48 ^{NS}
	LBWT	0.19		-4.09	0.43 ^{NS}	-4.53	-0.23 ^{NS}
	DSI	0.22	0.03 ^{NS}		4.53	-0.43 ^{NS}	3.86
	API	0.10	-0.09	-0.12		-4.96	-0.67 ^{NS}
	API ₁	-0.02 ^{NS}	-0.20	-0.23	-0.12		4.29
	API ₂	0.17	-0.02 ^{NS}	-0.05**	0.07	0.19	
205-d <i>WTd</i>	HCE		1.78	-5.30	0.09 ^{NS}	-4.82	-0.1 ^{NS}
	LBWT	0.12		-7.08	-1.69	-6.60	-1.89
	DSI	0.13	0.01 ^{NS}		5.40	0.48 ^{NS}	5.19
	API	0.07	-0.05	-0.06		-4.91	-0.20 ^{NS}
	API ₁	-0.02 ^{NS}	-0.14	-0.15	-0.09		4.71
	API ₂	0.12	0.01 ^{NS}	-0.01 ^{NS}	0.05**	0.14	
160-d <i>gaind</i>	HCE		3.15	-3.50	0.46 ^{NS}	-4.42	1.16
	LBWT	0.04**		-6.65	-2.69	-7.57	-1.99
	DSI	0.05	0.01 ^{NS}		3.96	-0.92	4.66
	API	0.03 ^{NS}	-0.01 ^{NS}	-0.02 ^{NS}		-4.88	0.70*
	API ₁	-0.02 ^{NS}	-0.05	-0.06	-0.05		5.58
	API ₂	0.04**	0.01 ^{NS}	-0.01 ^{NS}	0.01 ^{NS}	0.06	
365-d <i>WTd</i>	HCE		4.93	-8.80	0.55 ^{NS}	-9.24	1.05 ^{NS}
	LBWT	0.16		-13.73	-4.38	-14.17	-3.88
	DSI	0.17	0.01 ^{NS}		9.35	-0.43 ^{NS}	9.85
	API	0.10	-0.06 ^{NS}	-0.08**		-9.79	0.50 ^{NS}
	API ₁	-0.04 ^{NS}	-0.20	-0.21	-0.14		10.29
	API ₂	0.16	0.01 ^{NS}	-0.02 ^{NS}	0.06 ^{NS}	0.20	

¹ Differences between slopes = column-row; intercept differences = row-column

²NS = estimate is not significantly different ($P > 0.05$) from the control population; * = $P < 0.05$; ** = $P < 0.01$; no superscription = $P > 0.001$.

³*CEd* = calving ease standardized direct EPD; *BWTd* = birth weight standardized direct EPD; 205-d *WTd* = 205-d weight standardized direct EPD; 160-d *gaind* = 160-d postweaning gain direct EPD; 365-d *WTd* = 365-d weight standardized direct EPD

⁴HCE = high calving ease selection scenario; LBWT = low birth weight selection scenario; DSI = Dickerson's index; API = All-purpose index; API₁ = 0.2YWT + 1.3CE; API₂ = 0.2YWT - 1.8BWT

Table 4.11: Difference (X100) between regression coefficients^{1,2} (intercept above the diagonal, slope below the diagonal) of studied traits standardized *maternal* EPD regressed on birth year estimated from different selection scenarios in first-calf Simmental heifers.

Trait ³	Selection scenario ⁴	HCE	LBWT	DSI	API	API ₁	API ₂
CE _m	HCE		2.91	-1.85	1.16	-2.58	2.03
	LBWT	0.01 ^{NS}		-4.76	-1.75	-5.49	-0.88
	DSI	0.09	0.09		3.01	-0.73**	3.89
	API	0.01 ^{NS}	0.01 ^{NS}	-0.08		-3.74	0.87
	API ₁	0.04*	0.03*	-0.05	0.03 ^{NS}		4.61
	API ₂	0.02 ^{NS}	0.01 ^{NS}	-0.08	0.01 ^{NS}	-0.02 ^{NS}	
BWT _m	HCE		0.27 ^{NS}	-1.24	-0.03 ^{NS}	-2.32	-0.04 ^{NS}
	LBWT	-0.01 ^{NS}		-1.51	-0.30 ^{NS}	-2.59	-0.31 ^{NS}
	DSI	-0.02 ^{NS}	0.01 ^{NS}		1.21	-1.08	1.20
	API	-0.02 ^{NS}	-0.01 ^{NS}	-0.01 ^{NS}		-2.29	-0.01 ^{NS}
	API ₁	0.05	0.06	0.06	0.07		2.28
	API ₂	-0.03 ^{NS}	-0.01 ^{NS}	-0.01 ^{NS}	-0.01 ^{NS}	-0.08	
205-d WT _m	HCE		3.63	-0.43 ^{NS}	1.09	-2.07	2.55
	LBWT	-0.14		-4.05	-2.54	-5.69	-1.07
	DSI	-0.01 ^{NS}	0.13		1.52	-1.64	2.98
	API	-0.05	0.09	-0.04		-3.16	1.46
	API ₁	0.07	0.21	0.08	0.12		4.62
	API ₂	-0.12	0.02 ^{NS}	-0.10	-0.06	-0.19	

¹ Differences between slopes = column-row; differences between intercepts = row - column

²NS = estimate is not significantly different ($P > 0.05$) from the control population; * = $P < 0.05$; ** = $P < 0.01$; estimate with no superscription is significantly different ($P > 0.001$) from the control population.

³CE_m = calving ease standardized maternal EPD; BWT_m = birth weight standardized maternal EPD; 205-d WT_m = 205-d weight standardized maternal EPD

⁴HCE = high calving ease selection scenario; LBWT = low birth weight selection scenario; DSI = Dickerson's selection index; API = All-purpose index; API₁ = 0.2 YWT + 1.3 CE; API₂ = 0.2 YWT - 1.8 BWT

Selection for high calving ease (HCE) versus selection for low birth weight (LBWT): Genetic trends (1969-2004) of standardized average EPD for CE_d, BW_{Td}, 205-*d* WT_d, 160-*d* gain, 365-*d* WT, CE_m, BW_{Tm}, and 205-*d* WT_m under two selection scenarios: HCE vs. LBWT are presented in Fig. 4.2. In both selection scenarios, the direct effects of calving ease selection showed positive trends compared to the control. Here, the HCE substantially shifted the intercept (0.1199 SD) and the slope (0.0025 SD/yr) of the regression line (Table 4.9). The HCE intercept estimate was 57.7% higher than ($P < 0.001$) that obtained from the LBWT; however the CE slope from the HCE was lower ($P < 0.001$) by 30.5% (Table 4.10).

Conversely, the growth-related direct effects estimated from both selection scenarios decreased (Table 4.9). The estimated direct genetic trends for BWT, 205-*d* WT, and 160-*d* gain, and 365-*d* WT under the HCE were 27.9, 37.5, 16, and 28%, respectively, higher than ($P < 0.001$) those obtained from the LBWT selection scenario (Tables 4.9 and 4.10) but lower than control. For maternal effects, the genetic trends of CE in both selection scenarios were positive ($P < 0.001$) with similar rates of 0.0005 and 0.0005 SD/yr, respectively; however, the intercept from the HCE was, 60%, higher ($P < 0.001$) than that under the LBWT (Tables 4.9 and 4.10). Maternal genetic trends of birth weight from both selection scenarios showed decreasing rates of -0.0011 (HCE) and -0.0009 (LBWT) SD/yr. Maternal trends for 205-*d* WT under HCE decreased with a rate of -0.0004 SD/yr while an increasing rate of 0.0010 SD/yr was estimated under the LBWT scenario (Tables 4.9 and 4.11). Bennett (2008) used selection (1993-1999) to create two different lines, a select and a control line within each of 4 purebred (Charolais, Gelbvieh, Hereford, and Angus) and 3 composite cattle (MARC I, II, and III) populations. Selection for lower 2-yr-old heifer calving difficulty score EBV was applied in the select lines; whereas, animals in the control lines were selected for average birth weight EBV. The author reported

that selection for calving ease decreased the average EBV for calving difficulty and birth weight across populations by -1.06 and -3.5 kg, respectively. These results were in agreement with the current study where selection for high calving ease produced animals with lower birth weight and higher calving ease. However, in contrast to our results, Bennett (2008) reported that both lines did not show differences in maternal additive genetic effects on calving difficulty and birth weight; and direct genetic effects on weaning weight and postweaning gain. This was because of the selection for higher calving ease (select line) was compared to the control line, which was selected to maintain the average of birth weight (Bennett, 2008); whereas, in our study, the two lines (*i.e.*, selection scenarios) were actually two selected lines. Therefore, the differences between scenarios in the present study are expected to be higher in magnitude. To our knowledge, there is no study that applied single trait selection for low birth weight as in this evaluation. In previous reports, selection for low birth weight was always accompanied by selection for high weaning or yearling weight (Doornbos et al., 1994; Gould, 1996; MacNeil, 2003). However, the study closest in design to this was one that selected for below-average birth weight (MacNeil et al., 1998). In that report, there were two selected lines with the first applying independent culling levels for below-average birth weight and high yearling weight (YB) and a second single-trait mass selection for high yearling weight (YW) in the inbred population of Line 1 Hereford cattle. Authors suggested that direct selection for calving ease would be more effective than selection for low birth weight. Results from the current study revealed that selection for high calving ease (HCE) produced heavier animals with lower incidence of dystocia than selection for low birth weight (LBWT). Selection for low birth weight improved calving ease, but caused losses in growth at later ages which was a result of the high genetic correlations between birth weight and subsequent growth traits.

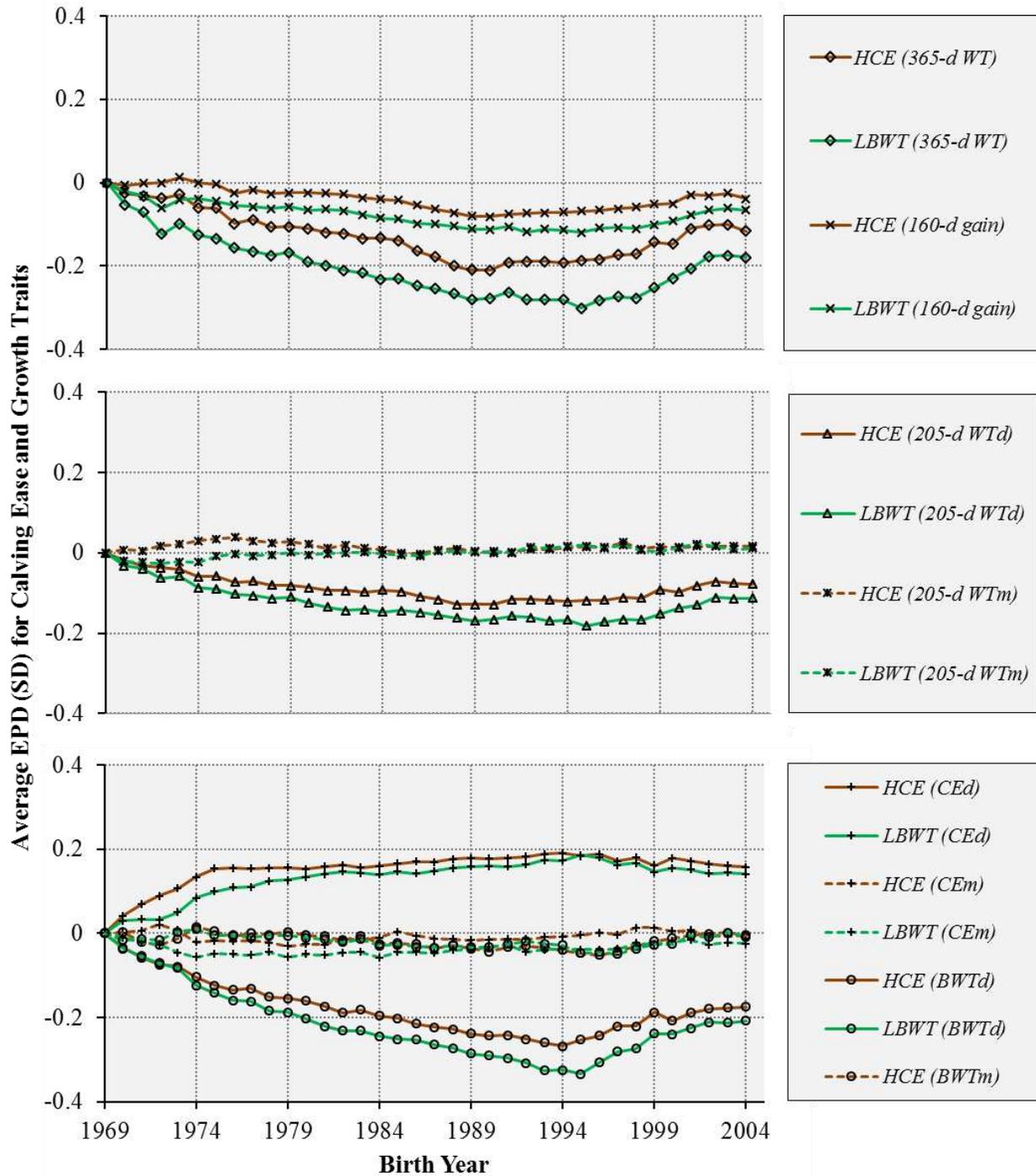


Figure 4.2: Genetic trend (1969-2004) of standardized average EPD for direct calving ease (*CEd*), direct birth weight (*BWTd*), direct 205-d weight (*205-d WTd*), direct 160-d postweaning gain (*160-d gain*), 365-d weight (*365-d WT*), maternal calving ease (*CEm*), maternal birth weight (*BWTm*), and maternal 205-d weight (*205-d WTm*) estimated from two selection scenarios: HCE Versus LBWT

The all-purpose selection index (API) versus Dickerson's selection index (DSI): The direct and maternal genetic trends for calving ease (CE), birth weight (BWT), and weaning weight (205-d WT) and the direct genetic trends for postweaning gain (160-d gain) and yearling weight (365-d WT) under the API and DSI selection scenarios are presented in Fig. 4.3. Even though the slope value for CE direct was higher ($P < 0.001$; Table 4.10) in the DSI, the API shifted the intercept (*i.e.*, gave higher average EPD) by 70% more than the intercept obtained from the DSI (0.1048 vs. 0.0616 SD, respectively; Table 4.9).

For growth traits, both selection scenarios reduced growth compared to the control. Despite the steeper trends (slopes) estimated from the DSI selection scenario, intercepts of the direct genetic trends for BWT, 205-d WT, and 365-d WT estimated from the API were lower than those of the DSI (Table 4.9 and 4.10). However, there were no differences ($P > 0.05$) between slopes for 160-d gain under both selection scenarios (Table 4.10). For maternal genetic trends of growth traits, maternal trends obtained from API and DSI showed decreasing rates (API vs. DSI) of (-0.0008 vs. -0.0009 SD/yr) and (-0.0002 vs. -0.0002 SD/yr) for BWT and 205-d WT, respectively (Table 4.9). Further, there were no differences ($P > 0.05$) between these estimates. The genetic trend of calving ease maternal under the API had an increasing rate; whereas, a negative trend was estimated under the DSI (Table 4.9). The decrease in growth-related genetic trends under both selection scenarios, compared to the control scenario, reflected the emphasis of Simmental breeders on selection for faster growing animals. Similar to the present results, Gould (1996) and MacNeil et al. (1998) reported that the DSI improved calving ease; however, MacNeil et al. (1998) recommended the direct selection for calving ease instead of selection for lower birth weight. The current results showed that, despite the lower growth rates of animals selected using API, the incidence of dystocia was much less than that in the DSI.

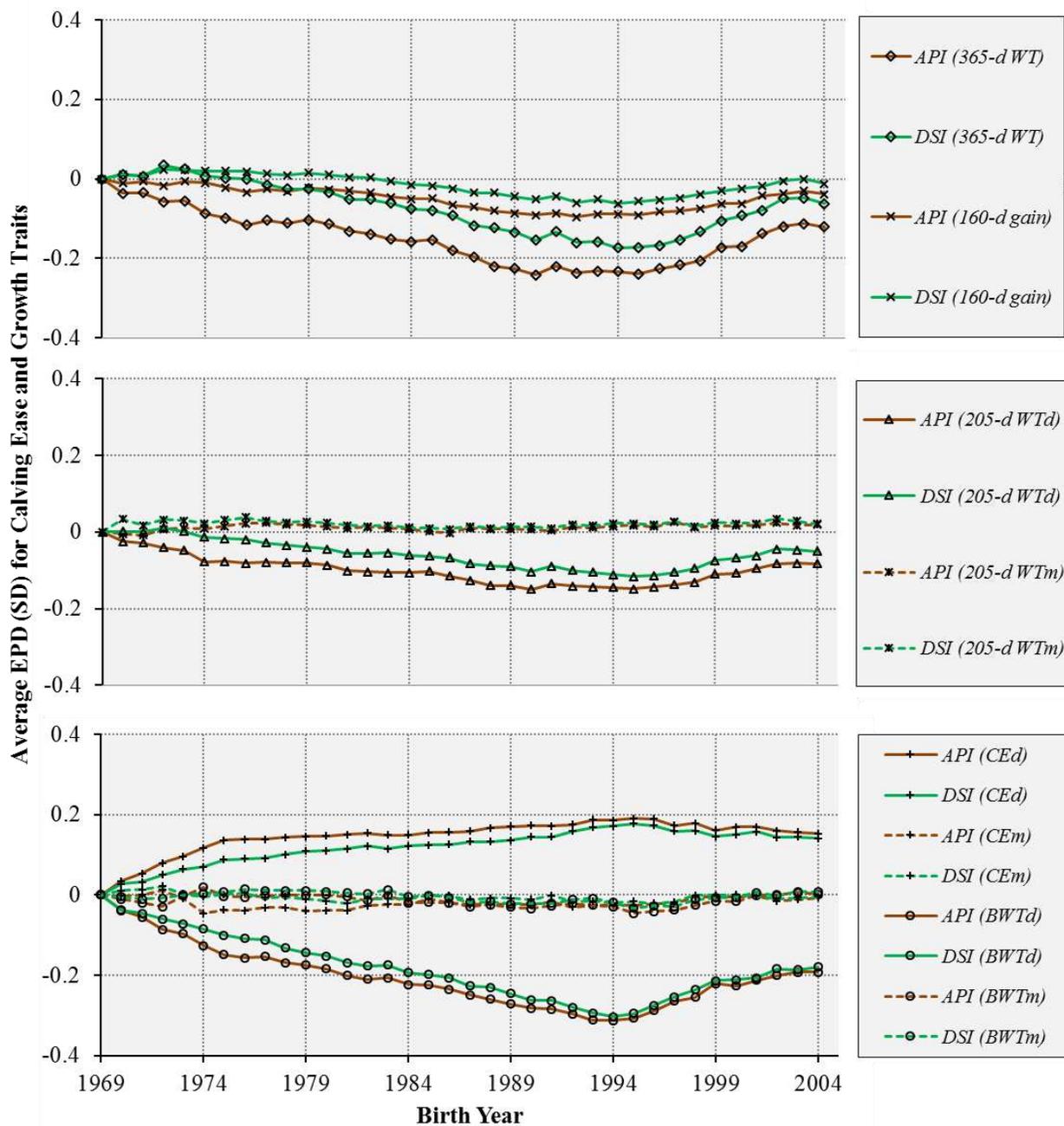


Figure 4.3: Genetic trend (1969-2004) of standardized average EPD for direct calving ease (*CEd*), direct birth weight (*BWTd*), direct 205-d weight (*205-d WTd*), direct 160-d postweaning gain (*160-d gain*), 365-d weight (*365-d WT*), maternal calving ease (*CEm*), maternal birth weight (*BWTm*), and maternal 205-d weight (*205-d WTm*) estimated from two selection scenarios: All purposes Index (API) = $0.2 YWT - 1.8 BWT + 0.1 WWT + 1.3 CE$ Versus Dickerson's selection index (DSI) = $YWT - 3.2 BWT$

The all-purpose sub-selection index (API₁) versus Dickerson's selection index (DSI): The API₁ is a sub-selection index of the API where yearling weight and calving ease are the only traits included in the API₁. Therefore, the comparison between the API₁ and DSI can be thought of as a comparison between a calving ease-based selection index (API₁) versus a birth weight-based selection index (DSI). Figure 4.4 depicts the direct and maternal average EPD of studied traits under both selection scenarios. In spite of the higher slope “rate of change” under the DSI, the regression line ($b_0 + b_1 \cdot \text{birth year}$) of estimated direct calving ease EPD under the API₁ scenario was higher than that obtained under the DSI (Tables 4.9 and 4.10). Here, selection using the API₁, in the early years of the study, greatly increased the average calving ease EPD which resulted in a higher intercept; therefore, the obtained rate of change “slope” was lower than that obtained under the DSI. This is a result of the rapid genetic change under the API₁, in the early years, which is constrained in the subsequent years by the already selected “low CE” animals in the data (See Fig. 4.1).

Direct genetic effects, for all growth traits, obtained under the API₁ were higher than ($P < 0.001$) the estimated direct effects under the DSI (Tables 4.9 and 4.10). Table 4.11 showed that maternal CE under the API₁ did not show a trend ($P > 0.05$) while a negative trend ($P < 0.001$) of -0.0004 SD/yr was estimated for maternal CE under the DSI. For maternal BWT and 205-d WT, negative trends were estimated under both selection scenarios (Tables 4.9 and 4.11). The superiority of API₁ “CE-based selection index” over DSI “BWT-based selection index”, across all traits, supports the speculation of MacNeil et al. (1998) that selection for higher calving ease would be more effective than selection for birth weight. The economic efficiency, in terms of profit, of both selection scenarios will be investigated later in this section.

