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Application of genetic markers for evaluation of residual feed intake in beef cattle

by

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Dedicated to the Nagwalla family

ABSTRACT

Improving feed efficiency has become a top priority in beef cattle production because of the rapidly increasing cost of feed provision. However, because of the expense associated with collecting individual animal feed intake data, only a relatively small number of animals have been tested, leading to low accuracies of estimated breeding values (EBV). Three studies were conducted to demonstrate the usefulness of including DNA marker information in RFI genetic evaluations. In the first study, the effect of period of testing on RFI was assessed. Beef cattle steers were tested for feed intake, with different cohorts tested in the fall-winter and winter-spring seasons. Seasonal differences were detected although these were confounded by differences in age and weight among the seasons. Additionally, mean EBV accuracy obtained was low, ranging between 0.47 and 0.51, implying that strategies to increase this accuracy are necessary. In the 2nd study, a suite of genetic markers predictive of RFI, DMI and ADG were pre-selected using single marker regression analysis and the top 100 SNPs analyzed further in 5 replicates of the training data to provide prediction equations for RFI, DMI and ADG. Cumulative marker phenotypes (CMP) were used to predict trait phenotypes and accuracy of prediction ranged between 0.007 and 0.414. Given that this prediction accuracy was lower than the polygenic EBV accuracy, the CMP would need to be combined with EBV for effective marker assisted selection. In study 3, genomic selection (GS) theory and methodology were used to derive genomic breeding values (GEBV) for RFI, DMI and ADG. The accuracy of prediction obtained with GEBV was low, ranging from 0.223 to

0.479 for marker panel with 200 SNPs, and 0.114 to 0.246 for a marker panel with 37,959 SNPs, depending on the GS method used. The results from these studies demonstrate that the utility of genetic markers for genomic prediction of RFI in beef cattle may be possible, but will likely be more effective if a tool that combines GEBV with traditional BLUP EBV is used for selection.

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LIST OF ABBREVIATIONS

ADG	Average daily gain
AFD	Assigned feed disappearance
AI	Artificial insemination
BIF	Beef improvement federation
BLUP	Best linear unbiased prediction
BWT	Birth weight
CCA	Canadian Charolais association
CCAC	Canadian council on animal care
CE	Calving ease
CHARM	Charolais herd recording and management program
CMP	Cumulative marker phenotype
CMP^{ADG}	Cumulative marker phenotype for ADG
CMP^{DMI}	Cumulative marker phenotype for DMI
CMP^{RFI}	Cumulative marker phenotype for RFI
d. f.	Degrees of freedom
DM	Dry matter
DMI	Dry matter intake
DNA	Deoxyribonucleic acid
EBV	Estimated breeding value
EFI	Expected feed intake
EPD	Estimated progeny differences

ERT	Economically relevant trait
FCR	Feed conversion ratio
GEBV	Genomic breeding Value
GEST	Gestation length
GH	Growth hormone
GHR	Growth hormone receptor
GS	Genomic selection
IGF-I	Insulin-like growth factor I
LD	Linkage disequilibrium
LD-MAS	Linkage disequilibrium-aided marker assisted selection
logL	Model log-likelihood
LR	Likelihood ratio
LS	Least square
MAGE	Marker assisted genetic evaluation
MAS	Marker assisted selection
MBV	Molecular breeding value
ME	Metabolizable energy
MEBV	Marker-assisted breeding value
mi-RNA	micro-ribonucleic acid
MMWT	Metabolic mid-weight
MS	Marker/molecular score
MWT	Mid weight on test
NBCEC	National beef cattle evaluation consortium

NFE	Net feed efficiency (also known as NFI, net feed intake)
PEG	Partial efficiency of growth
PLS	Partial least square
PS RR-BLUP	Random regression BLUP performed after pre-selection of SNPs using single marker regression analysis
QTL	Quantitative trait loci
RFI	Residual feed intake
RFI_C	Residual feed intake calculated within contemporary group
RFI_G	Genetic residual feed intake
RFI_O	Residual feed intake calculated across several test groups
RFI_P	Phenotypic residual feed intake
RFI_S	Residual feed intake accounting for season effects
RH	Relative humidity
RHP	Resting heat production
RR-BLUP	Random regression BLUP
SC	Snell score
SI	Selection index
SLTWT	Slaughter weight
SNP	Single nucleotide polymorphism
STWT	Weight at start of test
SWT	Weight at start of test
UBF	Ultrasound back fat

CHAPTER 1 : Literature review

1.1 INTRODUCTION

Profitability in any commercial system is dictated by the balance between input and output streams of the system. In a beef cattle production system, profit may be increased by minimizing the cost of inputs, which is dominated mainly by the cost of feed, whose provision constitutes one of the highest inputs of production (Herd et al., 2003). Given the rapidly increasing global demand for grain for human consumption, animal feed and bio-fuel production, and the consequent increase in grain prices, the cost of feeding animals will remain high for the foreseeable future. This heightens the need to increase the efficiency of feed utilization even though this has been the subject of research for many decades.

Most measures of feed efficiency in young growing animals are a function of live weight and growth rate, and are mostly expressed as a ratio relative to feed intake. These include partial efficiency of growth (PEG) and feed conversion ratio (FCR). Residual Feed Intake (RFI), also known as Net Feed Efficiency (NFE; Koch et al., 1963) has been proposed as a measure of efficiency that is independent of mature animal size and production. The trait is moderately heritable and as such is a good candidate for genetic improvement. Further, the lack of correlation with production traits ensures that selection for improved efficiency does not alter these traits for cattle under selection, thereby maintaining

uniformity in terms