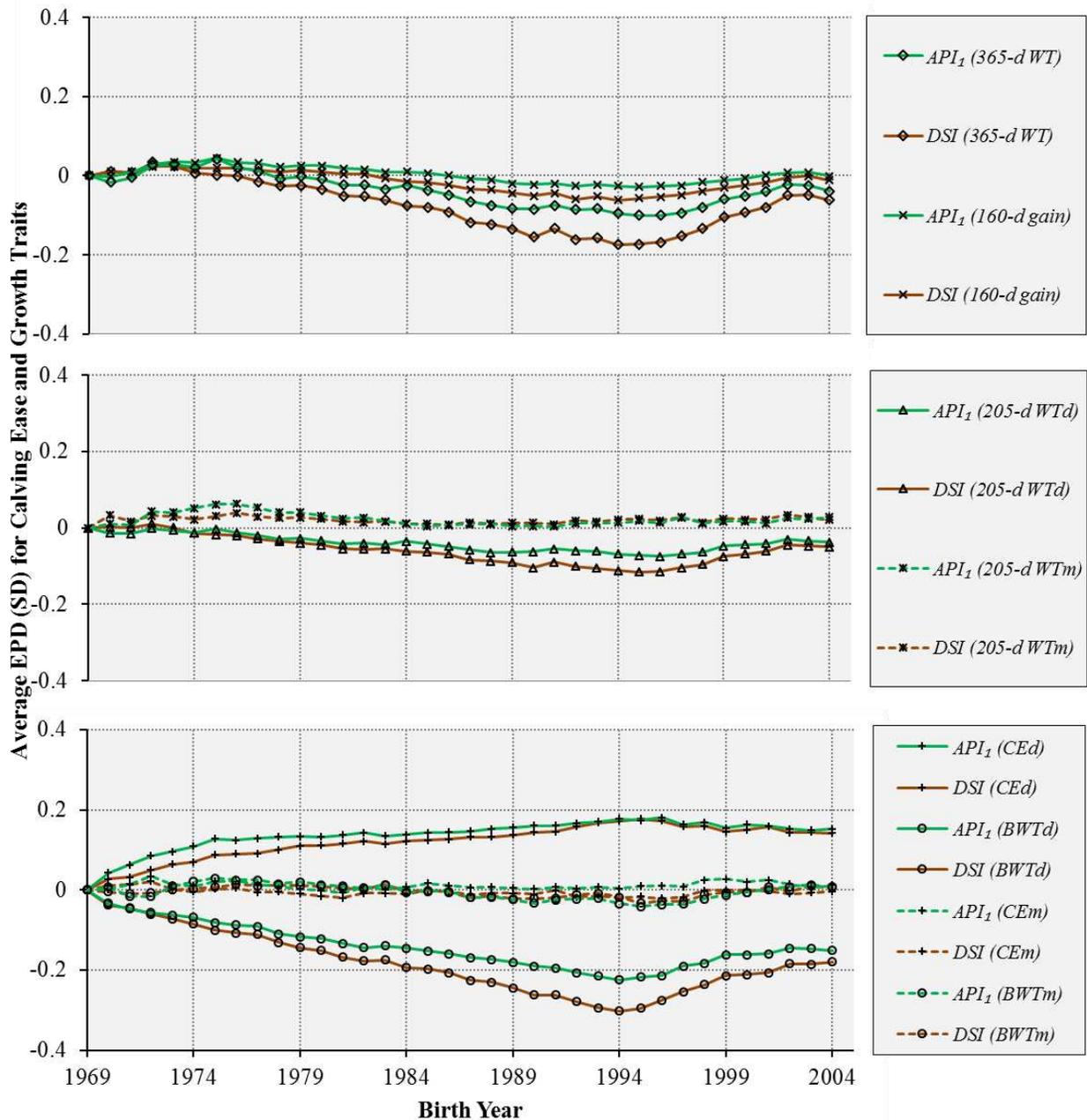


Figure 4.4: Genetic trend (1969-2004) of standardized average EPD for direct calving ease (CEd), direct birth weight (BWTd), direct 205-d weight (205-d WTd), direct 160-d postweaning gain (160-d gain), 365-d weight (365-d WT), maternal calving ease (CEm), maternal birth weight (BWTm), and maternal 205-d weight (205-d WTM) estimated from two selection scenarios: Dickerson's selection index (DSI) = $YWT - 3.2 BWT$ Versus $API_1 = 0.2 YWT + 1.3 CE$

The all-purpose sub-selection index (API₂) versus Dickerson's selection index (DSI): The API₂ is a sub-selection index of the API where yearling weight and birth weight are the only traits included in the API₂. Therefore, the comparison here is between two birth weight-based selection indices. Figure 4.5 shows genetic trends (1969-2004) of standardized average EPD for direct and maternal calving ease, birth weight, 205-*d* weight, and direct 160-*d* postweaning gain and 365-*d* weight under the API₂ and DSI selection scenarios. For direct and maternal trends for calving ease, the API₂ produced higher ($P < 0.001$) direct calving ease EPD and lower ($P < 0.001$) maternal calving ease EPD compared to the DSI (Tables 4.9 and 4.10). However, differences between DSI and API₂ were less than those between DSI and both API and API₁. This was expected since DSI and API₂ were both focus on lower birth weight whereas API and API₁ were selecting for higher calving ease. As compared to DSI, lower direct genetic trends were estimated for all growth-related traits under the API₂. The lower direct trends for 205-*d* WT 160-*d* gain, and 365-*d* WT obtained under the API₂ were essentially a result of the lower intercepts ($P < 0.001$) while slopes were not different ($P > 0.05$) between the two selection scenarios. The low direct trends for growth traits were a result of the higher downward selection for birth weight (the negative weight of BWT in the API₂ was 281% “-9 vs. -3.2” higher than that in the DSI).

Generally, results showed that the API₂ selection scenario, compared to the DSI, produced animals with higher calving ease and lower growth rates. Furthermore, these differences resulted from the higher selection pressure placed on birth weight under the API₂. Even though the differences between DSI and API₂ were significant, the magnitude of these differences was smaller than that of the differences between DSI, API and API₁. This illustrates the difference between the calving ease-based selection and birth weight-based selection indices where the former produced animals with higher calving ease and better growth rates.

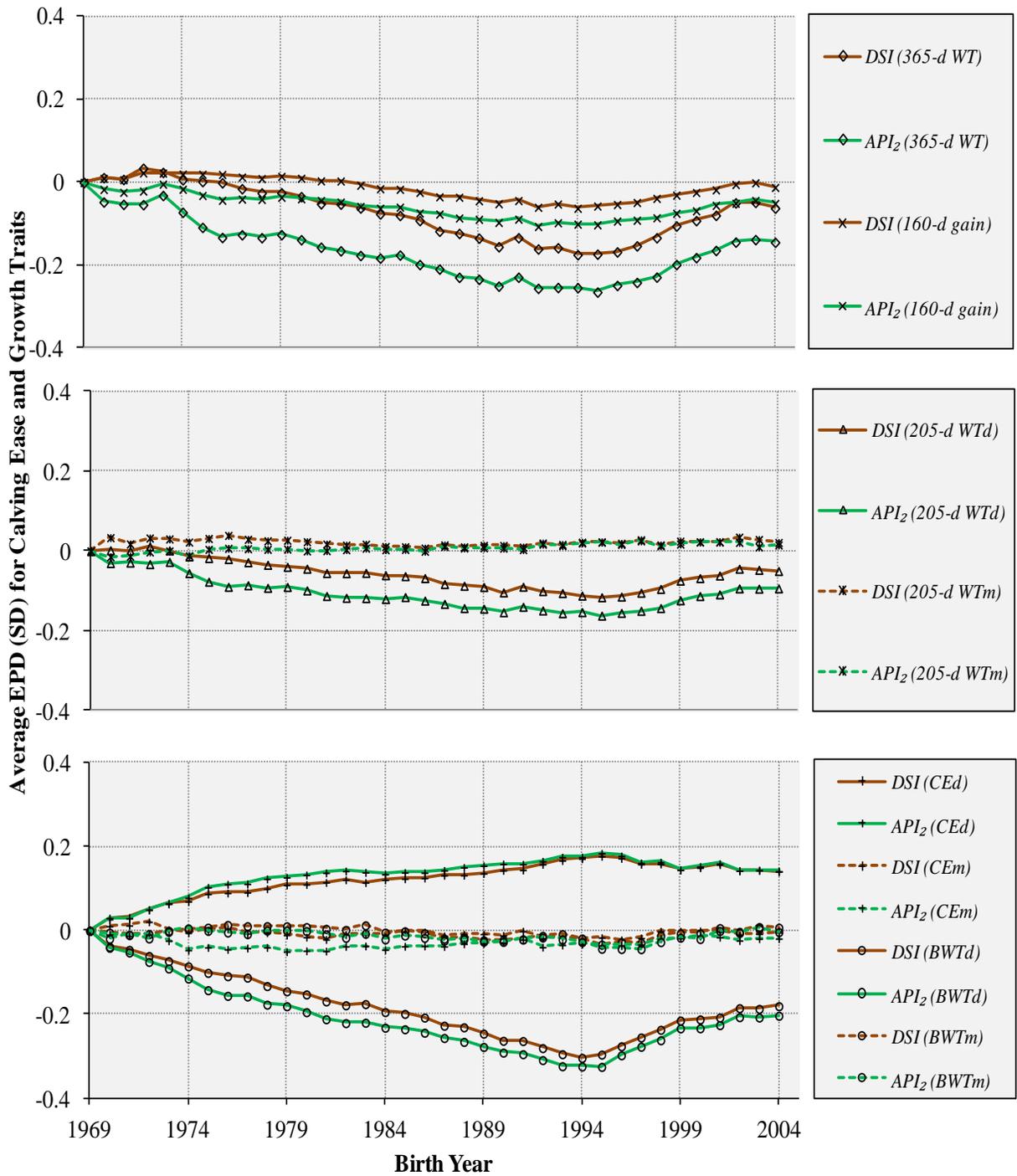


Figure 4.5: Genetic trend (1969-2004) of standardized average EPD for direct calving ease (CEd), direct birth weight ($BWTd$), direct 205-d weight (205-d WTd), direct 160-d postweaning gain (160-d gain), 365-d weight (365-d WT), maternal calving ease (CEm), maternal birth weight ($BWTm$), and maternal 205-d weight (205-d WTm) estimated from two selection scenarios: Dickerson's selection index ($DSI = YWT - 3.2 BWT$) Versus $API_2 = 0.2 YWT - 1.8 BWT$

The all-purpose selection index (*API*) versus all-purpose **sub**-selection index (*API₁*): the *API* selection index ($API = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT$) with its sub-index *API₁* ($API_1 = 1.3 CE + 0.20 YWT$) were compared in terms of the genetic trends of studied traits resulted under both selection scenarios. Figure 4.6 shows genetic trends (1969-2004) of standardized average EPD for direct and maternal calving ease, birth weight, 205-*d* weight, and direct 160-*d* postweaning gain and 365-*d* weight under the *API* and *API₁* selection scenarios. Estimates of intercepts and slopes of studied traits are presented in Table 4.9. As shown in Fig. 4.6 and Table 4.9, both selection scenarios produced similar slopes ($P > 0.05$) for direct CE; however, the intercept of the regression line was higher ($P < 0.001$) under the *API* meaning that *API* produced higher average calving ease EPD. For growth traits direct genetic trends, *API₁* consistently produced higher genetic trends across all growth traits. Rates of direct genetic change for BWT, 205-*d* WT, 160-*d* gain, and 365-*d* WT, under the *API₁*, were 20, 33, 20.8, and 27.4%, respectively, higher ($P < 0.001$) than their respective estimates under *API* (Tables 4.9 and 4.10). Positive average EPD for maternal CE were estimated under *API₁* were positive (i.e., positive intercept) and did not show a trend ($P > 0.05$); however, under the *API*, maternal CE EPD were negative and increased with a rate of 0.0004 SD/yr (Table 4.9). Maternal effects for BWT, under both scenarios, showed decreasing rates with higher EPD estimated under the *API₁* selection scenario. Nonetheless, maternal effects for 205-*d* WT showed a decreasing rate of -0.0011 SD/yr under the *API₁* while increased with a rate of 0.0002 SD/yr under the *API* (Table 4.9). These results showed that both selection scenarios produced animals with high CE EPD with a slight advantage for the *API*; however both scenarios reduced growth rate with higher EPD estimated under the *API₁*. The higher CE EPD under the *API* and the higher growth rates under the *API₁* were a result of incorporating BWT in the former and excluding it from the latter.

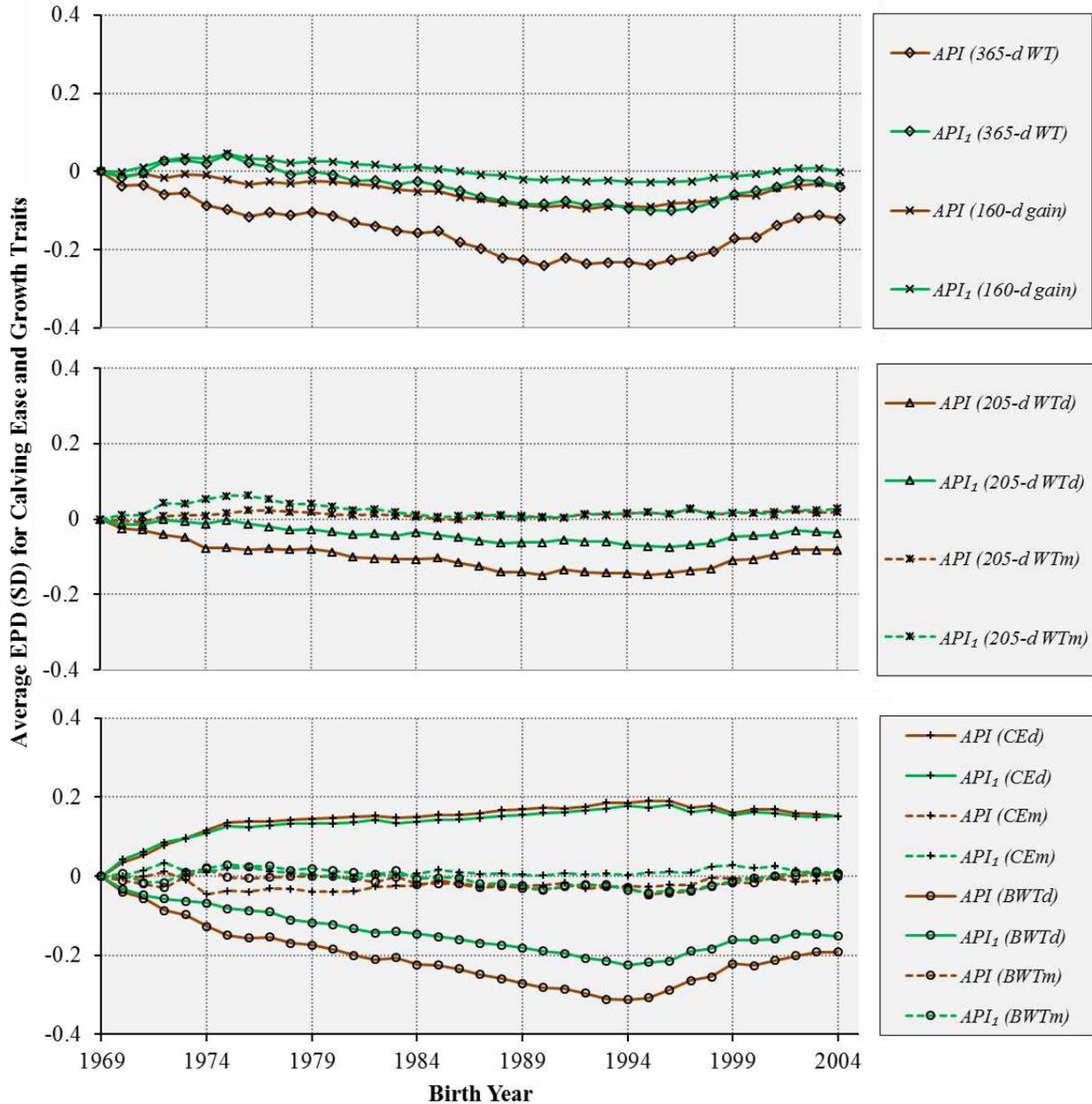


Figure 4.6: Genetic trend (1969-2004) of standardized average EPD for direct calving ease (CEd), direct birth weight (BWTd), direct 205-d weight (205-d WTd), direct 160-d postweaning gain (160-d gain), 365-d weight (365-d WT), maternal calving ease (CEm), maternal birth weight (BWTm), and maternal 205-d weight (205-d WTm) estimated from two selection scenarios: All purposes Index (API) = 0.2 YWT - 1.8 BWT + 0.1 WWT + 1.3 CE Versus API_1 = 0.2 YWT + 1.3 CE

The all-purpose selection index (API) versus all-purpose sub-selection index (API₂): the direct and maternal genetic trends of studied traits under the API selection index ($\mathbf{API} = -1.8 \text{ BWT} + 1.3 \text{ CE} + 0.10 \text{ WWT} + 0.20 \text{ YWT}$) with its BWT-based sub-index API₂ ($\mathbf{API}_2 = -1.8 \text{ BWT} + 0.20 \text{ YWT}$) were compared (Fig. 4.7 and Tables 4.10 and 4.11). Results showed that direct genetic trends for CE, BWT, and 205-d WT in the API were significantly ($P < 0.001$) higher than those under the API₂ (Table 4.10). Despite the similar slopes ($P > 0.05$) for the direct 160-d gain under both scenarios, higher ($P < 0.05$) average EPD (*i.e.*, higher intercept) were obtained from the API scenario. Genetic trends for direct 365-d WT were similar ($P > 0.05$) under both selection scenarios.

For maternal trends, the API maintained the superiority for maternal calving ease and maternal 205-d WT (Table 4.11). Conversely, there were no differences ($P > 0.05$), between the two scenarios, in the genetic trends of maternal birth weight (Table 4.11). These results showed that the absence of calving ease in the API₂ produced cattle with lower calving ease and growth trait EPD while the absence of birth weight in the API₁ (see Fig. 4.6) resulted in higher calving ease and growth trait EPD compared to the API selection scenario.

The all-purpose sub-selection index (API₁) versus all-purpose sub-selection index (API₂): The two sub-selection indices of the API were compared. The API₁ ($\mathbf{API}_1 = 1.3 \text{ CE} + 0.20 \text{ YWT}$) was considered the calving ease-based selection scenario while the API₂ ($\mathbf{API}_2 = -1.8 \text{ BWT} + 0.20 \text{ YWT}$) was considered the birth weight-based selection scenario. Direct and maternal genetic trends of calving ease and growth-related traits under API₁ and API₂ are shown in Fig. 4.8.

Results showed that the direct genetic trend for calving ease and all growth traits obtained under the API₁ were significantly higher than those estimated from the API₂ (Table 4.10). Further, The API₁ showed higher ($P < 0.001$) maternal genetic trends for calving ease and 205-*d* WT. However, birth weight maternal genetic trends were not different ($P > 0.05$) between the two selection scenarios. These findings were similar to those comparing the API and API₂. However, the API₁, compared to both API and API₂, produced animals with the highest average EPD for growth traits. The superiority of the API₁ was a result of the absence of restrictions on birth weight which is eventually reflected on growth rates at subsequent ages.

Results obtained from both calving ease-based and low birth weight-based selection scenarios showed that the various selection scenarios, compared to the control scenario, increased the ease of calving and reduced growth rate, which suggest that selection for heavier animals was practiced in the first-calf Simmental heifers (i.e., control; see Fig 4.1). However, since 1999, a noticeable improvement in calving ease was evident.

Generally, the calving ease-based selection scenarios (HCE, API, and API₁) showed higher genetic trends for calving ease and growth-related traits compared to the birth weight-based selection scenarios (LBWT, DSI, and API₂). The single trait, HCE, selection scenario has substantially improved calving ease and produced heavier animals compared to LBWT selection scenario. The API and API₁ were considered the more effective selection scenarios amongst the various selection indexes. In summary, we accept the hypothesis that direct selection for calving ease, as opposed to selection for low birth weight, improves the ease of calving and growth-related traits reduces the performance losses resulted from the indirect selection using birth weight.

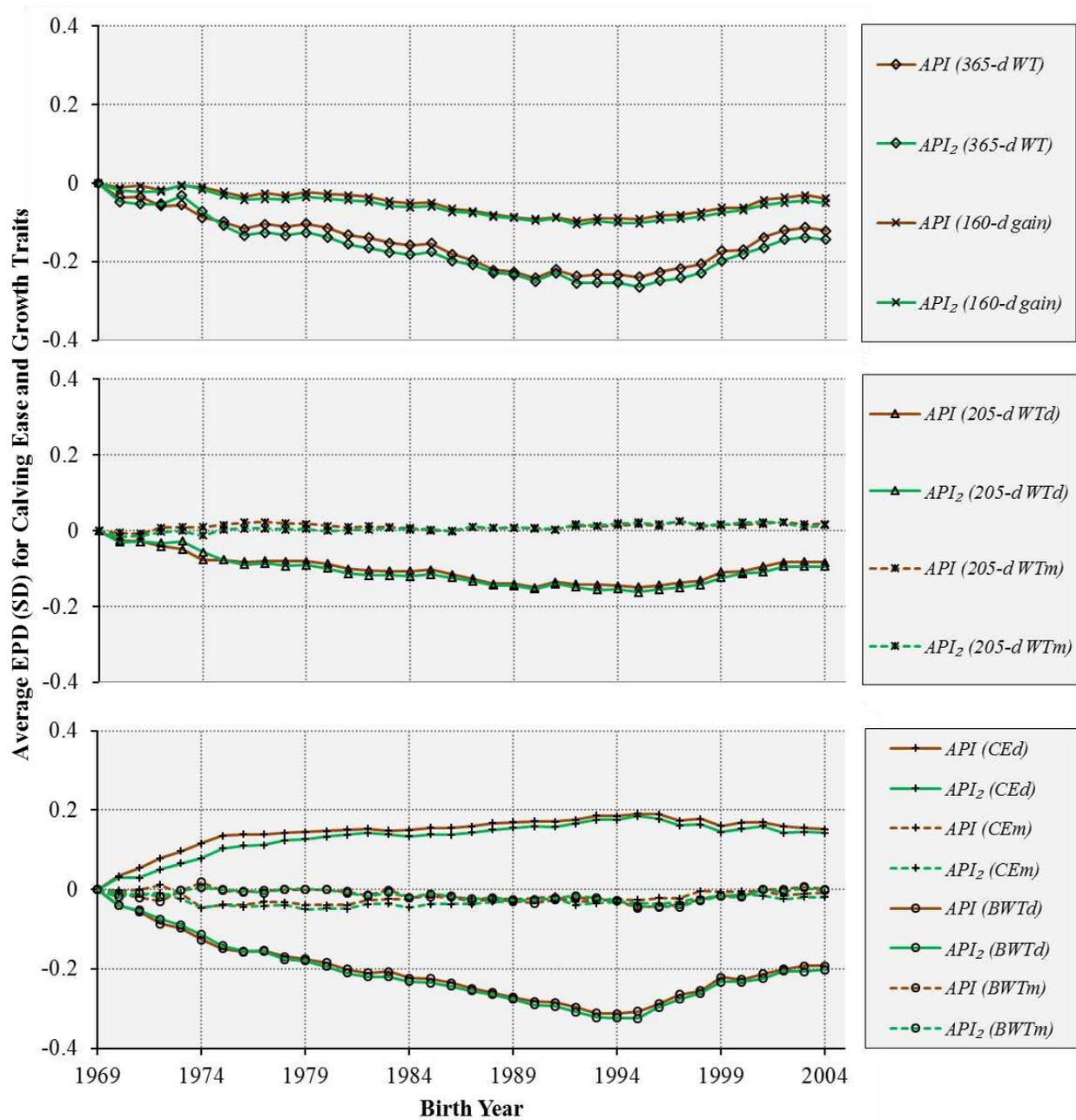


Figure 4.7: Genetic trend (1969-2004) of standardized average EPD for direct calving ease (CEd), direct birth weight ($BWTd$), direct 205-d weight (205-d WTd), direct 160-d postweaning gain (160-d gain), 365-d weight (365-d WT), maternal calving ease (CEm), maternal birth weight ($BWTm$), and maternal 205-d weight (205-d WTm) estimated from two selection scenarios: All purposes Index (API) = $0.2 YWT - 1.8 BWT + 0.1 WWT + 1.3 CE$ Versus $API_2 = 0.2 YWT - 1.8 BWT$

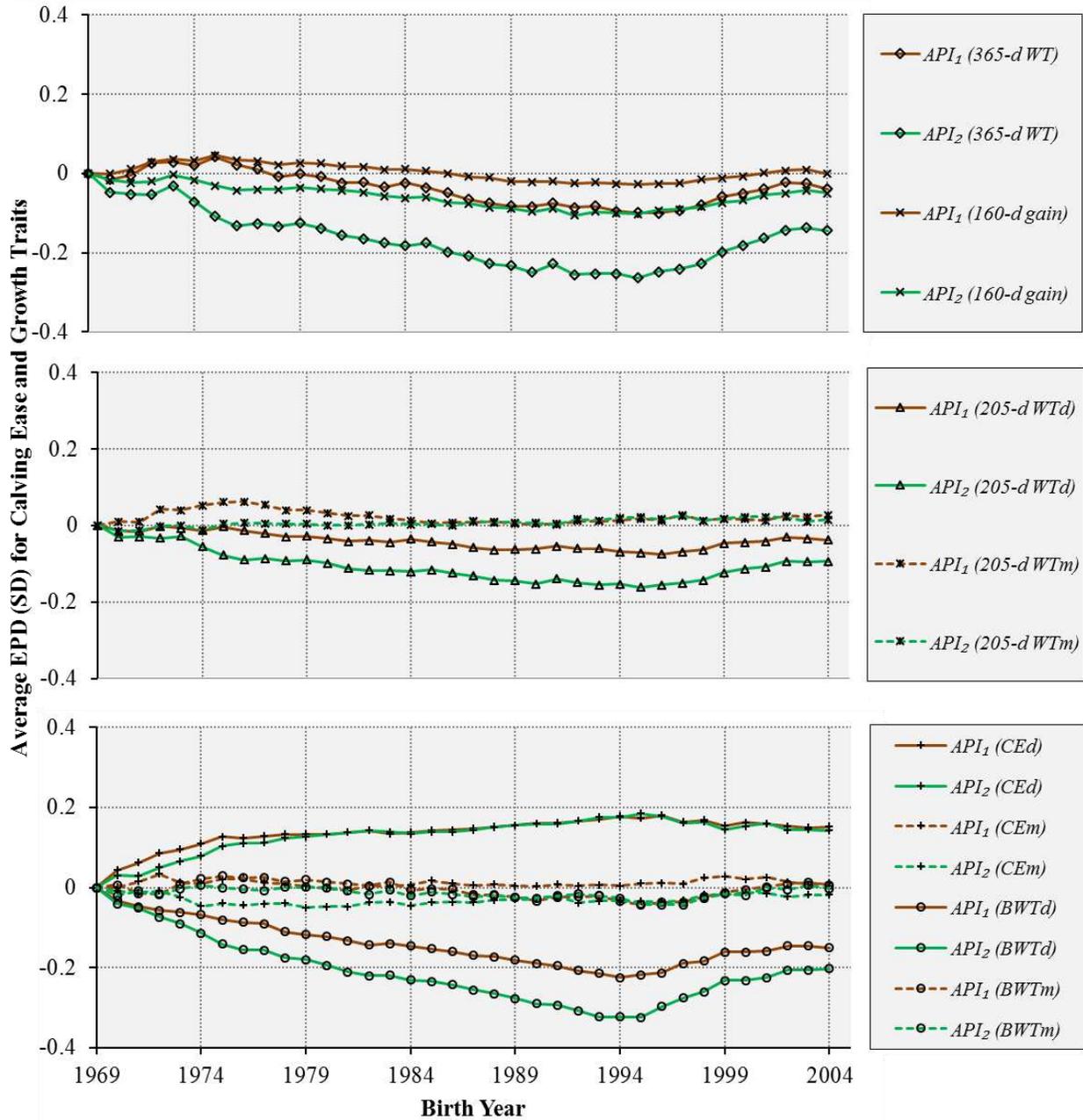


Figure 4.8: Genetic trend (1969-2004) of standardized average EPD for direct calving ease (CEd), direct birth weight (BWTd), direct 205-d weight (205-d WTd), direct 160-d postweaning gain (160-d gain), 365-d weight (365-d WT), maternal calving ease (CEm), maternal birth weight (BWTm), and maternal 205-d weight (205-d WTm) estimated from two selection scenarios: $API_1 = 0.2 \text{ YWT} + 1.3 \text{ CE}$ Versus $API_2 = 0.2 \text{ YWT} - 1.8 \text{ BWT}$

Net Profit for various selection scenarios: The profit for all selection scenarios was estimated using the API selection index ($API = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT$). In order to estimate the profit, the unstandardized EPD of traits were used in the API (*i.e.*, growth traits EPD were expressed in kg and calving ease EPD were expressed in % of unassisted calving with economic weights modified accordingly). The prices of production inputs were assumed to be constant throughout the period of study; consequently, the economic weights in the API were assumed to be constant. Therefore, for each selection scenario, the estimates of net profit were regressed on birth year. Intercepts and slopes (\$/yr) are presented in Table 4.12. The differences between intercepts and between slopes of different selection scenario were tested for significance (Table 4.13). Selection scenarios can be classified into 2 groups: 1) high calving ease selection scenarios which include the single trait selection scenario for high calving ease (HCE), the all-purpose selection index (API), and the all-purpose sub-selection index (API_1), and 2) low birth weight selection scenarios which include the single trait selection scenario for low birth weight (LBWT), Dickerson's selection index (DSI), and the all-purpose sub-selection index (API_2).

For high calving ease selection scenarios (Group 1), the HCE, API, and API_1 selection scenarios showed the highest net profit with intercept estimates of \$13.01, \$11.58, and \$11.09, respectively, and their estimated rates of change were 0.28, 0.33, and 0.30 \$/yr, respectively (Table 4.12). Rates of change in the profit for both API and API_1 selection scenarios (Table 4.13) did not significantly differ ($P > 0.05$). Compared to the LBWT selection scenario, selection for high calving (HCE) ease showed higher annual averages of net profit (Fig. 4.9) where it shifted the intercept by 58% (Table 4.12). The low birth weight selection scenarios (Group 2) can be ordered from the highest to the lowest net profit as follow: API_2 , LBWT, and DSI. Table 4.13 showed that the differences between the slope of LBWT and slopes of API_2 and DSI were not

different ($P > 0.05$). Nonetheless, differences between intercepts of the three selection scenarios were different. Intercepts estimates for API₂, LBWT, and DSI were 8.81, 8.23, and 7.36\$, respectively (Table 4.12).

Table 4.12: Regression coefficients¹ of the net profit² (\$) of various selection scenarios regressed on birth year in first-calf Simmental heifers

Item	Selection scenario ³											
	HCE		LBWT		DSI		API		API ₁		API ₂	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
Intercept, \$	13.010	0.174	8.228	0.163	7.357	0.153	11.580	0.169	11.090	0.165	8.811	0.163
Slope, \$/yr	0.280	0.009	0.407	0.009	0.426	0.008	0.328	0.009	0.303	0.009	0.389	0.009

¹All estimates were significantly different ($P < 0.001$) from the control

²Estimated net profit was estimated using the All-purpose selection index implemented by the ASA

³HCE = high calving ease selection scenario; LBWT = low birth weight selection scenario; DSI = Dickerson's selection index; API = All-purpose index; API₁ = 0.2 YWT + 1.3 CE; API₂ = 0.2 YWT – 1.8 BWT

Table 4.13: Differences between regression coefficients^{1,2} of the net profit (\$) of different selection scenarios regressed on birth year in first-calf Simmental heifers

Selection Scenario ³	HCE		LBWT		DSI		API		API ₁		API ₂	
	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE	Est.	SE
HCE			4.78 (0.21)		5.66 (0.20)		1.43 (0.21)		1.92 (0.21)		4.20 (0.21)	
LBWT	-0.13 (0.01)				0.87 (0.19)		-3.35 (0.20)		-2.86 (0.20)		-0.58* (0.20)	
DSI	-0.15 (0.01)		-0.02 ^{NS} (0.01)				-4.22 (0.20)		-3.73 (0.19)		-1.45 (0.19)	
API	-0.05 (0.01)		0.08 (0.01)		0.10 (0.01)				0.49 ^{NS} (0.21)		2.77 (0.20)	
API ₁	-0.02 ^{NS} (0.01)		0.10 (0.01)		0.12 (0.01)		0.02 ^{NS} (0.01)				2.28 (0.20)	
API ₂	-0.11 (0.01)		0.02 ^{NS} (0.01)		0.04** (0.01)		-0.06 (0.01)		-0.09 (0.01)			

¹ Differences between slopes are below the diagonal; differences between intercepts are above the diagonal

²NS = estimate is not significantly different ($P > 0.05$) from the control population; * = $P < 0.05$; ** = $P < 0.01$; estimate with no superscription is significantly different ($P < 0.001$) from the control population.

³HCE = high calving ease selection scenario; LBWT = low birth weight selection scenario; DSI = Dickerson's selection index; API = All-purpose index; API₁ = 0.2 YWT + 1.3 CE; API₂ = 0.2 YWT – 1.8 BWT

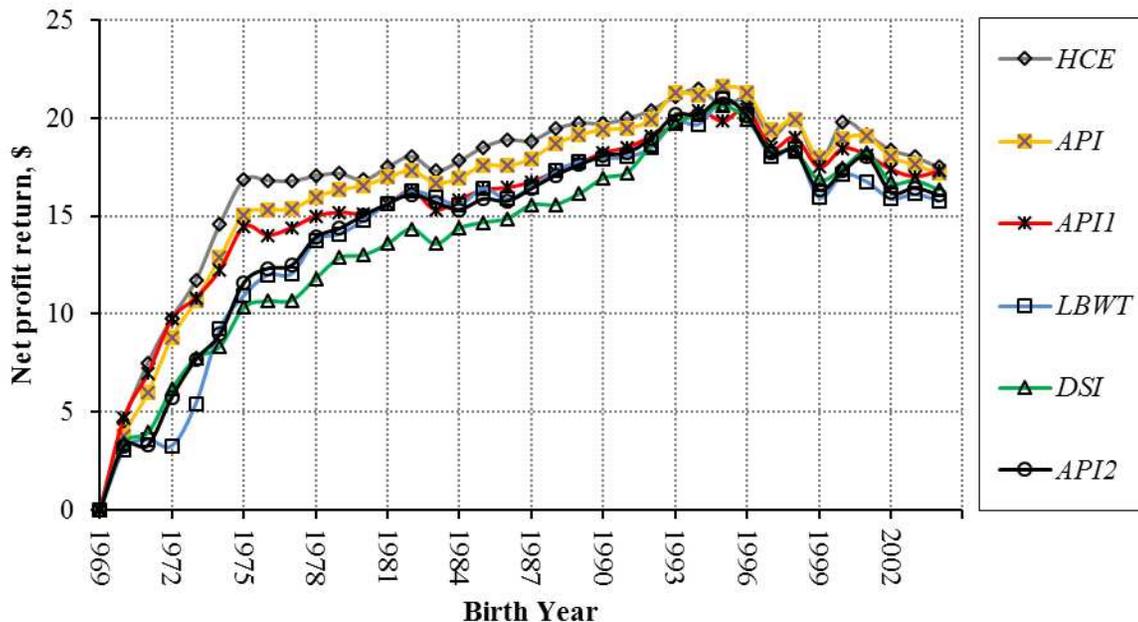


Figure 4.9: Average net profit (1969-2004) of various selection scenarios: HCE = selection for high calving ease; All-purpose selection index: $API = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT$; $API_1 = 1.3 CE + 0.20 YWT$; $API_2 = -1.8 BWT + 0.20 YWT$; LBWT = selection for low birth weight; $DSI = YWT - 3.2 BWT$

Generally, calving ease-based selection scenarios (HCE, API, and API_1) showed higher profit than the birth weight-based selection scenarios (LBWT, DSI, and API_2). Selection for high calving ease (HCE), as opposed to the LBWT selection scenario, shifted the intercept of the net returned by 58%, respectively. The highest change in profit was estimated from both HCE and API selection scenarios while the DSI selection scenario showed the least profit.

4.4. Summary

Costs associated with calving difficulty have a direct impact on the profitability of beef cattle operations. Traditionally, selection for low birth weight was used as means to reduce the incidence of dystocia. Nonetheless, the genetic antagonistic relationships between calving ease

and postnatal growth traits press the question about the appropriateness of using birth weight instead of calving ease as a selection tool. Therefore, we hypothesize that, instead of selection for low birth weight, direct selection for calving ease should be used as means to reduce both the incidence of calving difficulty and losses in growth-related traits. Our objective was to quantify the performance losses in the first-calf heifer population of the American Simmental beef cattle under six different selection scenarios for either low birth weight or selection for high calving ease. In order to quantify the performance losses under the different selection scenarios, genetic trends and the net profit were estimated for each scenario. Data on calving ease, birth weight, weaning weight, and yearling weight were obtained from the American Simmental Association (ASA). Given the multi-breed nature of the ASA database, only animals with $\geq 87.5\%$ Simmental were included in our study with data constructed beginning with a base population of 2 year old dams as they provide the most relevant calving ease observations (N=95,791). Weaning and yearling weights were adjusted to 205 and 365 *d* of age, respectively. Further, 160-*d* postweaning gain was calculated from the adjusted weights. Four-generation pedigrees were constructed to estimate sire and maternal grandsire (co)variance components for calving ease (CE), birth weight (BWT), and 205-*d* weight (205-*d* WT), and sire (co)variance components for 160-*d* postweaning gain (160-*d* gain) using the threshold-linear sire-maternal grandsire model with a Gibbs sampling algorithm. Following variance component estimation, the direct and maternal EPD for CE, BWT, and 205-*d* weight and direct EBV for 160-*d* gain and 365-*d* weight for 465,710 animals were estimated using a threshold-linear multivariate maternal animal model. Calving ease was modeled as a threshold trait (*i.e.*, underlying continuous liability was assumed) with 3 observed categories. The 365-*d* weight was not included in the model; however, its direct EBV were calculated as the summation of the estimated EBV for 205-*d* weight and 160-*d* gain.

A subpopulation of 2 year old (first-calf) Simmental heifers ($n = 277,897$) was extracted under the restriction of including only progeny of first-calf heifers. This subpopulation was used for estimating genetic trends of Simmental cattle, and was also used as a selection pool (control scenario) for different selection scenarios. Furthermore, six different selection scenarios, for low birth weight as opposed to selection for high calving ease, were created. Using the first-calf heifers data (the control), data for each selection scenario was created by selecting sires, within each year of birth, with $EBV \geq$ the average (either EBV in the single trait selection or the index value in the multiple trait selection), along with the top 75% of dams with progeny. Selection scenarios were two single trait selection approaches for both high calving ease (**HCE**) and low birth weight (**LBWT**) in addition to four alternate selection indices which were the all-purpose selection index ($API = -1.8 BWT + 1.3 CE + 0.10 WWT + 0.20 YWT$) of the ASA, and its two derived sub-indices: ($API_1 = 1.3 CE + 0.20 YWT$), and ($API_2 = -1.8 BWT + 0.20 YWT$), and lastly the Dickerson's selection index ($DSI = -3.2 BWT + YWT$; Dickerson et al. (1974)). For each selection scenario, EPD for studied traits were standardized by their respective genetic standard deviation and then expressed as a deviation from the average EPD, within birth year, of the control scenario. Comparison between different selection scenarios involved evaluating the direct and maternal genetic trends of studied traits and profit from these scenarios. Here, profit was calculated for all selection scenarios using the API.

Results showed that the estimated posterior means of the direct heritability for CE, on the underlying scale, BWT, 205-d WT, 160-d gain, and 365-d WT of the American Simmental were 0.23, 0.52, 0.28, 0.21, and 0.33, respectively. Maternal heritability estimates for CE, BWT, and 205-d WT were 0.14, 0.05, and 0.055, respectively. The high negative genetic correlation between calving ease and birth weight (-0.67) justified the importance of incorporating birth

weight in the genetic evaluation of calving ease. The moderate positive genetic correlations between birth weight and subsequent growth traits exposed the genetic antagonistic relationship between calving ease and postnatal growth traits when selection for birth weight is applied.

Results obtained from the comparisons of different selection scenarios for high calving ease and low birth weight showed that all selection scenarios, compared to the control scenario, produced reduced growth rate and increased the ease of calving suggesting selection for heavier animals was practiced on the first-calf Simmental heifer population. However, since 1999, a noticeable improvement in calving ease was evident. Generally, the calving ease-based selection scenarios (HCE, API, and API₁) had the highest profit and showed higher genetic trends for calving ease and growth-related traits compared to the birth weight-based selection scenarios. The single trait, HCE, selection scenario, as opposed to LBWT, improved calving ease and growth-related traits which resulted in shifting the intercept of profit by 58%. The DSI selection scenario showed the least genetic trend for calving ease and the least profit. Therefore, we accept the hypothesis that direct selection for high calving ease, as opposed to selection for low birth weight, produces cattle with higher calving ease and growth rates.

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CHAPTER V.

STATISTICAL MODEL COMPARISONS: THRESHOLD VERSUS LINEAR AND ANIMAL VERSUS SIRE USING AMERICAN SIMMENTAL FIELD DATA

5.1. Introduction

Although calving ease is a polygenic trait, it is classified as an ordered categorical trait since it is recorded in a data scoring system ranging from 1 = unassisted calving to 5 = malpresentation. The categorical nature of calving ease phenotypes poses the question of how suitable the linear methods are for the evaluation/analysis of such traits. The appropriateness of applying linear methodologies to such traits was intensively investigated by Thompson (1979) and Gianola (1982). Nonlinear methods were proposed to evaluate ordered categorical traits on the underlying continuous liability scale (Gianola and Foulley, 1983; Harville and Mee, 1984) and many studies have examined the advantages of the threshold methodology over the linear approach when used in genetic evaluation of ordered categorical trait. Most studies used either simulated or field data, yet few used both kinds of data to evaluate the threshold methodology. Results varied between supporting (Varona et al., 1999b; Ramirez-Valverde et al., 2001) and rejecting (Weller et al., 1988; Matos et al., 1997) the hypothesis that the threshold model is more suitable for the analysis of categorical responses. The objective of this study was to compare suitability of the threshold model versus the linear model in analysis of heifer calving ease score field data from the American Simmental Association.

5.2. Materials and Methods

In this section, the threshold model was compared to the linear model applied to heifer calving ease field data from the American Simmental Association. We also extended the comparison to include those between the animal and the sire model. Further, within these models, calving ease was analyzed using a univariate model, a bivariate model (with birth weight), and a multivariate model (with both birth and 205-*d* weights). In addition, calving ease was fitted either as a binary or polychotomous trait (*i.e.*, multiple categories (3 categories)). Only the direct genetic effects were fitted in all models. The total number of analyses required to compare all models was 240. Description of these analyses is presented in Table 5.1. The criterion of comparison was the model predictive ability estimated using a cross validation “data splitting” technique, followed by the calculation of correlations (Pearson’s and Spearman’s correlation coefficients) between predicted EPD obtained from two complementary data sets.

A balanced data was created for the analysis (Table 5.2). The data was prepared so that observations on all traits within animal were available and only large herd data were included ($n \geq 50$). Once accumulated, a data-splitting procedure was performed. First, data were duplicated (Data 1 and Data 2). Second, in data 1, 50% of calving ease observations was randomly set to be missing. Third, in data 2, the other 50% of calving ease observations were set to be missing. This procedure produced two complementary data subsets in term of calving ease observations. This sampling procedure was repeated for another four times resulting in a total of 5 pairs of complementary data subsets. Each animal, in each pair of data subsets, had a calving ease observation in one subset and missing observation in the other subset.

Description of models: Six models were used to perform all analyses. Models were: 1) Univariate linear model for calving ease 2) Univariate threshold model for calving ease 3) Bivariate linear-linear model for calving ease and birth weight 4) Bivariate threshold-linear model for calving ease and birth weight 5) Multivariate linear-linear-linear model for calving ease, birth weight, and 205-*d* weight; and 6) Multivariate threshold-linear-linear model for calving ease, birth weight, and 205-*d* weight. Each of the six models was fitted as both an animal model and a sire model with an additional 2 combinations super-imposed on the above where calving ease was fitted as a binary or a polychotomous outcome. Therefore, for each model, one through 6, four different analyses were performed. Applied to the five pairs of complementary data subsets (total of 10 subsets), each of the former analyses was replicated 10 times. This resulted in a total of 240 analyses to compare all different models (Table 5.1). Models and their equations are described as follow:

1) *Univariate linear model:*

The equation of the univariate linear model is described below.

$$Y_{ce} = X_{ce}\beta_{ce} + Z_{1ce}a_{ce} + Z_{2ce}h_{ce} + e_{ce}, \quad (5.1)$$

Where Y_{ce} was vector of observations with subscript ce denoting calving ease either with 2 categories or 3 categories; β were sex fixed effects; a were the random effects of either animal or sire; h were the random effects of herd-year-season; e were the residual effects; and X , Z_1 , and Z_2 were incidence matrices that link data with fixed effects, animal or sire random effects, and herd-year-season random effects, respectively.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} a \\ h \\ e \end{bmatrix} = \begin{bmatrix} \sigma_a^2 \mathbf{A} & 0 & 0 \\ 0 & \sigma_h^2 & 0 \\ 0 & 0 & \sigma_e^2 \end{bmatrix}$$

with σ_a^2 , σ_h^2 , and σ_e^2 denoting variances, on the observed scale, for either direct additive (under animal model) or sire (under sire model), herd-year-season, and residual random effects, \mathbf{A} was the additive genetic relationship matrix.

2) *Univariate threshold model:*

This model was fitted in the same manner of fitting the preceding model with the exception of fitting calving ease as a threshold trait (i.e., on the underlying continuous scale described in Eq. 4.2). The univariate threshold model is described as follow:

$$L_{ce} = X_{ce}\beta_{ce} + Z_{1ce}a_{ce} + Z_{2ce}h_{ce} + e_{ce}, \quad (5.2)$$

Where L_{ce} was vector of liabilities with subscript ce denoting calving ease either with 2 categories or 3 categories; β were sex fixed effects; a were the random effects of either animal or sire; h were the random effects of herd-year-season; e were the residual effects; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 were incidence matrices that link data with fixed effects, animal or sire random effects, and herd-year-season random effects, respectively.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} a \\ h \\ e \end{bmatrix} = \begin{bmatrix} \sigma_a^2 \mathbf{A} & 0 & 0 \\ 0 & \sigma_h^2 & 0 \\ 0 & 0 & \sigma_e^2 \end{bmatrix}$$

with σ_a^2 , σ_h^2 , and σ_e^2 denoting variances, on the underlying scale, for either direct additive (under animal model) or sire (under sire model), herd-year-season, and residual random effects, \mathbf{A} was the additive genetic relationship matrix.

3) *Bivariate linear-linear model fitted for calving ease and birth weight:*

The observed categories of calving ease were assumed to be normally distributed “continuous”; therefore, calving ease was evaluated on the observed scale. The model was fitted in both animal and sire model settings. Under each setting calving ease was evaluated twice with 2 and 3 categories. The model equation is represented below.

$$\begin{bmatrix} Y_{ce} \\ Y_{bwt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \end{bmatrix} + \begin{bmatrix} Z_1 a_{ce} \\ Z_1 a_{bwt} \end{bmatrix} + \begin{bmatrix} Z_2 h_{ce} \\ Z_2 h_{bwt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \end{bmatrix}, \quad (5.3)$$

In the above equation, \mathbf{Y} were vectors of observations for respective trait; subscriptions \mathbf{ce} and \mathbf{bwt} were calving ease (2 or 3 categories) and birth weight; $\boldsymbol{\beta}$ were effects associated with sex; \mathbf{a} were animal or sire random effects; \mathbf{h} were herd-year-season random effects, respectively; \mathbf{e} were the residuals; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 were incidence matrices that link data with fixed effects, animal or sire random effects, and herd-year-season random effects, respectively.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{H} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

where \mathbf{G} = a 2×2 genetic (co)variance matrix, with CE on the observed scale, for either direct genetic (animal model) or sires (sire model) random effects, \mathbf{A} = additive genetic relationship matrix, \mathbf{H} = a 2×2 diagonal matrix for herd-year-season random effects, \mathbf{R} = a 2×2 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations, and \otimes =Kronecker product.

4) *Bivariate threshold-linear model fitted for calving ease and birth weight:*

An underlying normal distribution “liability” was assumed for calving ease which was evaluated as a threshold trait. The model was fitted in both animal and sire model settings. Under each

setting calving ease was evaluated twice with 2 and 3 categories. The model equation is described as follow:

$$\begin{bmatrix} L_{ce} \\ Y_{bwt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \end{bmatrix} + \begin{bmatrix} Z_1 a_{ce} \\ Z_1 a_{bwt} \end{bmatrix} + \begin{bmatrix} Z_2 h_{ce} \\ Z_2 h_{bwt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \end{bmatrix}, \quad (5.4)$$

In the above equation, \mathbf{L} was a vector of underlying liabilities for calving ease; \mathbf{Y} was a vector of observations for birth weight; subscriptions \mathbf{ce} and \mathbf{bwt} were calving ease (2 or 3 categories) and birth weight; β were effects associated with sex; \mathbf{a} were animal or sire random effects; \mathbf{h} were herd-year-season random effects, respectively; \mathbf{e} were the residuals; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 were incidence matrices that link data with fixed effects, animal or sire random effects, and herd-year-season random effects, respectively.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{H} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

where \mathbf{G} = a 2×2 genetic (co)variance matrix, with CE on the underlying scale, for either direct genetic (animal model) or sires (sire model) random effects, \mathbf{A} = additive genetic relationship matrix, \mathbf{H} = a 2×2 diagonal matrix for herd-year-season random effects, \mathbf{R} = a 2×2 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations, and \otimes =Kronecker product.

5) *Multivariate linear-linear model fitted for calving ease, birth weight, and 205-d weight:*

As in models 1 and 3, calving ease was fitted as a linear trait. Under both animal and sire models, calving ease observations were fitted twice with 2 and 3 categories. The multivariate linear-linear model used in these analyses is presented in Eq. 5.5 below.

$$\begin{bmatrix} Y_{ce} \\ Y_{bwt} \\ Y_{205wt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{205wt}\beta_{205wt} \end{bmatrix} + \begin{bmatrix} Z_1 a_{ce} \\ Z_1 a_{bwt} \\ Z_1 a_{205wt} \end{bmatrix} + \begin{bmatrix} Z_2 h_{ce} \\ Z_2 h_{bwt} \\ Z_2 h_{205wt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{205wt} \end{bmatrix}, \quad (5.5)$$

In the above equation, β were effects associated with sex, and weaning contemporary group subclasses; \mathbf{a} were sire or animal random effects; \mathbf{h} were herd-year-season random effects, respectively; \mathbf{e} were the residuals; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 were incidence matrices that link data with fixed effects, animal or sire random effects, and herd-year-season random effects, respectively. \mathbf{Y} was vector of observations for respective trait.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{H} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

where \mathbf{G} = a 3×3 genetic (co)variance matrix, with CE on the observed scale, for either direct genetic (animal model) or sires (sire model) random effects, \mathbf{A} = additive genetic relationship matrix, \mathbf{H} = a 3×3 diagonal matrix for herd-year-season random effects, \mathbf{R} = a 3×3 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations, and \otimes =Kronecker product.

6) *Multivariate threshold-linear model fitted for calving ease, birth weight, and 205-d weight:*

As in models 2 and 4, calving ease was fitted as a threshold trait with an underlying distribution described in Eq. 4.2. Under both animal and sire models, calving ease observations were fitted twice with 2 and 3 categories. The multivariate threshold-linear model used in these analyses is presented in Eq. 5.6 below.

$$\begin{bmatrix} L_{ce} \\ Y_{bwt} \\ Y_{205wt} \end{bmatrix} = \begin{bmatrix} X_{ce}\beta_{ce} \\ X_{bwt}\beta_{bwt} \\ X_{205wt}\beta_{205wt} \end{bmatrix} + \begin{bmatrix} Z_1 a_{ce} \\ Z_1 a_{bwt} \\ Z_1 a_{205wt} \end{bmatrix} + \begin{bmatrix} Z_2 h_{ce} \\ Z_2 h_{bwt} \\ Z_2 h_{205wt} \end{bmatrix} + \begin{bmatrix} e_{ce} \\ e_{bwt} \\ e_{205wt} \end{bmatrix}, \quad (5.6)$$

In the above equation, β were effects associated with sex, and weaning contemporary group subclasses; \mathbf{a} were sire or animal random effects; \mathbf{h} were herd-year-season random effects, respectively; \mathbf{e} were the residuals; and \mathbf{X} , \mathbf{Z}_1 , and \mathbf{Z}_2 were incidence matrices that link data with fixed effects, animal or sire random effects, and herd-year-season random effects, respectively: \mathbf{L} was a vector of calving ease liabilities; \mathbf{Y} was vector of observations for birth weight and weaning weight.

The (co)variance structure of random effects was defined as:

$$\text{var} \begin{bmatrix} \mathbf{a} \\ \mathbf{h} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{G} \otimes \mathbf{A} & 0 & 0 \\ 0 & \mathbf{H} \otimes \mathbf{I} & 0 \\ 0 & 0 & \mathbf{R} \otimes \mathbf{I} \end{bmatrix}$$

where \mathbf{G} = a 3×3 genetic (co)variance matrix, with CE on the underlying scale, for either direct genetic (animal model) or sires (sire model) random effects, \mathbf{A} = additive genetic relationship matrix, \mathbf{H} = a 3×3 diagonal matrix for herd-year-season random effects, \mathbf{R} = a 3×3 residual (co)variance matrix, \mathbf{I} = identity matrix of order appropriate to the numbers of observations, and \otimes =Kronecker product.

Table 5.1: Description of models used in analyses to compare their predictive ability of calving ease EPD of Simmental data.

Model ¹	CE ²	Fitted traits ³	Sire model		Animal model	
			Subset pairs	Analyses	Subset pairs	analyses
Univariate						
L-CE ₂	L+B	CE	5	10	5	10
L-CE ₃	L+P	CE	5	10	5	10
T-CE ₂	T+B	CE	5	10	5	10
T-CE ₃	T+P	CE	5	10	5	10
Bivariate						
LL-CE ₂	L+B	CE BWT	5	10	5	10
LL-CE ₃	L+P	CE BWT	5	10	5	10
TL-CE ₂	T+B	CE BWT	5	10	5	10
TL-CE ₃	T+P	CE BWT	5	10	5	10
Multivariate						
LLL-CE ₂	L+B	CE BWT 205-d WT	5	10	5	10
LLL-CE ₃	L+P	CE BWT 205-d WT	5	10	5	10
TLL-CE ₂	T+B	CE BWT 205-d WT	5	10	5	10
TLL-CE ₃	T+P	CE BWT 205-d WT	5	10	5	10
Total			60	120	60	120

¹L = linear; T = threshold; CE₂ = 2 categories; CE₃ = 3 categories.

²L = linear; T = threshold; B = binary; P = polychotomous.

³CE = calving ease; BWT = birth weight; 205-d WT = adjusted 205-d weight.

Table 5.2: Summary statistics of Simmental data used in model comparisons “threshold vs. linear” and “Animal vs. sire”.

Item ¹	N	Calving difficulty score				Mean	SD	Min.	Max.
		1	2	3	4				
<i>Data file:</i>									
Animal	19,012								
Dam	19,012								
CE	19,012	11,661	5,407	1,372	572	1.51	0.75	1	4
Males	9,272	4,944	2,998	832	453	1.65	0.83	1	4
Females	9,785	6,717	2,409	540	119	1.39	0.65	1	4
BWT, kg	19,012	11,661	5,407	1,372	572	40.91	5.04	24.09	55.45
Males	9,272	4,944	2,998	832	453	42.28	5.00	24.09	55.45
Females	9,785	6,717	2,409	540	119	39.61	4.74	24.09	55.45
205- <i>d</i> WT, kg	19,012	11,661	5,407	1,372	572	270.96	44.81	104.94	433.15
Males	9,272	4,944	2,998	832	453	285.26	47.56	113.50	433.15
Females	9,785	6,717	2,409	540	119	257.47	37.34	104.94	407.48
WCG	347								
HYS	1,737								

Pedigree:

Animal Model

Animal 80,007

Sire 9,011

Dam 54,118

Sire Model

Sire 9,011

Sire of sire 2,490

MGS 2,128

¹CE = Calving ease; BWT = Birth weight; 205-*d* WT = 205 days adjusted weight; WCG = Weaning contemporary group; HYS = Herd-Year-Season; MGS = Maternal grandsire.

5.3. Results and Discussion

In the present study, we examined the threshold model suitability for the analysis of categorical traits as opposed to linear approaches for calving ease. Furthermore, we addressed not only the linearity of the trait, but also the number of the trait categories, model complexity (i.e., the number of fitted traits) and extended the comparison to include the comparison of the animal model versus the sire model. Efficiency of each model was determined by assessing the predictive ability of the model. The predictive ability of model was estimated using the correlation between predicted calving ease EPD from two complementary data sets under each model (see section 5.2 for further explanation). The distribution of calving ease scores of first-calf Simmental heifers was: 61.33% unassisted calving, 28.44% minor assistance, 7.22% major assistance, and 3% Cesarean. However for this study, the last two categories (major assistance + Cesarean = 10.22%) were merged. Effects included in both animal and sire models were the fixed effects of sex and weaning contemporary group (included only in the multivariate models), herd-year-season random effects, and either direct additive genetic random effects in the animal model or sire random effects in the sire model. Description of analyses used to compare the predictive ability of models for the estimation of calving ease EPD of the American Simmental beef cattle is presented in Table 5.1.

Estimates of posterior means for sire and residual (co)variance components, obtained using Bayesian inference via means of a Gibbs sampling algorithm, of calving ease (CE), birth weight (BWT), and 205-*d* weight (205-*d* WT) for the American Simmental data under different sire models are presented in Table 5.3. Estimates of posterior means for direct genetic and residual (co)variance components for the same data under different animal models are presented in Table

5.4. These values were used to estimate EPD of these traits, in the complementary data set, between which correlations were calculated to estimate each model's predictive ability.

Table 5.3: Posterior means for sire and residual (co)variance components¹ of calving ease (CE), birth weight (BWT), and 205-*d* weight (205-*d* WT) for the American Simmental data using different sire models.

Model	Effect	Trait	CE ²				BWT	205- <i>d</i> WT
			L-CE ₂	L-CE ₃	T-CE ₂	T-CE ₃		
Univariate								
	Sire	CE	0.011	0.020	0.068	0.060		
	Residual	CE	0.210	0.395	1.000	0.856		
Bivariate								
	Sire	CE	0.020	0.395	0.067	0.056		
		BWT	0.107	0.943	0.293	0.238	3.147	
	Residual	CE	0.210	0.020	1.000	0.852		
		BWT	0.631	0.139	1.820	1.694	15.09	
Multivariate								
	Sire	CE	0.008	0.018	0.061	0.052		
		BWT	0.105	0.135	0.281	0.227	3.346	
		205- <i>d</i> WT	0.078	0.071	0.173	0.116	11.11	89.07
	Residual	CE	0.210	0.395	1.000	0.851		
		BWT	0.631	0.943	1.816	1.688	15.11	
		205- <i>d</i> WT	0.423	0.429	1.305	0.967	25.58	638.6

¹variances (bold faced) and covariances (below diagonal of the effect block).

²L-CE₂ = calving ease is fitted as a linear binary trait; L-CE₃ = calving ease is fitted as a linear trait with 3 categories; T-CE₂ = calving ease is fitted as a threshold binary trait; and T-CE₃ = calving ease is fitted as a threshold trait with 3 categories.

Table 5.4: Posterior means for direct genetic and residual (co)variance components¹ of calving ease (CE), birth weight (BWT), and 205-*d* weight (205-*d* WT) for the American Simmental data using different animal models.

Model	Effect	Trait	CE ²				BWT	205- <i>d</i> WT
			L-CE ₂	L-CE ₃	T-CE ₂	T-CE ₃		
Univariate								
	Direct	CE	0.046	0.105	0.491	0.301		
	Residual	CE	0.175	0.318	1.000	0.632		
Bivariate								
	Direct	CE	0.047	0.104	0.521	0.306		
		BWT	0.372	0.516	1.210	0.882	10.39	
	Residual	CE	0.175	0.319	1.000	0.625		
		BWT	0.372	0.580	1.292	1.066	7.970	
Multivariate								
	Direct	CE	0.045	0.100	0.500	0.298		
		BWT	0.373	0.516	1.217	0.892	10.65	
		205- <i>d</i> WT	0.260	0.436	0.754	0.582	30.15	291.3
	Residual	CE	0.176	0.321	1.000	0.630		
		BWT	0.370	0.578	1.269	1.053	7.842	
		205- <i>d</i> WT	0.660	0.816	2.232	1.512	5.427	437.1

¹variances (bold faced) and covariances (below diagonal of the effect block).

²L-CE₂ = calving ease is fitted as a linear binary trait; L-CE₃ = calving ease is fitted as a linear trait with 3 categories; T-CE₂ = calving ease is fitted as a threshold binary trait; and T-CE₃ = calving ease is fitted as a threshold trait with 3 categories.

Comparison of models was done using Pearson's correlation (r) and Spearman rank Correlation (R) between observed and estimated calving ease EPD is presented in Table 5.5. The correlations presented in Table 5.5 were the averages of correlations obtained from 5 replicates of complementary subset pairs.

The acronyms for models used in the results were previously described in Table 5.1. Here, traits were ordered so that calving ease was first followed by BWT and 205-*d* WT, respectively. Models were defined as follows:

L = the trait was fitted as a linear trait, **T** = the trait was fitted as a threshold trait, **CE₂** = calving ease is measured as 2 categories, and **CE₃** = calving ease is measured as 3 categories. Therefore, the univariate models (only CE) fitted under either animal model or sire model were L-CE₂, L-CE₃, T-CE₂, and T-CE₃. The bivariate models (CE and BWT) fitted under either animal model or sire model were LL-CE₂, LL-CE₃, TL-CE₂, and TL-CE₃. The multivariate models (CE, BWT, and 205-*d* WT) fitted under either animal model or sire model were LLL-CE₂, LLL-CE₃, TLL-CE₂, and TLL-CE₃.

Comparison of “threshold vs. linear” with a sire model:

Regardless of the number of calving ease categories, the average correlation (**R** and **r**) obtained from the univariate threshold models were higher than their counterparts from the linear models. The superiority of the threshold models was consistent across sires groups, except for sires with large number of progeny (sires >100 progeny). In those instances, there were smaller differences between the two methodologies. The superiority of the threshold model was more pronounced in the low accuracy sires (<50 records). This was in agreement with reports of Clutter et al. (1989) who speculated that sires with limited number of records might be ranked differently when the threshold model is used instead of the linear model. The largest differences in average rank correlations were between the L-CE₂ and T-CE₂ (0.42 vs. 0.45), respectively, which represented 7.14% increase in the average rank correlation. These results were consistent with those reported by Varona et al. (1999b) who showed that the threshold model outperformed the linear. Further, Gevrekci et al. (2011) evaluated dystocia in Holsteins under different models. They compared threshold sire (TS), threshold sire-maternal grandsire (TS-MGS), and linear sire-maternal grandsire (L) models. Authors concluded that the threshold model was superior to the linear model for the genetic evaluation of dystocia. Nonetheless, these findings were in contrast

with those by Ramirez-Valverde et al. (2001) who reported an increase of 7.14% in favor of the linear model for the average correlation of sires with <50 progeny (low accuracy sires). Results of the current study revealed that, within the same model, when the number of calving ease categories increased (from 2 to be 3), both **R** and **r** for sires with >100 progeny were notably increased. The rank correlations of the linear and the threshold models were increased by 6.45 and 4.76%, respectively; however, other sire groups did not show any change.

In all bivariate sire models, incorporating birth weight substantially increased the predictive ability of the model (Table 5.5). Furthermore, the threshold models (TL-CE₂ and TL-CE₃) showed the highest improvement in the model predictive ability increasing the rank of sires by 77 and 68%, respectively. The bivariate threshold models (TL-CE₂ and TL-CE₃) showed considerable increase in model predictive ability compared to the linear models. The average **R** and **r** of the TL-CE₂ were 41% (0.79 vs. 0.56) and 40% (0.84 vs. 0.60), respectively, higher than that of the LL-CE₂. For high accuracy sires (sire > 100 progeny), all models performed the same with the exception of LL-CE₂ which had average **R** and **r** that were 14.3 and 13.3%, respectively, lower than the average of other bivariate models. This illustrates the inadequacy of the linear model when calving ease is fitted as a binary trait even with birth weight included in the analysis of calving ease as a second trait. When the number of calving ease categories was increased, the linear-linear model has the highest improvement in predictive ability (**R** and **r** were increased by 14.3 and 13.3%, respectively). This improvement is a result of the calving ease distribution moving toward normality. These results agreed with those obtained by Ramirez-Valverde et al. (2001) who found that including birth weight in the analysis of calving difficulty greatly improved the model predictive ability, especially for low accuracy sires (sires < 50). Nonetheless, they did not report differences in the model predictive ability between the

threshold-linear and the linear-linear sire-maternal grandsire models. Several studies using field data reported similar results relative to the superiority of the threshold-linear over the linear-linear model (Casellas et al., 2007; Negussie et al., 2008; Vostrý et al., 2014).

Even though the predictive ability of all models was improved when another continuous trait (205-d WT) was added to the model, the linear models for calving ease exhibited the most significant increase (bivariate linear vs. multivariate linear). The average \mathbf{R} and \mathbf{r} of the LL-CE₂ were increased by 46.4 and 45%, respectively, when 205-d WT was included in the model (LLL-CE₂) in addition to BWT. The TLL-CE₂ maintained the superiority over other models; however, the difference with the LLL-CE₂ was the smallest and they performed similarly with respect to the high accuracy sires (sires > 100). Under the sire model, the inclusion of two continuous traits in the genetic evaluation of categorical traits overcame the inadequacy of the linear methodologies for the analysis of such traits. However, since the data used in the present study was a balanced data, an analysis using unbalanced data could give larger differences between the multivariate threshold-linear model and the multivariate linear-linear model as suggested by Meijering and Gianola (1985) who found that the threshold model is more efficient than the linear when unbalanced data is used. To our knowledge, the comparison of the threshold and linear models that include the analysis of one categorical trait with two Gaussian traits in a multivariate setting has not been reported in the literature.

Comparison of “threshold vs. linear” with an animal model:

Results from the univariate animal models (Table 5.5) were very consistent with the hypotheses of: 1) the threshold model superiority in the analysis of categorical traits 2) The higher the number of categories, regardless of the trait linearity, the better the model predictive ability. The average rank correlation from the T-CE₂ was 2.17% higher than the L-CE₂.

Table 5.5: Comparison of models “Threshold vs. linear” and “Animal vs. sire” using Pearson’s correlation (r) and Spearman rank Correlation (R) between predicted calving ease EPD obtained from two complementary data sets of American Simmental cattle

		Model ¹															
		Sire								Animal							
		L-CE ₂		L-CE ₃		T-CE ₂		T-CE ₃		L-CE ₂		L-CE ₃		T-CE ₂		T-CE ₃	
		R	r	R	r	R	r	R	r	R	r	R	r	R	r	R	r
Univariate ²																	
	All sires	0.42	0.48	0.42	0.48	0.45	0.52	0.44	0.50	0.46	0.51	0.47	0.52	0.47	0.52	0.48	0.54
	Sires ≤ 50	0.42	0.47	0.42	0.47	0.45	0.51	0.44	0.49	0.45	0.49	0.47	0.51	0.46	0.51	0.48	0.53
	50 < Sires ≤ 100	0.49	0.55	0.51	0.57	0.50	0.58	0.50	0.58	0.58	0.60	0.62	0.64	0.59	0.61	0.62	0.64
	Sires > 100	0.62	0.67	0.66	0.69	0.63	0.69	0.66	0.70	0.72	0.72	0.75	0.75	0.73	0.73	0.76	0.75
Bivariate ³																	
	All sires	0.56	0.60	0.72	0.76	0.79	0.84	0.74	0.78	0.68	0.72	0.66	0.71	0.67	0.72	0.66	0.71
	Sires ≤ 50	0.57	0.60	0.72	0.76	0.80	0.84	0.74	0.78	0.68	0.72	0.66	0.70	0.67	0.72	0.66	0.71
	50 < Sires ≤ 100	0.58	0.62	0.70	0.74	0.78	0.81	0.72	0.76	0.69	0.72	0.70	0.73	0.68	0.72	0.69	0.73
	Sires > 100	0.70	0.72	0.80	0.80	0.81	0.84	0.80	0.81	0.78	0.79	0.79	0.80	0.77	0.78	0.78	0.79
Multivariate ⁴																	
	All sires	0.82	0.87	0.74	0.79	0.83	0.88	0.77	0.82	0.75	0.79	0.72	0.76	0.74	0.78	0.72	0.77
	Sires ≤ 50	0.82	0.87	0.74	0.79	0.83	0.88	0.77	0.82	0.75	0.79	0.72	0.76	0.74	0.78	0.72	0.76
	50 < Sires ≤ 100	0.84	0.86	0.74	0.77	0.85	0.86	0.77	0.80	0.77	0.78	0.75	0.77	0.76	0.77	0.75	0.77
	Sires > 100	0.86	0.87	0.81	0.82	0.86	0.87	0.83	0.84	0.83	0.83	0.82	0.82	0.82	0.82	0.82	0.82

¹L = calving ease fitted as a linear trait; T = calving ease fitted as a threshold trait; CE₂ = calving ease fitted as a binary trait; CE₃ = calving ease fitted as a polychotomous trait (3 categories).

²Univariate = model included calving ease only

³Bivariate = model included calving ease and birth weight

⁴Multivariate = model included calving ease, birth weight, and 205-d weight.

Furthermore, the average rank correlation from the T-CE₃ was 2.12% higher than the L-CE₃. However, correlations estimated from all univariate animal models were relatively low, except for sires with progeny > 100 which showed the highest correlations with small differences between the different models. The current results were consistent with those reported in the literature (Varona et al., 1999b; Ramirez-Valverde et al., 2001; Casellas et al., 2007; Gevrekci et al., 2011).

As anticipated, the inclusion of birth weight “Gaussian trait” in the genetic evaluation of calving ease as a “categorical trait” improved the predictive ability of all models independent of CE linearity (threshold or linear). The linear models, especially the LL-CE₂, had a considerable gain in their predictive ability when birth weight was included. The average rank correlations of LL-CE₂, LL-CE₃, TL-CE₂, and TL-CE₃ were increased by 47.82, 40.42, 42.55, and 37.50%, respectively. Generally, all bivariate animal models showed similar performance with a slight advantage of the linear models. Ramirez-Valverde et al. (2001), in their study of Gelbvieh cattle, reported similar findings. They found that the threshold-linear animal model did not outperform the linear-linear animal model. Conversely, Varona et al. (1999b), Casellas et al. (2007), and Negussie et al. (2008) reported that the threshold-linear model outperformed the linear-linear model based on their assessment parameters which were: MSE (Varona et al., 1999b) and correlation between EBV (Casellas et al., 2007; Negussie et al., 2008).

In multivariate animal models, in terms of the improved predictive ability compared to the bivariate models, results were similar to those obtained from the sire model. The increase in average rank correlations of LLL-CE₂, LLL-CE₃, TLL-CE₂, and TLL-CE₃ were 10.3, 9.1, 10.4, and 9.1%, respectively, over the bivariate analysis. Further, all multivariate models “threshold-linear vs. linear-linear” produced similar correlations. Here, the added information, when two

continuous traits were incorporated in the genetic evaluation of the threshold trait, compensated for the deficiency of the linear approach.

Generally, the comparison of predictive ability of threshold versus Linear, and animal versus sire models using Pearson's correlation (r) and Spearman rank Correlation (R) between predicted calving ease EPD indicated that: 1) There was superiority of the univariate threshold model "animal or sire" over the univariate linear model, 2) The inclusion of linear trait(s) improved the prediction of categorical traits, 3) Analysis of categorical trait data with two continuous traits resulted in small differences between the threshold and linear models, 4) The higher the number of categories the better the linear model prediction; in contrast, the threshold-linear models had better predictive ability when calving ease was fitted as a binary outcome, 5) Differences between the threshold and linear models were more pronounced in low accuracy (progeny < 50) sires and were the least in high accuracy (progeny > 100) sires, 6) The predictive ability of all univariate animal models was higher than that of the univariate sire models; however, in the more complex models (bivariate and multivariate), the predictive ability of the sire models was greatest, 7) The highest predictive ability among all models was obtained from the threshold-linear models with CE fitted as a binary trait. In conclusion, we accept the hypothesis that the threshold model is more suitable than the linear model for the analysis of categorical traits.

5.4. Summary

The categorical nature of calving ease phenotypes poses the question of how suitable the linear methods are to be implemented in the analysis of such traits. Researchers have investigated the advantages of the threshold model over the linear model. Obtained results varied between supporting and opposing the superiority of the threshold model in the analysis of

categorical traits. Therefore, our second objective was to compare the threshold model to the linear model applied to heifer calving ease field data from the American Simmental Association. We examined the threshold model suitability for the analysis of categorical traits as opposed to linear methods for calving ease. Furthermore, we addressed not only the linearity of the trait, but also the number of the trait categories, model complexity (i.e., the number of fitted traits) and extended the comparison to include evaluation of the animal model versus the sire model. Only the direct genetic effects were fitted in all models. Using a balanced data with herd size ≥ 50 animals, the efficiency of models was determined by the predictive ability of the model using the cross validation “data splitting” technique. The predictive ability of models was estimated using the correlations (Pearson’s and Spearman’s) between predicted calving ease EPD obtained from two complementary data sets.

The comparison of models predictive ability using Pearson’s correlation (r) and Spearman rank Correlation (R) between predicted calving ease EPD revealed that: 1) The univariate threshold model, either animal or sire, was superior to the univariate linear model, 2) The inclusion of linear trait(s) has improved the prediction of categorical traits (CE), 3) Analysis of categorical traits with two additional continuous traits results in small differences between the threshold and linear models, 4) The higher the number of categories the better the linear model prediction, 5) Differences between the threshold and linear models were more pronounced in low accuracy (progeny < 50) sires and were the least in high accuracy (progeny > 100) sires, 6) The predictive ability of all univariate animal models was higher than that of the univariate sire models; however, in the more complex models (bivariate and multivariate) the predictive ability of the sire models was the highest, 7) The highest predictive ability among all compared models was obtained from the threshold-linear sire model with calving ease fitted as a binary outcome.

In conclusion, we accept the hypothesis that the threshold model is more suitable than the linear model for the analysis of ordered categorical traits.

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CHAPTER VI.

CONCLUSIONS

Results from simulated data using single trait selection for low birth weight versus high calving ease revealed that the rate of genetic change in calving ease (% unassisted calving/yr) from the high calving ease selection scenario was higher ($P < 0.001$) than that from the low birth weight scenario. Both selection scenarios reduced growth rate. The decrease in growth rate genetic trend, from the single trait selection, was expected, since postnatal growth traits were not included in the selection. However, genetic trends of growth traits obtained from the high calving ease selection scenario were higher ($P < 0.001$) than those when selection occurred for low birth. Selection for high calving ease increased ($P < 0.001$) the annual genetic change for calving ease, weaning weight, and yearling weight over selection for low birth weight by 0.37%, 1.65 kg, and 1.77 kg, respectively. Therefore, selection for high calving ease produced animals with better calving ease EPD and higher growth rates at later ages. In conclusion, we accept the hypothesis that direct selection for high calving ease, as opposed to selection for low birth weight, produces cattle with higher calving ease and growth rates.

In the simulation study, both the threshold and linear approaches to evaluating calving ease showed similar predictive ability. In this case, these results were likely due to the highly balanced data used in current simulation study and might not reflect typical calving ease field data where observations are likely skewed with high incidences of calving ease, different incidences across levels of fixed effects, and potentially small numbers of records per sire. This was evident when Simmental field data was used to compare models.

Results from the American Simmental beef cattle field data showed that the estimated direct heritabilities for calving ease (on the underlying scale), birth weight, 205-*d* weight, 160-*d* postweaning gain, and 365-*d* weight were within the literature estimates of the Simmental beef cattle. Maternal heritability estimates for calving ease, birth weight, and 205-*d* weight were also in agreement with the Simmental estimates reported in the literature. The highest genetic correlations amongst studied traits were between the 365-*d* weight and its component traits (*i.e.*, 205-*d* weight and 160-*d* gain). The high negative genetic correlation between calving ease and birth weight (-0.67) and the high heritability of birth weight (0.52) justify the importance of incorporating birth weight in the genetic evaluation of calving ease, especially given relatively high reporting rates in most seedstock herds. The moderate positive genetic correlations between birth weight and subsequent growth traits exposed the genetic antagonistic relationship between calving ease and postnatal growth traits when selection for birth weight is applied.

Results obtained from the Simmental field data showed that all selection scenarios compared to the control scenario, reduced growth rate and increased the ease of calving, which suggested that, in the first generations of Simmental breed, selection for heavier animals was practiced. However, since 1999, a noticeable improvement in calving ease was evident in the breed. Generally, the calving ease-based selection scenarios (HCE, API, and API₁) had the highest net profit and showed higher genetic trends for calving ease and growth-related traits compared to the birth weight-based selection scenarios (LBWT, DSI, and API₂). The calving ease-based selection scenarios (HCE, API, and API₁) shifted the intercept of the net profit of the control scenario by 13, 11.6, and 11.1 \$, respectively; whereas, the birth weight-based selection scenarios (LBWT, DSI, and API₂) showed lower intercepts of 8.2, 7.3, and 8.8 \$, respectively. The single trait selection scenario (HCE) substantially improved calving ease over LBWT and

resulted in shifting the intercept of the net profit by 58% in the favorable direction. The DSI selection scenario showed the least genetic improvement in calving ease and the least net profit. Therefore, we accept the hypothesis that direct selection for high calving ease, as opposed to selection for low birth weight, produces cattle with higher calving ease and growth rates.

The comparison of threshold and linear models, and comparisons of animal versus sire models using Pearson's and Spearman's correlations between predicted calving ease EPD revealed that the univariate threshold model was superior to the univariate linear model, no matter whether the animal or sire relationships were used. The inclusion of linear trait(s) improved the prediction of categorical traits (e.g. BW with CE). Furthermore, the analysis of categorical traits with two continuous traits resulted in small differences between the threshold and linear models. The higher the number of categories the better the linear model prediction; in contrast, the threshold-linear models showed better prediction ability when calving ease was fitted as a binary outcome. Differences between the threshold and linear models were more pronounced in low accuracy sires and were the least in high accuracy sires. The predictive ability of all univariate animal models was higher than that of the univariate sire models; however, in the more complex models (bivariate and multivariate) the predictive ability of the sire models was the highest. The highest predictive ability among all compared models was in the threshold-linear sire model with calving ease as a binary outcome. In conclusion, we accept the hypothesis that the threshold model is more suitable than the linear model for the analysis of ordered categorical traits.

APPENDIXES

APPENDIX A: THE THRGIBBS1F90 PARAMETER FILE USED TO ESTIMATE EPD FOR CALVING EASE AND GROWTH-RELATED TRAITS OF FIRST-CALF HEIFER POPULATION OF THE AMERICAN SIMMENTAL BEEF CATTLE UNDER THE MULTIVARIATE MATERNAL ANIMAL MODEL

DATAFILE

allanimdata

NUMBER_OF_TRAITS

4

NUMBER_OF_EFFECTS

6

OBSERVATION(S)

3 4 5 6

WEIGHT(S)

EFFECTS: POSITIONS_IN_DATAFILE

NUMBER_OF_LEVELS

TYPE_OF_EFFECT[EFFECT NESTED]

7 7 0 0 2 cross

0 0 8 0 15833 cross

0 0 0 9 7040 cross

1 1 1 1 465710 cross

2 2 2 0 465710 cross

10 10 10 10 29393 cross

RANDOM_RESIDUAL VALUES

1 1.26 0.81 1.49

1.26 7.463 14.91 6.99

0.81 14.91 408.35 -12.92

1.49 6.99 -12.92 454.4

RANDOM_GROUP

4 5

RANDOM_TYPE

add_animal

FILE

pedanimVC1

(CO)VARIANCES

0.396 1.53 3.46 1.12 -0.03 0 0 0

1.53 13.212 37.52 19.96 0 -0.486 0 0

3.46 37.52 295.92 130.12 0 0 -7.32 0

1.12 19.96 130.12 220 0 0 0 0

-0.03 0 0 0 0.2588 0 0 0

0 -0.486 0 0 0 1.211 0 0

0 0 -7.32 0 0 0 58.74 0

0 0 0 0 0 0 0 0

RANDOM_GROUP

6

RANDOM_TYPE

diagonal

FILE

(CO)VARIANCES

0.09 0 0 0

0 3.406 0 0
0 0 310.1 0
0 0 0 521.5
OPTION cat 3 0 0 0
OPTION fixed_var mean

**APPENDIX B: R CODE USED TO CREATE THE SIMULATED DATA FOR HIGH
CALVING EASE SELECTION SCENARIO**

```

#R code based on Dr. Larry Schaeffer's R code for multiple trait models
#Creating a simulated data (Selection for high calving ease)
## Traits were: Calving eas (CE), birth weight (BW), weaning weight (WW), and postweaning
gain (PWG)
# First creating the base population and its F1 progeny (No selection)

library(MASS)

set.seed(1234)
# Herd effects (120 herds) on CE, BWT, WWT, and PWG
herdCE=(rnorm(120,0))*0.05
set.seed(1234)
herdBW=(rnorm(120,0))
set.seed(1234)
herdWW=(rnorm(120,0))*2
set.seed(1234)
herdPWG=(rnorm(120,0))*0.1
herd=matrix(data=c(herdCE,herdBW,herdWW,herdPWG),byrow=TRUE,nrow=4)
# sex effects (120 herds) on CE, BWT, WWT, and PWG
sex=matrix(data=c(0.108,-0.108,2,-1,10,-7,0.060,-0.040),byrow=TRUE,nrow=4)
# Residual matrix
R=matrix(data=c(1,1.13,0.46,0.48,1.13,20.5,30.37,8.78,0.46,30.37,534,29.87,0.48,8.78,29.87,26
1),byrow=TRUE,nrow=4)
# G matrix
G=matrix(data=c(0.24,1.11,1.6,1.51,1.11,9.67,23.11,14.65,1.6,23.11,221,103,1.51,14.65,103,217
),byrow=TRUE,nrow=4)
# Traits averages
mu=c(1.73,39,250,980)
## ID for F1 animals with record (n=36000)
anwr=c(37201:73200)
#ID for all animals (founders (36000 dams, 1200 sires) and their F1 progeny (36000))
aid = c(1:73200)
##ctreating fields in the data file for sire (30 progeny each), dams (1 progeny each), herds (size
of 300 each), sex (60% females and 40% males)
sid = c(numeric(37200),rep(1:1200, by=1, each=30))
did <- c(numeric(37200),1201:37200)
bi=c(rep(1,37200),rep(0.5,36000))
set.seed(1234)
iherd=c(sample(rep(1:120, by=1, each=300),36000,replace=F))
set.seed(1234)
isex=(rbinom(36000, 1, 0.6))+1

# heritability of traits
gd=diag(G)
rd=diag(R)
h2=gd/(gd+rd)

```

h2

```
# correlations among traits
# Function to calculate correlations from a covariance matrix
CORMAT=function(Q) {
  D = diag(Q)
  D = sqrt(D)
  B = diag(1/D)
  HC = B %**% Q %**% B
  HC }
CORMAT(R)
CORMAT(G)
# Get cholesky decompositions of G and R
LG = t(chol(G))
LR = t(chol(R))

nam=73200
# Simulate true breeding values for all animals (founders and their F1 progeny)
# J MATRIX FUNCTION
jd = function(n,m){
  matrix(c(1),nrow=n,ncol=m)}

tbv = jd(nam,4)*0
for(i in 1:nam){
  x = LG %**% (sqrt(bi[i])*rnorm(4,0,1))
  if(sid[i]>0){
    ks=sid[i]
    kd=did[i]
    x = x + 0.5*(tbv[ks, ]+tbv[kd, ]) }
  tbv[i, ] = x }
nrec=36000
# Make an observation for all traits for animals (only F1 progeny)
## observations were created by combining (trait average, herd effect, sex effect, TBV,
residual)
obs = jd(nrec,4)*0
for(k in 1:nrec){
  kanm=anwr[k]
  kherd=iherd[k]
  ksex=isex[k]

  obs[k, ]=mu + herd[ ,kherd] + sex[ ,ksex] + tbv[kanm, ]
  res = LR %**% rnorm(4,0,1)
  obs[k, ]=obs[k, ] + res
}
## scale CE and create the observed categories
obs[ ,1] = scale(obs[ ,1], center = TRUE, scale = FALSE)
```

```

obs[,1] = cut(obs[,1], c(-Inf, 0, 1, 1.4, Inf), labels = FALSE, ordered = TRUE)
#(1=50%, 2=34.13%, 3=7.79%, 4=8.08%)
## rounding observations
#obs[,1] = round(obs[,1], digits=5)
obs[,2] = round(obs[,2], digits=2)
obs[,3] = round(obs[,3], digits=2)
obs[,4] = round(obs[,4])
#####
#####
ped <- data.frame(id = aid, sire = sid, dam = did)
attach(ped)
#####
# creating data file for animals with records(F1)
dataped <- ped[ped$Sid>37200,]
animtbv <- tbv[37201:73200, ]
simulateddata <- data.frame(id = dataped$Sid, sire = dataped$sire, dam = dataped$dam, sex =
isex, herd = iherd, CE = obs[,1], BW = obs[,2], ww = obs[,3], pwg = obs[,4], CEtbv =
animtbv[,1], BWtbv = animtbv[,2], wwtbv = animtbv[,3], pwgtbv = animtbv[,4])
attach(simulateddata)

BWave=mean(BW)
BWave
BWsd=sd(BW)
BWsd
BWave-(3*BWsd)
BWave+(3*BWsd)
## using only BW observations that fall within 3 standard deviations
simudata <- subset(simulateddata, BW > (BWave-(3*BWsd)))
simulateddata <- subset(simudata, BW < (BWave+(3*BWsd)))
summary(BW)
animlist = c(simulateddata[,1],simulateddata[,2], simulateddata[,3])
detach(simulateddata)
uniqueanimlist = c(sort(unique(animlist)))
pedigree=ped[uniqueanimlist,]
attach(pedigree)
length(pedigree[,1])
length(uniqueanimlist)
#####
# creating data file for all animals "including founders which will have TBV, but missing
observations"
#Header: id sire dam sex herd CE BW ww pwg CEtbv BWtbv wwtbv pwgtbv
sexofparents = c(rep(1,1200),rep(2,36000))
herdofparents = c(rep(NA,1200),iherd)
allsimdata <- data.frame(id = ped$id, sire = ped$sire, dam = ped$dam, sex =
c(sexofparents,isex), herd = c(herdofparents,iherd), CE = c(rep(NA,37200),obs[,1]), BW =

```

```

c(rep(NA,37200),obs[,2]), ww = c(rep(NA,37200),obs[,3]), pwg = c(rep(NA,37200),obs[,4]),
CEtbv = tbv[,1], BWtbv = tbv[,2], wwtbv = tbv[,3], pwgtbv = tbv[,4])
basepopdata <- allsimdata[allsimdata[,1] %in% pedigree[,1], ]
attach(basepopdata)

#####
#####
#####
###SELECTION FOR CALVING EASE
#####
# 1 2 3 4 5 6 7 8 9 10 11 12 13
# id sire dam sex herd CE BW ww pwg CEtbv BWtbv wwtbv pwgtbv
#####
## creating F2
#####
## redefine the total number of all animals and number of base population in previous simulation
#####
#total number of all animals
nam = 73200
#number of sires and dams(founders) (1200+36000) in base population
nbase = 37200
#####
## selecting top 5% sirs and 80% dams (TBV for CE is the selection criteria)
## selection of sires
## average CE TBV for sires and dams
averages=by( basepopdata$CEtbv, basepopdata$sex, mean)
ave1males=averages[1]
ave1females=averages[2]
## standard deviation of CE TBV for sires and dams
SDs=by( basepopdata$CEtbv, basepopdata$sex, sd)
sd1males=SDs[1]
sd1females=SDs[2]
## selecting top 5% of sires
males <- subset(basepopdata, sex == 1)
kull2males= (males[,10]>(ave1males-(1.65*sd1males)))
males[kull2males,11]=0
selectedmales <- subset(males, males[,11] != 0)
summary(selectedmales[,7], na.rm=TRUE)
nrow(males)
nrow(selectedmales)
nrow(selectedmales)/nrow(males)

#####
## selection of dams
females <- subset(basepopdata, sex == 2)
kull2females= (females[,10]>(ave1females+(0.85*sd1females)))

```

```

females[kull2females,11]=0
# all selected females (females with progeny (base pop.) and 2 years (F1)females without
progeny)
selectedallfemales <- subset(females, females[,11] != 0)
summary(selectedallfemales[,7], na.rm=TRUE)
nrow(females)
nrow(selectedallfemales)
nrow(selectedallfemales)/nrow(females)
## only 2 years old females
selectedfemales <- subset(selectedallfemales, selectedallfemales[,1] > nbase)
nrow(selectedfemales)
nrow(selectedfemales)/nrow(females)
damlistf2 = c(selectedallfemales[,1])
#####
#### 783 selected males and 46130 selected females
n_sel_males = nrow(selectedmales)
n_sel_females = nrow(selectedallfemales)
n_progeny = n_sel_females
# number of females per sire = 58.9
n_females_per_sire = n_sel_females/n_sel_males
n_females_per_sire
# because number of dams per sire is 58.9, then sires will have different numbers of progeny
(some will have 58 and others will have 59 progeny)
rounded_n_females_per_sire = round(n_females_per_sire)
rounded_n_females_per_sire

if(rounded_n_females_per_sire < n_females_per_sire) {
  n1records_per_sire = (rounded_n_females_per_sire)
  n2records_per_sire = (n1records_per_sire)+1
} else {
  n1records_per_sire = (rounded_n_females_per_sire)-1
  n2records_per_sire = (rounded_n_females_per_sire)
}

#number of sires with 58 progeny (67 out of 783)
nsires_with_n1records = (n_sel_males)-((n_sel_females)-(n_sel_males*n1records_per_sire))
#number of sires with 59 progeny (716 out of 783)
nsires_with_n2records = (n_sel_males)-(nsires_with_n1records)
##pulling out the first 67 sires of sire list(783)
own_record_sires_with_n1records = selectedmales[1:nsires_with_n1records, ]
## replicate each sire 58 times
selectedmales1=own_record_sires_with_n1records[rep(seq_len(nrow(own_record_sires_with_n
1records)), each=n1records_per_sire),]
##pulling out the remained 716 sires of sire list(783)
own_record_sires_with_n2records = selectedmales[((nsires_with_n1records)+1):n_sel_males, ]
## replicate each sire 59 times

```

```

selectedmales2=own_record_sires_with_n2records[rep(seq_len(nrow(own_record_sires_with_n
2records)), each=n2records_per_sire),]
## Create random list os sires with length of 46130 which is number of selected dams
allselectedmales=rbind(selectedmales1,selectedmales2)
randomlymatedsires=allselectedmales[sample(nrow(allselectedmales)),]
sirelistf2 = randomlymatedsires[ ,1]

#####
selectedparents=rbind(selectedmales, selectedallfemales)
sortedselectedparents <- selectedparents[order(selectedparents[ ,1]),]
# pulling out selected parents and their pedigree
animlist = c(selectedparents[ ,1],selectedparents[ ,2], selectedparents[ ,3])
uniqueanimlist = c(sort(unique(animlist)))
uniqueanimlist = uniqueanimlist[-1]
subdata <- basepopdata[basepopdata[ ,1] %in% uniqueanimlist, ]
subdata <- data.matrix(subdata)

length(subdata[,1])
length(uniqueanimlist)
## creating F2 pedigree which include(selected parents and their pedigree+ new F2 ID with their
selected parents)
pedf2 = rbind(subdata[
,1:3],cbind(c((nam+1):(nam+n_progeny)),sirelistf2[1:n_progeny],damlistf2[1:n_progeny]))
#####
## calculating averages of traits of selected parents to create F2 observations
CEave=mean(selectedparents[ ,6], na.rm=TRUE)
CEave
BWave=mean(selectedparents[ ,7], na.rm=TRUE)
BWave
WWave=mean(selectedparents[ ,8], na.rm=TRUE)
WWave
PWGave=mean(selectedparents[ ,9], na.rm=TRUE)
PWGave
#####
## For F2 progeny, repeating the same code used to create F1.

library(MASS)

set.seed(1234)
herdCE=(rnorm(120,0))*0.05
set.seed(1234)
herdBW=(rnorm(120,0))
set.seed(1234)
herdWW=(rnorm(120,0))*2
set.seed(1234)
herdPWG=(rnorm(120,0))*0.1

```

```

herd=matrix(data=c(herdCE,herdBW,herdWW,herdPWG),byrow=TRUE,nrow=4)
sex=matrix(data=c(0.108,-0.108,2,-1,10,-7,0.060,-0.040),byrow=TRUE,nrow=4)
# Residual matrix
R=matrix(data=c(1,1.13,0.46,0.48,1.13,20.5,30.37,8.78,0.46,30.37,534,29.87,0.48,8.78,29.87,26
1),byrow=TRUE,nrow=4)
# G matrix
G=matrix(data=c(0.24,1.11,1.6,1.51,1.11,9.67,23.11,14.65,1.6,23.11,221,103,1.51,14.65,103,217
),byrow=TRUE,nrow=4)

#####averages:
mu=c(CEave,BWave,WWave,PWGave)
anwr=c((nam+1):(nam+n_progeny))
aid = c(pedf2[ ,1])
sid = c(pedf2[ ,2])
did <- c(pedf2[ ,3])

#number of herds
length(unique(selectedallfemales[ ,5]))
iherd=c(selectedallfemales[ ,5])
set.seed(123)
isex=(rbinom(n_progeny, 1, 0.6))+1

# heritability of traits
gd=diag(G)
rd=diag(R)
h2=gd/(gd+rd)
h2

# correlations among traits
# Function to calculate correlations from a covariance matrix
CORMAT=function(Q) {
  D = diag(Q)
  D = sqrt(D)
  B = diag(1/D)
  HC = B %*% Q %*% B
  HC }
CORMAT(R)
CORMAT(G)
# Get cholesky decompositions of G and R
LG = t(chol(G))
LR = t(chol(R))

# Simulate true breeding values for all animals
# J MATRIX FUNCTION
jd = function(n,m){
  matrix(c(1),nrow=n,ncol=m)}

```

```

nam1=n_progeny
mendelian = jd(nam1,4)*0
for(i in 1:nam1){
  mendelian[i, ] = LG %**% (rnorm(4,0,1))
}
damtbv= selectedallfemales[ ,10:13]
siretbv= randomlymatedsires[ ,10:13]
parentsaveragetbv=0.5*(damtbv + siretbv)
tbv=mendelian+parentsaveragetbv

nrec=n_progeny
# Make an observation for all traits for all animals
obser = jd(nrec,4)*0
for(k in 1:nrec){
  kherd=iherd[k]
  ksex=isex[k]

  obser[k, ]=mu + herd[ ,kherd] + sex[ ,ksex]
  res = LR %**% rnorm(4,0,1)
  obser[k, ]=obser[k, ] + res
}
obs = obser + tbv
obs[ ,1] = scale(obs[ ,1], center = TRUE, scale = FALSE)
obs[ ,1] = cut(obs[ ,1], c(-Inf, 0, 1, 1.4, Inf), labels = FALSE, ordered = TRUE)
obs[ ,2] = round(obs[ ,2], digits=2)
obs[ ,3] = round(obs[ ,3], digits=2)
obs[ ,4] = round(obs[ ,4])
#####
pedigree1 <- data.frame (id = aid, sire = sid, dam = did)
attach(pedigree1)
dataped <- pedigree1[pedigree1$Sid>nam,]
simdataf2 <- data.frame (id = dataped$id, sire = dataped$sire, dam = dataped$dam, sex = isex,
herd = iherd, CE = obs[ ,1], BW = obs[ ,2], ww = obs[ ,3], pwg = obs[ ,4], CEtbv = tbv[ ,1],
BWtbv = tbv[ ,2], wwtbv = tbv[ ,3], pwgtbv = tbv[ ,4])
attach(simdataf2)
nrow(simdataf2)
## pulling out only the 2 yr old dams data
two_year_females_list <- c(sort(selectedfemales[ ,1]))
length(two_year_females_list)
simdataf2 <- simdataf2[simdataf2[ ,3] %in% two_year_females_list, ]
nrow(simdataf2)
## combine the data file of (base+F1) with F2 data file (This file include 1. founders with no
observations, but with TBV 2. F1 progeny observations and TBV 3. F2 progeny with
observations and TBV)
f2andbasepopdata <- rbind(basepopdata,simdataf2)

```

```

## Data file for F1 and F2 (has both observations and TBV)
f2andbasepopdata <- subset(f2andbasepopdata, f2andbasepopdata[,1] > nbase)
# keeping BW observations within 3 SD
BWave_f1_f2=mean(f2andbasepopdata$BW)
BWave_f1_f2

BWsd_f1_f2=sd(f2andbasepopdata$BW)
BWsd_f1_f2
BWave_f1_f2-(3*BWsd_f1_f2)
BWave_f1_f2+(3*BWsd_f1_f2)
f2andbasepopdata <- subset(f2andbasepopdata, BW > (BWave_f1_f2-(3*BWsd_f1_f2)))
f2andbasepopdata <- subset(f2andbasepopdata, BW < (BWave_f1_f2+(3*BWsd_f1_f2)))
summary(f2andbasepopdata$BW)
nrow(f2andbasepopdata)

simdataf2 <- subset(f2andbasepopdata, f2andbasepopdata[,1] > nam)
summary(simdataf2$BW)
nrow(simdataf2)
N_sires = length(c(sort(unique(simdataf2$sire))))
N_sires
basepop_f2_data <- rbind(basepopdata,simdataf2)

pedigreef2 <- data.frame (id = simdataf2$id, sire = simdataf2$sire, dam = simdataf2$dam)
pedigreef2andbase<- rbind(pedigree,pedigreef2)

#####
#####
## Creating F3
# 1 2 3 4 5 6 7 8 9 10 11 12 13
# id sire dam sex herd CE BW ww pwg CEtbv BWtbv wwtbv pwgtbv

#####
#####
## redefine (the total number of all animals) and (number of base population and F1+F2) in
previous simulation
#####
#total number of all animals (Used unique IDs up to now)
nam2 = nam+nam1
#number of sires and dams in base population (1200+36000) and in f1 generartion (36000)
nbaseandf1 = nam = 73200
#####
## selecting top 5% sirs and 80% dams
## selection of sires
averages=by( basepop_f2_data$CEtbv, basepop_f2_data$sex, mean)
ave1males=averages[1]
ave1females=averages[2]

```

```

SDs=by( basepop_f2_data$CEtbv, basepop_f2_data$sex, sd)
sd1males=SDs[1]
sd1females=SDs[2]

males <- subset(basepop_f2_data, sex == 1)
kull2males= (males[,10]>(ave1males-(1.7*sd1males)))
males[kull2males,11]=0
selectedmales <- subset(males, males[,11] != 0)
summary(selectedmales[,7], na.rm=TRUE)
nrow(males)
nrow(selectedmales)
nrow(selectedmales)/nrow(males)
#####
## selection of dams
females <- subset(basepop_f2_data, sex == 2)
kull2females= (females[,10]>(ave1females+(0.85*sd1females)))
females[kull2females,11]=0
# all selected females (females with progeny (base pop.and F1) and 2 years (F2)females without
progeny)
selectedallfemales <- subset(females, females[,11] != 0)
summary(selectedallfemales[,7], na.rm=TRUE)
nrow(females)
nrow(selectedallfemales)
nrow(selectedallfemales)/nrow(females)
## only 2 years old females
selectedfemales <- subset(selectedallfemales, selectedallfemales[,1] > nbaseandf1)
nrow(selectedfemales)
nrow(selectedfemales)/nrow(females)
damlistf3 = c(selectedallfemales[,1])
#####
#### 1110 selected males and 54565 selected females
n_sel_males = nrow(selectedmales)
n_sel_females = nrow(selectedallfemales)
n_progeny = n_sel_females
# number of females per sire = 49.15
n_females_per_sire = n_sel_females/n_sel_males
n_females_per_sire
# because number of dams per sire is 49.15, then sires will have different numbers of progeny
(some will have 49 and others will have 50 progeny)
rounded_n_females_per_sire = round(n_females_per_sire)
rounded_n_females_per_sire

if(rounded_n_females_per_sire < n_females_per_sire) {
  n1records_per_sire = (rounded_n_females_per_sire)
  n2records_per_sire = (n1records_per_sire)+1
} else {

```

```

n1records_per_sire = (rounded_n_females_per_sire)-1
n2records_per_sire = (rounded_n_females_per_sire)
}

nsires_with_n1records = (n_sel_males)-((n_sel_females)-(n_sel_males*n1records_per_sire))
nsires_with_n2records = (n_sel_males)-(nsires_with_n1records)
own_record_sires_with_n1records = selectedmales[1:nsires_with_n1records, ]
selectedmales1=own_record_sires_with_n1records[rep(seq_len(nrow(own_record_sires_with_n
1records)), each=n1records_per_sire),]
own_record_sires_with_n2records = selectedmales[((nsires_with_n1records)+1):n_sel_males, ]
selectedmales2=own_record_sires_with_n2records[rep(seq_len(nrow(own_record_sires_with_n
2records)), each=n2records_per_sire),]
allselectedmales=rbind(selectedmales1,selectedmales2)
randomlymatedsires=allselectedmales[sample(nrow(allselectedmales)),]
sirelistf3 = randomlymatedsires[ ,1]

#####
selectedparents=rbind(selectedmales, selectedallfemales)
sortedselectedparents <- selectedparents[order(selectedparents[ ,1]),]

animlist = c(selectedparents[ ,1],selectedparents[ ,2], selectedparents[ ,3])
uniqueanimlist = c(sort(unique(animlist)))
uniqueanimlist = uniqueanimlist[-1]
subdata <- basepop_f2_data[basepop_f2_data[ ,1] %in% uniqueanimlist, ]
subdata <- data.matrix(subdata)

length(subdata[,1])
length(uniqueanimlist)
pedf3 = rbind(subdata[
,1:3],cbind(c((nam2+1):(nam2+n_progeny)),sirelistf3[1:n_progeny],damlistf3[1:n_progeny]))

#####
CEave=mean(selectedparents[ ,6], na.rm=TRUE)
CEave
BWave=mean(selectedparents[ ,7], na.rm=TRUE)
BWave
WWave=mean(selectedparents[ ,8], na.rm=TRUE)
WWave
PWGave=mean(selectedparents[ ,9], na.rm=TRUE)
PWGave
#####
library(MASS)

set.seed(1234)
herdCE=(rnorm(120,0))*0.05
set.seed(1234)

```

```

herdBW=(rnorm(120,0))
set.seed(1234)
herdWW=(rnorm(120,0))*2
set.seed(1234)
herdPWG=(rnorm(120,0))*0.1
herd=matrix(data=c(herdCE,herdBW,herdWW,herdPWG),byrow=TRUE,nrow=4)
sex=matrix(data=c(0.108,-0.108,2,-1,10,-7,0.060,-0.040),byrow=TRUE,nrow=4)
# Residual matrix
R=matrix(data=c(1,1.13,0.46,0.48,1.13,20.5,30.37,8.78,0.46,30.37,534,29.87,0.48,8.78,29.87,26
1),byrow=TRUE,nrow=4)
# G matrix
G=matrix(data=c(0.24,1.11,1.6,1.51,1.11,9.67,23.11,14.65,1.6,23.11,221,103,1.51,14.65,103,217
),byrow=TRUE,nrow=4)

####averages:
mu=c(CEave,BWave,WWave,PWGave)
anwr=c((nam2+1):(nam2+n_progeny))
aid = c(pedf3[ ,1])
sid = c(pedf3[ ,2])
did <- c(pedf3[ ,3])

#number of herds
length(unique(selectedallfemales[ ,5]))
iherd=c(selectedallfemales[ ,5])
set.seed(123)
isex=(rbinom(n_progeny, 1, 0.6))+1

# heritability of traits
gd=diag(G)
rd=diag(R)
h2=gd/(gd+rd)
h2

# correlations among traits
# Function to calculate correlations from a covariance matrix
CORMAT=function(Q) {
  D = diag(Q)
  D = sqrt(D)
  B = diag(1/D)
  HC = B %*% Q %*% B
  HC }
CORMAT(R)
CORMAT(G)
# Get cholesky decompositions of G and R
LG = t(chol(G))
LR = t(chol(R))

```

```

# Simulate true breeding values for all animals
# J MATRIX FUNCTION
jd = function(n,m){
  matrix(c(1),nrow=n,ncol=m)}

nam3=n_progeny
mendelian = jd(nam3,4)*0
for(i in 1:nam3){
  mendelian[i, ] = LG %**% (rnorm(4,0,1))
}
damtbv= selectedallfemales[ ,10:13]
siretbv= randomlymatedsires[ ,10:13]
parentsaveragetbv=0.5*(damtbv + siretbv)
tbv=mendelian+parentsaveragetbv

nrec=n_progeny
# Make an observation for all traits for all animals
obser = jd(nrec,4)*0
for(k in 1:nrec){
  kherd=iherd[k]
  ksex=isex[k]

  obser[k, ]=mu + herd[ ,kherd] + sex[ ,ksex]
  res = LR %**% rnorm(4,0,1)
  obser[k, ]=obser[k, ] + res
}
obs = obser + tbv
obs[ ,1] = scale(obs[ ,1], center = TRUE, scale = FALSE)
obs[ ,1] = cut(obs[ ,1], c(-Inf, 0, 1, 1.4, Inf), labels = FALSE, ordered = TRUE)
obs[ ,2] = round(obs[ ,2], digits=2)
obs[ ,3] = round(obs[ ,3], digits=2)
obs[ ,4] = round(obs[ ,4])

#####
pedigree2 <- data.frame (id = aid, sire = sid, dam = did)
attach(pedigree2)
dataped <- pedigree2[pedigree2$Sid>nam2,]
simdataf3 <- data.frame (id = dataped$id, sire = dataped$sire, dam = dataped$dam, sex = isex,
herd = iherd, CE = obs[ ,1], BW = obs[ ,2], ww = obs[ ,3], pwg = obs[ ,4], CETbv = tbv[ ,1],
BWtbv = tbv[ ,2], wwtbv = tbv[ ,3], pwgtbv = tbv[ ,4])
attach(simdataf3)
nrow(simdataf3)

two_year_females_list <- c(sort(selectedfemales[ ,1]))
length(two_year_females_list)

```

```

simdataf3 <- simdataf3[simdataf3[,3] %in% two_year_females_list, ]
nrow(simdataf3)

## data file for all animals (base population, animals with records): contains true breeding values
for all animal which will be needed for calculating rank correlation (TBV with EBV from
thrgibbs1f90)
all_data_basepop_f2_f3 <- rbind(basepop_f2_data, simdataf3)
all_data_basepop_f2_f3 <- subset(all_data_basepop_f2_f3, all_data_basepop_f2_f3[,1] > nbase)

BWave_f1_f2_f3=mean(all_data_basepop_f2_f3$BW)
BWave_f1_f2_f3

BWsd_f1_f2_f3=sd(all_data_basepop_f2_f3$BW)
BWsd_f1_f2_f3
BWave_f1_f2_f3-(3*BWsd_f1_f2_f3)
BWave_f1_f2_f3+(3*BWsd_f1_f2_f3)
all_data_basepop_f2_f3 <- subset(all_data_basepop_f2_f3, BW > (BWave_f1_f2_f3-
(3*BWsd_f1_f2_f3)))
all_data_basepop_f2_f3 <- subset(all_data_basepop_f2_f3, BW <
(BWave_f1_f2_f3+(3*BWsd_f1_f2_f3)))
summary(all_data_basepop_f2_f3$BW)
nrow(all_data_basepop_f2_f3)

simdataf3 <- subset(all_data_basepop_f2_f3, all_data_basepop_f2_f3[,1] > nam2)
summary(simdataf3$BW)
nrow(simdataf3)
N_sires = length(c(sort(unique(simdataf3$sire))))
N_sires
basepop_f2_f3_data <- rbind(basepop_f2_data, simdataf3)

pedigreef3 <- data.frame (id = simdataf3$id, sire = simdataf3$sire, dam = simdataf3$dam)
base_f2_f3_ped <- rbind(pedigreef2andbase, pedigreef3)
#####
#####
# Creating F4
# 1 2 3 4 5 6 7 8 9 10 11 12 13
# id sire dam sex herd CE BW ww pwg CEtbv BWtbv wwtbv pwgtbv
#####
#####
## redefine (the total number of all animals) and (number of base population, F1, F2 and F3) in
previous simulation
#####
#total number of all animals (Used unique IDs up to now)
nam4 = nam+nam1+nam3

```

```

nbaseandf1f2 = nam2

#####
## selecting top 5% sirs and 80% dams
## selection of sires
averages=by( basepop_f2_f3_data$CEtbv, basepop_f2_f3_data$sex, mean)
ave1males=averages[1]
ave1females=averages[2]
SDs=by( basepop_f2_f3_data$CEtbv, basepop_f2_f3_data$sex, sd)
sd1males=SDs[1]
sd1females=SDs[2]

males <- subset(basepop_f2_f3_data, sex == 1)
kull2males= (males[,10]>(ave1males-(1.75*sd1males)))
males[kull2males,11]=0
selectedmales <- subset(males, males[,11] != 0)
summary(selectedmales[,7], na.rm=TRUE)
nrow(males)
nrow(selectedmales)
nrow(selectedmales)/nrow(males)

#####
## selection of dams
females <- subset(basepop_f2_f3_data, sex == 2)
kull2females= (females[,10]>(ave1females+(0.85*sd1females)))
females[kull2females,11]=0
# all selected females (females with progeny (base pop., F1 and F2) and 2 years (F3)females
without progeny)
selectedallfemales <- subset(females, females[,11] != 0)
summary(selectedallfemales[,7], na.rm=TRUE)
nrow(females)
nrow(selectedallfemales)
nrow(selectedallfemales)/nrow(females)
## only 2 years old females
selectedfemales <- subset(selectedallfemales, selectedallfemales[,1] > nbaseandf1f2)
nrow(selectedfemales)
nrow(selectedfemales)/nrow(females)
damlistf4 = c(selectedallfemales[,1])
#####
#### 1310 selected males and 59473 selected females
n_sel_males = nrow(selectedmales)
n_sel_females = nrow(selectedallfemales)
n_progeny = n_sel_females
# number of females per sire = 45.3
n_females_per_sire = n_sel_females/n_sel_males
n_females_per_sire

```

```

# because number of dams per sire is 45.3, then sires will have different numbers of progeny
(some will have 45 and others will have 46 progeny)
rounded_n_females_per_sire = round(n_females_per_sire)
rounded_n_females_per_sire
if(rounded_n_females_per_sire < n_females_per_sire) {
  n1records_per_sire = (rounded_n_females_per_sire)
  n2records_per_sire = (n1records_per_sire)+1
} else {
  n1records_per_sire = (rounded_n_females_per_sire)-1
  n2records_per_sire = (rounded_n_females_per_sire)
}

nsires_with_n1records = (n_sel_males)-((n_sel_females)-(n_sel_males*n1records_per_sire))
nsires_with_n2records = (n_sel_males)-(nsires_with_n1records)
own_record_sires_with_n1records = selectedmales[1:nsires_with_n1records, ]
selectedmales1=own_record_sires_with_n1records[rep(seq_len(nrow(own_record_sires_with_n
1records)), each=n1records_per_sire),]
own_record_sires_with_n2records = selectedmales[((nsires_with_n1records)+1):n_sel_males, ]
selectedmales2=own_record_sires_with_n2records[rep(seq_len(nrow(own_record_sires_with_n
2records)), each=n2records_per_sire),]
allselectedmales=rbind(selectedmales1,selectedmales2)
randomlymatedsires=allselectedmales[sample(nrow(allselectedmales)),]
sirelistf4 = randomlymatedsires[ ,1]

#####
selectedparents=rbind(selectedmales, selectedallfemales)
sortedselectedparents <- selectedparents[order(selectedparents[ ,1]),]

animlist = c(selectedparents[ ,1],selectedparents[ ,2], selectedparents[ ,3])
uniqueanimlist = c(sort(unique(animlist)))
uniqueanimlist = uniqueanimlist[-1]
subdata <- basepop_f2_f3_data[basepop_f2_f3_data[ ,1] %in% uniqueanimlist, ]
subdata <- data.matrix(subdata)

length(subdata[,1])
length(uniqueanimlist)
pedf4 = rbind(subdata[
,1:3],cbind(c((nam4+1):(nam4+n_progeny)),sirelistf4[1:n_progeny],damlistf4[1:n_progeny]))

#####
CEave=mean(selectedparents[ ,6], na.rm=TRUE)
CEave
BWave=mean(selectedparents[ ,7], na.rm=TRUE)
BWave
WWave=mean(selectedparents[ ,8], na.rm=TRUE)
WWave

```

```

PWGave=mean(selectedparents[ ,9], na.rm=TRUE)
PWGave
#####
library(MASS)

set.seed(1234)
herdCE=(rnorm(120,0))*0.05
set.seed(1234)
herdBW=(rnorm(120,0))
set.seed(1234)
herdWW=(rnorm(120,0))*2
set.seed(1234)
herdPWG=(rnorm(120,0))*0.1
herd=matrix(data=c(herdCE,herdBW,herdWW,herdPWG),byrow=TRUE,nrow=4)
sex=matrix(data=c(0.108,-0.108,2,-1,10,-7,0.060,-0.040),byrow=TRUE,nrow=4)
# Residual matrix
R=matrix(data=c(1,1.13,0.46,0.48,1.13,20.5,30.37,8.78,0.46,30.37,534,29.87,0.48,8.78,29.87,26
1),byrow=TRUE,nrow=4)
# G matrix
G=matrix(data=c(0.24,1.11,1.6,1.51,1.11,9.67,23.11,14.65,1.6,23.11,221,103,1.51,14.65,103,217
),byrow=TRUE,nrow=4)

####averages: 1.36198 34.59145 235.868 977.412
mu=c(CEave,BWave,WWave,PWGave)
anwr=c((nam4+1):(nam4+n_progeny))
aid = c(pedf4[ ,1])
sid = c(pedf4[ ,2])
did <- c(pedf4[ ,3])

#number of herds
length(unique(selectedallfemales[ ,5]))
iherd=c(selectedallfemales[ ,5])
set.seed(123)
isex=(rbinom(n_progeny, 1, 0.6))+1

# heritability of traits
gd=diag(G)
rd=diag(R)
h2=gd/(gd+rd)
h2

# correlations among traits
# Function to calculate correlations from a covariance matrix
CORMAT=function(Q) {
  D = diag(Q)
  D = sqrt(D)

```

```

B = diag(1/D)
HC = B %**% Q %**% B
HC }
CORMAT(R)
CORMAT(G)
# Get cholesky decompositions of G and R
LG = t(chol(G))
LR = t(chol(R))

# Simulate true breeding values for all animals
# J MATRIX FUNCTION
jd = function(n,m){
  matrix(c(1,n),nrow=n,ncol=m)}

nam5=n_progeny
mendelian = jd(nam5,4)*0
for(i in 1:nam5){
  mendelian[i, ] = LG %**% (rnorm(4,0,1))
}
damtbv= selectedallfemales[ ,10:13]
siretbv= randomlymatedsires[ ,10:13]
parentsaveragetbv=0.5*(damtbv + siretbv)
tbv=mendelian+parentsaveragetbv

nrec=n_progeny
# Make an observation for all traits for all animals
obser = jd(nrec,4)*0
for(k in 1:nrec){
  kherd=iherd[k]
  ksex=isex[k]

  obser[k, ]=mu + herd[ ,kherd] + sex[ ,ksex]
  res = LR %**% rnorm(4,0,1)
  obser[k, ]=obser[k, ] + res
}
obs = obser + tbv
obs[ ,1] = scale(obs[ ,1], center = TRUE, scale = FALSE)
obs[ ,1] = cut(obs[ ,1], c(-Inf, 0, 1, 1.4, Inf), labels = FALSE, ordered = TRUE)
obs[ ,2] = round(obs[ ,2], digits=2)
obs[ ,3] = round(obs[ ,3], digits=2)
obs[ ,4] = round(obs[ ,4])

#####

pedigree3 <- data.frame (id = aid, sire = sid, dam = did)
attach(pedigree3)

```

```

dataped <- pedigree3[pedigree3$Id>nam4,]
simdataf4 <- data.frame (id = dataped$Id, sire = dataped$sire, dam = dataped$dam, sex = isex,
herd = iherd, CE = obs[ ,1], BW = obs[ ,2], ww = obs[ ,3], pwg = obs[ ,4], CEtbv = tbv[ ,1],
BWtbv = tbv[ ,2], wwtbv = tbv[ ,3], pwgtbv = tbv[ ,4])
attach(simdataf4)
nrow(simdataf4)

two_year_females_list <- c(sort(selectedfemales[ ,1]))
length(two_year_females_list)
simdataf4 <- simdataf4[simdataf4[ ,3] %in% two_year_females_list, ]
nrow(simdataf4)

## data file for all animals (base population, animals with records): contains true breeding values
for all animal which will be needed for calculating rank correlation
all_data_basepop_f2_f3_f4 <- rbind(basepop_f2_f3_data, simdataf4)
all_data_basepop_f2_f3_f4 <- subset(all_data_basepop_f2_f3_f4, all_data_basepop_f2_f3_f4[
,1] > nbase)

BWave_f1_f2_f3_f4 = mean(all_data_basepop_f2_f3_f4$BW)
BWave_f1_f2_f3_f4

BWsd_f1_f2_f3_f4 = sd(all_data_basepop_f2_f3_f4$BW)
BWsd_f1_f2_f3_f4
BWave_f1_f2_f3_f4 - (3 * BWsd_f1_f2_f3_f4)
BWave_f1_f2_f3_f4 + (3 * BWsd_f1_f2_f3_f4)
all_data_basepop_f2_f3_f4 <- subset(all_data_basepop_f2_f3_f4, BW > ((BWave_f1_f2_f3_f4) -
(3 * BWsd_f1_f2_f3_f4)))
all_data_basepop_f2_f3_f4 <- subset(all_data_basepop_f2_f3_f4, BW <
((BWave_f1_f2_f3_f4) + (3 * BWsd_f1_f2_f3_f4)))
summary(all_data_basepop_f2_f3_f4$BW)
nrow(all_data_basepop_f2_f3_f4)

simdataf4 <- subset(all_data_basepop_f2_f3_f4, all_data_basepop_f2_f3_f4[ ,1] > nam4)
summary(simdataf4$BW)
nrow(simdataf4)
N_sires = length(c(sort(unique(simdataf4$sire))))
N_sires
basepop_f2_f3_f4_data <- rbind(basepop_f2_f3_data, simdataf4)
nrow(basepop_f2_f3_f4_data)
pedigreef4 <- data.frame (id = simdataf4$id, sire = simdataf4$sire, dam = simdataf4$dam)
base_f2_f3_f4_ped <- rbind(base_f2_f3_ped, pedigreef4)

#####
#####
## see how many records per sire
try <- subset(basepop_f2_f3_f4_data, basepop_f2_f3_f4_data[ ,1] > nbase)

```

```

nrow(try)
ones = c(rep(1,(nrow(try))))
try = data.matrix(try)
try = cbind(try,ones)
ham=sort(by( try[ ,14], try[ ,2], length))
head(ham)
#####
#####
## Final data files (2 and 3 calving ease categories)
## pedigree file
## data file for animals with records (will be used for thrigibbs1f90)
data_anim_with_record <- subset(basepop_f2_f3_f4_data, basepop_f2_f3_f4_data[ ,1] > nbase)
summary(data_anim_with_record$CE)
## change CE scores to be 3 categories
data_anim_with_record$CE <- replace(data_anim_with_record$CE, data_anim_with_record$CE
== 4,3)
## Final data (3 categories) ready for thrigibbs1f90
sel_CE_3cat_data <- data_anim_with_record
summary(sel_CE_3cat_data$CE)

## pedigree file
sel_CE_pedigree<- base_f2_f3_f4_ped

## change CE scores to be 2 categories (binary)
sel_CE_3cat_data$CE <- replace(sel_CE_3cat_data$CE, sel_CE_3cat_data$CE == 3,2)
sel_CE_bin_data <- sel_CE_3cat_data
summary(sel_CE_bin_data$CE)

```

**APPENDIX C: AVERAGE STANDARDIZED EPD FOR CALVING EASE AND
GROWTH-RELATED TRAITS OF FIRST-CALF HEIFER POPULATION OF THE
SIMMENTAL BEEF CATTLE**

Table C.1: Average standardized EPD for calving ease and growth-related traits of first-calf Simmental heifers

Birth year	Trait _{effect} ¹							
	CE _d	BWT _d	205-d WT _d	160-d gain	365-d WT	CE _m	BWT _m	205-d WT _m
≤ 1969	0.00001	0.00834	-0.01357	-0.01335	-0.02692	0.00001	-0.01276	-0.02982
1970	0.04789	-0.03613	-0.10249	-0.06637	-0.16886	-0.06885	-0.05867	-0.14234
1971	0.01398	-0.02843	-0.08225	-0.05290	-0.13515	-0.06096	-0.04233	-0.11976
1972	-0.02130	-0.03226	-0.09273	-0.08329	-0.17602	-0.05126	-0.04569	-0.11699
1973	-0.04084	-0.03303	-0.08706	-0.07945	-0.16651	-0.01867	-0.06067	-0.12290
1974	-0.07218	-0.02244	-0.07249	-0.07772	-0.15022	0.01171	-0.07012	-0.13064
1975	-0.08460	-0.01729	-0.06044	-0.05552	-0.11596	0.03129	-0.06169	-0.12780
1976	-0.08846	-0.01593	-0.03328	-0.03759	-0.07087	0.05133	-0.03632	-0.11077
1977	-0.09817	-0.00872	-0.00822	-0.01782	-0.02604	0.07717	-0.03662	-0.10320
1978	-0.09151	-0.00069	0.01196	0.00657	0.01853	0.11021	-0.03111	-0.09787
1979	-0.09893	0.00941	0.02850	0.01682	0.04533	0.13272	-0.03055	-0.09055
1980	-0.09992	0.02848	0.06416	0.04500	0.10916	0.16106	-0.02432	-0.08458
1981	-0.11005	0.05349	0.09211	0.05442	0.14653	0.17761	-0.01491	-0.08149
1982	-0.11706	0.07764	0.12573	0.08517	0.21091	0.21070	-0.01296	-0.08174
1983	-0.12037	0.09843	0.15457	0.10949	0.26406	0.23553	-0.00878	-0.07013
1984	-0.13006	0.13072	0.19201	0.13940	0.33142	0.26449	0.00128	-0.06617
1985	-0.12902	0.14962	0.23025	0.17552	0.40578	0.28748	0.01428	-0.06217
1986	-0.14431	0.17920	0.26511	0.20628	0.47139	0.30032	0.01645	-0.05678
1987	-0.14059	0.19365	0.29605	0.23604	0.53210	0.31258	0.02330	-0.05647
1988	-0.14978	0.21649	0.33647	0.25846	0.59494	0.32295	0.01265	-0.05479
1989	-0.14923	0.23361	0.37138	0.29107	0.66245	0.34083	0.01818	-0.04934
1990	-0.14598	0.24740	0.40096	0.31089	0.71185	0.35094	0.01909	-0.04491
1991	-0.14537	0.25706	0.42701	0.32623	0.75324	0.36169	0.01551	-0.04129
1992	-0.14560	0.28967	0.47646	0.36164	0.83810	0.37392	0.02574	-0.03775
1993	-0.15632	0.31891	0.50371	0.38018	0.88389	0.38087	0.03064	-0.03762
1994	-0.14977	0.33445	0.52217	0.39548	0.91765	0.38300	0.02215	-0.02411
1995	-0.15943	0.36738	0.54570	0.41242	0.95812	0.38769	0.01710	-0.02217

¹CE_d = calving ease direct; BWT_d = birth weight direct; 205-d WT_d = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; ¹CE_m = calving ease maternal; BWT_m = birth weight maternal; 205-d WT_m = 205-d weight maternal

Table C.1 (cont.)

Birth year	Trait _{effect} ¹							
	<i>CEd</i>	<i>BWTd</i>	205-d <i>WTd</i>	160-d gain	365-d WT	<i>CEm</i>	<i>BWTm</i>	205-d <i>WTm</i>
1996	-0.16494	0.39318	0.56706	0.41922	0.98628	0.39146	0.01869	-0.00010
1997	-0.17093	0.41368	0.58362	0.43351	1.01712	0.38761	0.02497	0.00823
1998	-0.17534	0.42649	0.60148	0.43736	1.03883	0.38286	0.01796	0.02371
1999	-0.18387	0.44720	0.62055	0.44683	1.06738	0.37938	0.01319	0.03185
2000	-0.15738	0.42365	0.61613	0.44415	1.06028	0.36007	0.01076	0.04474
2001	-0.15978	0.43007	0.62390	0.45547	1.07936	0.34418	-0.00201	0.05184
2002	-0.13122	0.40222	0.61694	0.45289	1.06983	0.33829	0.00601	0.06975
2003	-0.13003	0.39308	0.60706	0.44519	1.05225	0.31294	-0.01165	0.07981
2004	-0.10288	0.35681	0.60029	0.44580	1.04609	0.30557	-0.00046	0.07171
2005	-0.08362	0.32949	0.58302	0.42818	1.01119	0.28180	-0.01138	0.08001
2006	-0.07916	0.31133	0.55908	0.41513	0.97420	0.26984	-0.00161	0.06932
2007	-0.07758	0.30601	0.55471	0.39884	0.95355	0.27473	-0.01144	0.06727
2008	-0.07942	0.30807	0.56059	0.39657	0.95716	0.25880	-0.02375	0.08398
2009	-0.05169	0.26851	0.53637	0.38726	0.92363	0.24765	-0.01287	0.08567
2010	-0.05541	0.27816	0.56471	0.39516	0.95987	0.25427	-0.02976	0.08913

¹*CEd* = calving ease direct; *BWTd* = birth weight direct; 205-d *WTd* = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; ¹*CEm* = calving ease maternal; *BWTm* = birth weight maternal; 205-d *WTm* = 205-d weight maternal

**APPENDIX D: AVERAGE STANDARDIZED EPD FOR CALVING EASE AND
GROWTH-RELATED TRAITS FROM DIFFERENT SELECTION SCENARIOS FOR
LOW BIRTH WEIGHT VERSUS HIGH CALVING EASE**

Table D.1: Average standardized EPD¹ for calving ease and growth traits of first-calf Simmental heifers from the high calving ease selection scenario (HCE)²

BY	CE _d	BWT _d	205-d WT _d	160-d gain	365-d WT	CE _m	BWT _m	205-d WT _m
≤ 1969	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
1970	0.04141	-0.03455	-0.01964	-0.00637	-0.02602	0.00159	0.00308	0.00758
1971	0.06829	-0.05773	-0.03064	-0.00102	-0.03166	0.00560	-0.01929	0.00453
1972	0.08883	-0.07443	-0.03720	0.00007	-0.03713	0.01974	-0.02762	0.01736
1973	0.10655	-0.07914	-0.04091	0.01260	-0.02831	0.00739	-0.01313	0.02123
1974	0.13382	-0.10369	-0.05952	-0.00011	-0.05962	-0.02077	0.01560	0.03041
1975	0.15336	-0.12328	-0.05788	-0.00350	-0.06138	-0.01806	0.00475	0.03478
1976	0.15459	-0.13422	-0.07291	-0.02526	-0.09817	-0.01922	-0.00639	0.03825
1977	0.15405	-0.13033	-0.07087	-0.01732	-0.08819	-0.01650	0.00055	0.02952
1978	0.15551	-0.15078	-0.08029	-0.02652	-0.10681	-0.02230	-0.00341	0.02443
1979	0.15625	-0.15414	-0.08122	-0.02469	-0.10591	-0.03020	0.00357	0.02739
1980	0.15256	-0.16093	-0.08600	-0.02366	-0.10966	-0.02603	-0.00444	0.02059
1981	0.15816	-0.17376	-0.09400	-0.02520	-0.11919	-0.02660	-0.00699	0.01163
1982	0.16183	-0.18867	-0.09411	-0.02820	-0.12231	-0.01461	-0.01584	0.01936
1983	0.15625	-0.18206	-0.09784	-0.03606	-0.13390	-0.01451	-0.00595	0.01069
1984	0.15919	-0.19624	-0.09300	-0.03948	-0.13249	-0.01062	-0.02515	0.00753
1985	0.16597	-0.20188	-0.09664	-0.04251	-0.13915	0.00382	-0.02364	-0.00114
1986	0.16987	-0.21430	-0.10906	-0.05433	-0.16339	-0.00513	-0.02632	-0.00276
1987	0.16949	-0.22313	-0.11566	-0.06316	-0.17883	-0.01258	-0.03572	0.00747
1988	0.17656	-0.22827	-0.12859	-0.07158	-0.20017	-0.01447	-0.02756	0.00953
1989	0.17863	-0.23799	-0.12857	-0.08032	-0.20890	-0.01607	-0.03675	0.00441
1990	0.17795	-0.24286	-0.12822	-0.08177	-0.20998	-0.01518	-0.04403	0.00023
1991	0.17880	-0.24238	-0.11610	-0.07556	-0.19165	-0.01404	-0.03283	0.00224
1992	0.18175	-0.25185	-0.11610	-0.07309	-0.18919	-0.01378	-0.03034	0.00892
1993	0.18758	-0.25953	-0.11718	-0.07180	-0.18898	-0.00944	-0.03447	0.00908
1994	0.19059	-0.26754	-0.12171	-0.07124	-0.19294	-0.00805	-0.04016	0.01328
1995	0.18375	-0.25210	-0.11867	-0.06830	-0.18698	-0.00498	-0.04710	0.01462
1996	0.18804	-0.24334	-0.11739	-0.06644	-0.18383	0.00150	-0.05141	0.01298
1997	0.17190	-0.22080	-0.11147	-0.06240	-0.17387	-0.00313	-0.04204	0.02621
1998	0.17979	-0.22092	-0.11228	-0.05909	-0.17137	0.01319	-0.03034	0.00949
1999	0.16050	-0.18748	-0.09164	-0.05111	-0.14275	0.01304	-0.01864	0.01467
2000	0.17811	-0.20727	-0.09710	-0.05056	-0.14767	0.00485	-0.01204	0.01340
2001	0.17135	-0.18865	-0.08150	-0.02916	-0.11065	0.00679	-0.00444	0.01568
2002	0.16407	-0.17954	-0.07117	-0.03113	-0.10230	-0.00566	-0.00143	0.01600
2003	0.16086	-0.17746	-0.07519	-0.02539	-0.10058	-0.00702	0.00184	0.01720
2004	0.15716	-0.17432	-0.07733	-0.03850	-0.11583	-0.00399	-0.00465	0.01566

¹CE_d = calving ease direct; BWT_d = birth weight direct; 205-d WT_d = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; CE_m = calving ease maternal; BWT_m = birth weight maternal; 205-d WT_m = 205-d weight maternal

²HCE: selection for high CE (selecting above the average sires and the top 75% dams within sires)

Table D.2: Average standardized EPD¹ for calving ease and growth traits of first-calf Simmental heifers from the low birth weight selection scenario (LBWT)²

BY	CE _d	BWT _d	205-d WT _d	160-d gain	365-d WT	CE _m	BWT _m	205-d WT _m
≤ 1969	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
1970	0.02936	-0.03650	-0.03254	-0.02012	-0.05266	-0.01043	-0.01655	-0.02129
1971	0.03356	-0.05470	-0.03948	-0.03149	-0.07097	-0.02109	-0.01271	-0.02297
1972	0.03244	-0.07023	-0.06273	-0.06097	-0.12370	-0.02653	-0.01589	-0.02613
1973	0.04998	-0.08301	-0.05774	-0.04074	-0.09848	-0.04623	0.00371	-0.02237
1974	0.08440	-0.12329	-0.08702	-0.03871	-0.12574	-0.05596	0.00971	-0.02363
1975	0.09929	-0.14175	-0.08986	-0.04467	-0.13453	-0.04781	-0.00442	-0.00821
1976	0.10908	-0.15923	-0.10225	-0.05463	-0.15688	-0.04995	-0.00457	-0.00197
1977	0.11002	-0.16191	-0.10642	-0.05825	-0.16467	-0.05135	-0.01013	-0.00716
1978	0.12448	-0.18437	-0.11320	-0.06186	-0.17506	-0.04445	-0.00543	-0.00466
1979	0.12696	-0.18702	-0.11054	-0.05735	-0.16789	-0.05667	-0.00607	0.00095
1980	0.13342	-0.20326	-0.12490	-0.06568	-0.19057	-0.04905	-0.00996	-0.00425
1981	0.14067	-0.22027	-0.13474	-0.06339	-0.19813	-0.05201	-0.01385	-0.00284
1982	0.14621	-0.23189	-0.14301	-0.06756	-0.21057	-0.04593	-0.02087	0.00073
1983	0.14363	-0.23083	-0.14072	-0.07631	-0.21703	-0.04496	-0.01349	0.00156
1984	0.13952	-0.24373	-0.14710	-0.08461	-0.23171	-0.05788	-0.02911	-0.00239
1985	0.14640	-0.25098	-0.14372	-0.08707	-0.23079	-0.04473	-0.02731	-0.00619
1986	0.14213	-0.25215	-0.14899	-0.09885	-0.24784	-0.04522	-0.03149	-0.00705
1987	0.14735	-0.26468	-0.15467	-0.10003	-0.25471	-0.04676	-0.03431	0.00324
1988	0.15551	-0.27297	-0.16264	-0.10454	-0.26719	-0.03956	-0.02759	0.00371
1989	0.15899	-0.28583	-0.16910	-0.11165	-0.28074	-0.03845	-0.03241	0.00184
1990	0.15996	-0.29001	-0.16579	-0.11203	-0.27782	-0.03312	-0.03338	0.00348
1991	0.15883	-0.29596	-0.15760	-0.10602	-0.26361	-0.02733	-0.02580	0.00011
1992	0.16307	-0.30814	-0.16139	-0.11907	-0.28046	-0.04448	-0.01879	0.01492
1993	0.17393	-0.32547	-0.17004	-0.11142	-0.28146	-0.03880	-0.02477	0.01098
1994	0.17303	-0.32438	-0.16729	-0.11388	-0.28117	-0.03708	-0.02847	0.01794
1995	0.18595	-0.33418	-0.18210	-0.11961	-0.30171	-0.03881	-0.04691	0.01716
1996	0.18013	-0.30647	-0.17205	-0.10958	-0.28163	-0.03854	-0.04462	0.01348
1997	0.16212	-0.28126	-0.16549	-0.10784	-0.27332	-0.03712	-0.04933	0.01811
1998	0.16696	-0.27419	-0.16681	-0.11018	-0.27698	-0.02332	-0.03606	0.00605
1999	0.14531	-0.23837	-0.15206	-0.10084	-0.25290	-0.02638	-0.02706	0.00367
2000	0.15442	-0.23918	-0.13740	-0.09280	-0.23020	-0.01925	-0.02606	0.01190
2001	0.15096	-0.22520	-0.12935	-0.07742	-0.20677	-0.01651	-0.00490	0.02217
2002	0.14176	-0.21165	-0.11074	-0.06637	-0.17711	-0.02668	-0.00947	0.01671
2003	0.14396	-0.21225	-0.11353	-0.06067	-0.17420	-0.02195	0.00161	0.00933
2004	0.14137	-0.20735	-0.11271	-0.06661	-0.17933	-0.02485	-0.00848	0.01168

¹CE_d = calving ease direct; BWT_d = birth weight direct; 205-d WT_d = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; CE_m = calving ease maternal; BWT_m = birth weight maternal; 205-d WT_m = 205-d weight maternal

²LBWT: selection for high CE (selecting below the average sires and the top 75% dams within sires)

Table D.3: Average standardized EPD¹ for calving ease and growth traits of first-calf Simmental heifers from Dickerson's selection index scenario (DSI)²

BY	CEd	BWTd	205-d WTd	160-d gain	365-d WT	CEm	BWTm	205-d WTm
≤ 1969	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
1970	0.02729	-0.03806	0.00178	0.00982	0.01160	0.01102	-0.00461	0.03336
1971	0.03184	-0.04553	0.00047	0.00669	0.00716	0.01272	-0.01010	0.01741
1972	0.04952	-0.06004	0.01133	0.02296	0.03429	0.02136	-0.00768	0.03243
1973	0.06412	-0.07240	0.00151	0.02270	0.02421	0.00224	0.00012	0.03011
1974	0.06993	-0.08476	-0.01354	0.01997	0.00643	-0.00462	0.00376	0.02241
1975	0.08766	-0.10022	-0.01761	0.01971	0.00210	0.00193	0.00754	0.03130
1976	0.09015	-0.10812	-0.02013	0.01932	-0.00081	0.00486	0.01391	0.03898
1977	0.09126	-0.11154	-0.02813	0.01307	-0.01506	-0.00643	0.01102	0.02921
1978	0.10035	-0.13167	-0.03464	0.00940	-0.02524	-0.00455	0.01116	0.02549
1979	0.10924	-0.14416	-0.03979	0.01483	-0.02496	-0.01014	0.01077	0.02693
1980	0.11043	-0.15159	-0.04434	0.01014	-0.03420	-0.01499	0.00888	0.02320
1981	0.11525	-0.16818	-0.05518	0.00387	-0.05132	-0.02062	0.00460	0.01712
1982	0.12166	-0.17742	-0.05565	0.00352	-0.05213	-0.00891	0.00204	0.01463
1983	0.11502	-0.17455	-0.05486	-0.00662	-0.06149	-0.00878	0.01302	0.01693
1984	0.12144	-0.19362	-0.06066	-0.01512	-0.07578	-0.00906	-0.00414	0.01110
1985	0.12411	-0.19790	-0.06300	-0.01650	-0.07950	-0.00078	-0.00115	0.01050
1986	0.12580	-0.20671	-0.06793	-0.02389	-0.09182	-0.00258	-0.00580	0.00710
1987	0.13223	-0.22604	-0.08286	-0.03461	-0.11747	-0.01203	-0.01874	0.01502
1988	0.13244	-0.22990	-0.08723	-0.03556	-0.12279	-0.00833	-0.01598	0.01029
1989	0.13663	-0.24499	-0.09021	-0.04400	-0.13421	-0.00778	-0.02263	0.01396
1990	0.14401	-0.26203	-0.10383	-0.05113	-0.15495	-0.01112	-0.02191	0.01372
1991	0.14485	-0.26265	-0.08955	-0.04358	-0.13314	-0.00083	-0.02052	0.00972
1992	0.15840	-0.27945	-0.10049	-0.05977	-0.16027	-0.01752	-0.01195	0.01978
1993	0.16750	-0.29398	-0.10542	-0.05196	-0.15738	-0.01478	-0.00801	0.01627
1994	0.17185	-0.30285	-0.11187	-0.06213	-0.17400	-0.02039	-0.01841	0.02195
1995	0.17757	-0.29491	-0.11588	-0.05685	-0.17273	-0.01614	-0.03293	0.02284
1996	0.17262	-0.27512	-0.11430	-0.05307	-0.16737	-0.02155	-0.02682	0.01911
1997	0.15860	-0.25414	-0.10459	-0.04820	-0.15278	-0.01731	-0.02875	0.02796
1998	0.15928	-0.23580	-0.09503	-0.03829	-0.13331	-0.00106	-0.01139	0.01512
1999	0.14504	-0.21391	-0.07436	-0.03051	-0.10487	-0.00092	-0.00637	0.02453
2000	0.15031	-0.21113	-0.06796	-0.02406	-0.09202	-0.00023	-0.00597	0.02269
2001	0.15772	-0.20656	-0.06141	-0.01778	-0.07919	-0.00222	0.00643	0.02232
2002	0.14315	-0.18436	-0.04435	-0.00483	-0.04917	-0.00918	-0.00241	0.03460
2003	0.14382	-0.18603	-0.04726	-0.00084	-0.04811	-0.00735	0.00896	0.02873
2004	0.14109	-0.17960	-0.05014	-0.01184	-0.06199	-0.00400	0.00747	0.02123

¹CEd = calving ease direct; BWTd = birth weight direct; 205-d WTd = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; CEm = calving ease maternal; BWTm = birth weight maternal; 205-d WTm = 205-d weight maternal

²DSI = YWT - 3.2BWT (selecting the above average sires and the top 75% dams within sires)

Table D.4: Average standardized EPD¹ for calving ease and growth traits of first-calf Simmental heifers from the all-purpose selection index scenario (API)²

BY	CE _d	BWT _d	205-d WT _d	160-d gain	365-d WT	CE _m	BWT _m	205-d WT _m
≤ 1969	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
1970	0.03463	-0.03928	-0.02504	-0.01169	-0.03672	-0.00243	-0.01080	-0.00513
1971	0.05375	-0.05585	-0.02882	-0.00617	-0.03499	-0.00031	-0.01976	-0.00811
1972	0.07921	-0.08639	-0.04105	-0.01696	-0.05801	0.01169	-0.02934	0.00814
1973	0.09608	-0.09672	-0.04844	-0.00656	-0.05501	-0.00908	-0.00191	0.00973
1974	0.11659	-0.12676	-0.07740	-0.00979	-0.08720	-0.04579	0.01868	0.00937
1975	0.13575	-0.14870	-0.07638	-0.02183	-0.09821	-0.03742	-0.00283	0.01550
1976	0.13852	-0.15654	-0.08220	-0.03351	-0.11571	-0.03932	-0.00559	0.02264
1977	0.13850	-0.15341	-0.07893	-0.02546	-0.10439	-0.03120	-0.00222	0.02310
1978	0.14304	-0.16919	-0.08059	-0.03099	-0.11158	-0.03206	-0.00036	0.01952
1979	0.14539	-0.17436	-0.08014	-0.02343	-0.10357	-0.03956	-0.00049	0.01825
1980	0.14713	-0.18447	-0.08688	-0.02653	-0.11341	-0.03924	0.00007	0.01359
1981	0.15064	-0.20050	-0.10084	-0.03041	-0.13125	-0.03850	-0.00455	0.01001
1982	0.15347	-0.21034	-0.10401	-0.03527	-0.13928	-0.02643	-0.01437	0.01255
1983	0.14862	-0.20638	-0.10623	-0.04579	-0.15203	-0.02394	-0.00134	0.00990
1984	0.14937	-0.22325	-0.10686	-0.05074	-0.15760	-0.02384	-0.02015	0.00741
1985	0.15511	-0.22442	-0.10324	-0.04989	-0.15313	-0.01086	-0.01828	0.00082
1986	0.15561	-0.23444	-0.11549	-0.06555	-0.18104	-0.01816	-0.01932	-0.00197
1987	0.15881	-0.24862	-0.12584	-0.07091	-0.19676	-0.02473	-0.02910	0.00994
1988	0.16686	-0.25946	-0.14027	-0.08035	-0.22063	-0.02235	-0.02472	0.00760
1989	0.17002	-0.27107	-0.14031	-0.08622	-0.22653	-0.02459	-0.02996	0.00795
1990	0.17265	-0.28191	-0.14937	-0.09160	-0.24097	-0.02288	-0.03424	0.00589
1991	0.17106	-0.28493	-0.13434	-0.08589	-0.22024	-0.01684	-0.02658	0.00331
1992	0.17520	-0.29581	-0.14101	-0.09580	-0.23682	-0.03073	-0.02058	0.01388
1993	0.18632	-0.31131	-0.14290	-0.08920	-0.23210	-0.02617	-0.02522	0.01176
1994	0.18531	-0.31241	-0.14435	-0.08829	-0.23264	-0.02491	-0.02877	0.01507
1995	0.19060	-0.30724	-0.14800	-0.09113	-0.23912	-0.02639	-0.04621	0.01765
1996	0.18926	-0.28794	-0.14412	-0.08221	-0.22633	-0.02167	-0.04164	0.01329
1997	0.17297	-0.26402	-0.13687	-0.07993	-0.21680	-0.02265	-0.03795	0.02640
1998	0.17823	-0.25469	-0.13137	-0.07389	-0.20526	-0.00422	-0.02526	0.01206
1999	0.16048	-0.22097	-0.10954	-0.06247	-0.17201	-0.00608	-0.01528	0.01577
2000	0.16915	-0.22625	-0.10733	-0.06223	-0.16956	-0.00491	-0.01657	0.01630
2001	0.16952	-0.21294	-0.09464	-0.04261	-0.13725	-0.00262	-0.00059	0.01893
2002	0.15945	-0.20099	-0.08283	-0.03687	-0.11970	-0.01514	0.00059	0.02313
2003	0.15612	-0.19233	-0.08213	-0.03026	-0.11238	-0.01124	0.00644	0.01724
2004	0.15243	-0.19215	-0.08249	-0.03831	-0.12080	-0.00678	0.00118	0.01819

¹CE_d = calving ease direct; BWT_d = birth weight direct; 205-d WT_d = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; CE_m = calving ease maternal; BWT_m = birth weight maternal; 205-d WT_m = 205-d weight maternal

²API = 1.3CE + 0.1WWT+0.2YWT-1.8BWT (above average sires and the top 75% dams within sires)

Table D.5: Average standardized EPD¹ for calving ease and growth traits of first-calf Simmental heifers from all-purpose sub-selection index scenario (API₁)²

BY	CE _d	BWT _d	205-d WT _d	160-d gain	365-d WT	CE _m	BWT _m	205-d WT _m
≤ 1969	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
1970	0.04260	-0.03270	-0.01428	-0.00146	-0.01574	0.00085	0.00666	0.01097
1971	0.06213	-0.04758	-0.01548	0.01064	-0.00484	0.01446	-0.01526	0.00896
1972	0.08537	-0.05718	-0.00189	0.02819	0.02630	0.03396	-0.01615	0.04298
1973	0.09534	-0.06248	-0.00674	0.03545	0.02872	0.01291	0.00905	0.04031
1974	0.10906	-0.06813	-0.01245	0.03281	0.02036	0.00977	0.02140	0.05232
1975	0.12718	-0.08140	-0.00309	0.04512	0.04203	0.02100	0.02887	0.06110
1976	0.12389	-0.08711	-0.01257	0.03396	0.02139	0.02178	0.02480	0.06265
1977	0.12806	-0.09071	-0.02022	0.03135	0.01113	0.01244	0.02500	0.05321
1978	0.13276	-0.11038	-0.02962	0.02146	-0.00816	0.00863	0.01514	0.04074
1979	0.13330	-0.11750	-0.02739	0.02598	-0.00141	0.00271	0.01965	0.04024
1980	0.13264	-0.12227	-0.03410	0.02552	-0.00858	-0.00177	0.01322	0.03230
1981	0.13717	-0.13308	-0.04172	0.01793	-0.02379	-0.00754	0.00928	0.02479
1982	0.14252	-0.14374	-0.03951	0.01664	-0.02287	0.00529	0.00460	0.02700
1983	0.13438	-0.13979	-0.04376	0.00928	-0.03448	0.00138	0.01328	0.01769
1984	0.13783	-0.14538	-0.03477	0.01051	-0.02426	0.00660	-0.00597	0.01237
1985	0.14261	-0.15297	-0.04226	0.00612	-0.03615	0.01670	-0.00339	0.00526
1986	0.14377	-0.16012	-0.04869	0.00008	-0.04862	0.01013	-0.00404	0.00819
1987	0.14679	-0.16954	-0.05706	-0.00822	-0.06527	0.00584	-0.01885	0.00945
1988	0.15207	-0.17350	-0.06401	-0.01074	-0.07476	0.00722	-0.01806	0.01095
1989	0.15587	-0.18116	-0.06276	-0.02013	-0.08289	0.00427	-0.02386	0.00453
1990	0.16000	-0.18999	-0.06186	-0.02184	-0.08370	0.00251	-0.03328	0.00415
1991	0.16109	-0.19519	-0.05447	-0.02016	-0.07463	0.00739	-0.02445	0.00384
1992	0.16603	-0.20675	-0.06010	-0.02526	-0.08537	0.00374	-0.02308	0.01192
1993	0.17037	-0.21461	-0.06029	-0.02230	-0.08259	0.00675	-0.02114	0.01186
1994	0.17752	-0.22513	-0.06864	-0.02633	-0.09497	0.00370	-0.03439	0.01393
1995	0.17347	-0.21741	-0.07181	-0.02766	-0.09947	0.00955	-0.04164	0.01799
1996	0.18033	-0.21362	-0.07437	-0.02594	-0.10031	0.01093	-0.03720	0.01326
1997	0.16317	-0.18971	-0.06842	-0.02500	-0.09341	0.00857	-0.03612	0.02756
1998	0.16829	-0.18354	-0.06371	-0.01588	-0.07959	0.02457	-0.02273	0.01233
1999	0.15423	-0.16141	-0.04684	-0.01178	-0.05863	0.02759	-0.01256	0.01737
2000	0.16297	-0.16162	-0.04350	-0.00677	-0.05027	0.02026	-0.00567	0.01675
2001	0.15922	-0.15917	-0.04134	0.00177	-0.03957	0.02502	0.00123	0.01242
2002	0.15248	-0.14581	-0.03029	0.00761	-0.02267	0.01392	0.00871	0.02529
2003	0.14908	-0.14634	-0.03379	0.00905	-0.02474	0.00687	0.01234	0.02327
2004	0.15219	-0.15105	-0.03765	-0.00115	-0.03880	0.01122	0.00711	0.02780

¹CE_d = calving ease direct; BWT_d = birth weight direct; 205-d WT_d = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; CE_m = calving ease maternal; BWT_m = birth weight maternal; 205-d WT_m = 205-d weight maternal

²API₁ = 1.3CE + 0.2YWT (above average sires and the top 75% dams within sires)

Table D.6: Average standardized EPD¹ for calving ease and growth traits of first-calf Simmental heifers from the all-purpose sub-selection index scenario (API₂)²

BY	CEd	BWTd	205-d WTd	160-d gain	365-d WT	CEm	BWTm	205-d WTm
≤ 1969	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000	0.00000
1970	0.03037	-0.04039	-0.03029	-0.01682	-0.04711	-0.00876	-0.01901	-0.01444
1971	0.02957	-0.05152	-0.02909	-0.02365	-0.05274	-0.01223	-0.00938	-0.01317
1972	0.05066	-0.07413	-0.03289	-0.02063	-0.05352	-0.00864	-0.01817	-0.00246
1973	0.06568	-0.08983	-0.02736	-0.00404	-0.03140	-0.02361	-0.00249	0.00007
1974	0.07858	-0.11373	-0.05556	-0.01636	-0.07192	-0.04608	0.00561	-0.01231
1975	0.10358	-0.14148	-0.07699	-0.03129	-0.10828	-0.03960	-0.00005	0.00407
1976	0.11089	-0.15488	-0.08978	-0.04284	-0.13263	-0.04429	-0.00397	0.00663
1977	0.11177	-0.15632	-0.08586	-0.04015	-0.12601	-0.04103	-0.00785	0.00570
1978	0.12381	-0.17591	-0.09232	-0.04075	-0.13308	-0.03956	0.00056	0.00410
1979	0.12727	-0.17966	-0.09015	-0.03565	-0.12581	-0.04981	0.00057	0.00481
1980	0.13309	-0.19386	-0.09881	-0.03918	-0.13799	-0.04767	-0.00069	0.00009
1981	0.13819	-0.21064	-0.11268	-0.04335	-0.15603	-0.04826	-0.00871	0.00082
1982	0.14252	-0.21992	-0.11735	-0.04729	-0.16464	-0.03707	-0.01667	0.00324
1983	0.13927	-0.21901	-0.11814	-0.05776	-0.17590	-0.03609	-0.00680	0.00715
1984	0.13465	-0.23084	-0.12042	-0.06190	-0.18232	-0.04510	-0.02044	0.00314
1985	0.13887	-0.23454	-0.11545	-0.05943	-0.17488	-0.03688	-0.01128	0.00395
1986	0.13839	-0.24274	-0.12427	-0.07347	-0.19774	-0.03612	-0.01676	-0.00060
1987	0.14400	-0.25535	-0.13249	-0.07616	-0.20865	-0.03727	-0.02354	0.01124
1988	0.15106	-0.26460	-0.14302	-0.08549	-0.22851	-0.03085	-0.01999	0.00754
1989	0.15506	-0.27677	-0.14453	-0.08881	-0.23334	-0.03012	-0.02588	0.00816
1990	0.15927	-0.29024	-0.15358	-0.09619	-0.24977	-0.02769	-0.02635	0.00719
1991	0.15852	-0.29399	-0.13984	-0.08848	-0.22832	-0.02107	-0.02082	0.00352
1992	0.16576	-0.30802	-0.14897	-0.10607	-0.25504	-0.03887	-0.01587	0.01704
1993	0.17564	-0.32261	-0.15603	-0.09705	-0.25307	-0.03390	-0.02091	0.01342
1994	0.17576	-0.32323	-0.15318	-0.10032	-0.25350	-0.03196	-0.02687	0.01999
1995	0.18476	-0.32420	-0.16200	-0.10205	-0.26405	-0.03480	-0.04274	0.02190
1996	0.17825	-0.29654	-0.15505	-0.09302	-0.24807	-0.03524	-0.04328	0.01665
1997	0.16182	-0.27620	-0.14997	-0.09098	-0.24094	-0.03243	-0.04359	0.02521
1998	0.16357	-0.26076	-0.14295	-0.08508	-0.22803	-0.01868	-0.02693	0.01287
1999	0.14513	-0.23244	-0.12343	-0.07426	-0.19770	-0.01777	-0.01625	0.01743
2000	0.15328	-0.23220	-0.11287	-0.06831	-0.18118	-0.01281	-0.01943	0.02257
2001	0.16009	-0.22465	-0.10861	-0.05512	-0.16373	-0.01526	-0.00026	0.02310
2002	0.14308	-0.20570	-0.09373	-0.04998	-0.14371	-0.02322	-0.00519	0.02149
2003	0.14475	-0.20649	-0.09433	-0.04333	-0.13765	-0.01869	0.00487	0.01014
2004	0.14210	-0.20236	-0.09364	-0.05058	-0.14422	-0.01856	-0.00301	0.01504

¹CEd = calving ease direct; BWTd = birth weight direct; 205-d WTd = 205-d weight direct; 160-d gain = 160-d postweaning gain direct; 365-d WT = 365-d weight direct; CEm = calving ease maternal; BWTm = birth weight maternal; 205-d WTm = 205-d weight maternal

²API₂ = 0.2YWT-1.8BWT (above average sires and the top 75% dams within sires)

**APPENDIX E: AVERAGE NET PROFIT FROM VARIOUS SELECTION SCENARIOS
EXPRESSED AS A DEVIATION FROM THE SIMMENTAL CATTLE NET PROFIT
(CONTROL)**

Table E.1: Average net profit¹ (\$), as deviation from Simmental cattle, for various selection scenarios

BY	Selection scenario ²					
	<i>HCE</i>	<i>LBWT</i>	<i>DSI</i>	<i>API</i>	<i>API₁</i>	<i>API₂</i>
≤ 1969	0.0000	0.0000	0.0000	0.0000	0.0000	0.0000
1970	4.5052	3.0670	3.4040	3.7772	4.6892	3.2646
1971	7.5099	3.6008	3.9420	5.9683	6.9655	3.2996
1972	9.7905	3.2731	6.1716	8.8121	9.7387	5.7591
1973	11.7179	5.4288	7.7423	10.6757	10.8314	7.6753
1974	14.5793	9.2275	8.3336	12.8657	12.2459	8.9581
1975	16.8381	10.9420	10.3255	15.0633	14.4554	11.5930
1976	16.8228	11.9934	10.6576	15.3209	14.0276	12.3220
1977	16.7851	12.0605	10.6976	15.3589	14.4099	12.4875
1978	17.0502	13.7529	11.8103	15.9817	14.9946	13.9138
1979	17.1706	14.0967	12.8692	16.3403	15.1925	14.3711
1980	16.8380	14.7758	13.0147	16.5628	15.1148	15.0455
1981	17.4883	15.6552	13.5786	16.9651	15.5981	15.6206
1982	18.0398	16.2652	14.3527	17.3225	16.3020	16.1159
1983	17.2971	15.9588	13.5797	16.6881	15.3273	15.6993
1984	17.8129	15.5898	14.3803	16.9494	15.8545	15.3308
1985	18.5257	16.4111	14.6786	17.5962	16.3416	15.8788
1986	18.8880	15.8644	14.8725	17.5588	16.4512	15.7626
1987	18.8437	16.4979	15.5694	17.9335	16.7490	16.4022
1988	19.4507	17.3341	15.5903	18.6939	17.2560	17.0844
1989	19.7368	17.7500	16.1380	19.1341	17.7025	17.6183
1990	19.7262	17.9361	16.9357	19.4181	18.2408	18.0879
1991	19.9687	18.0176	17.2214	19.4849	18.5058	18.2473
1992	20.4083	18.4945	18.6218	19.9220	19.0742	18.9740
1993	21.0992	19.7881	19.7390	21.2793	19.6370	20.1547
1994	21.4672	19.6959	20.1727	21.1806	20.3944	20.1854
1995	20.6175	20.9555	20.6434	21.5979	19.8392	21.0157
1996	20.9644	20.1633	19.9177	21.3021	20.4741	20.1143
1997	19.1074	18.0701	18.3376	19.4154	18.4744	18.2341
1998	19.9264	18.4463	18.3249	19.9237	19.0201	18.3189
1999	17.7780	15.9666	16.8392	17.9608	17.4898	16.3237
2000	19.7843	17.1105	17.4470	18.9414	18.4520	17.3010
2001	19.1380	16.7483	18.2524	19.0532	18.1094	18.0227
2002	18.3697	15.8844	16.7209	18.0220	17.3925	16.2145
2003	18.0056	16.1231	16.8052	17.6144	17.0231	16.4300
2004	17.4859	15.7659	16.3453	17.1822	17.3038	16.0680

¹ The net profit was calculated using the all-purpose selection index (API)

²HCE = single trait selection for high calving ease; LBWT = single trait selection for low birth weight; DSI = YWT - 3.2 BWT; API = 1.3CE + 0.1WWT+0.2YWT-1.8BWT; API₁ = 1.3CE + 0.2YWT; API₂ = 0.2YWT-1.8BWT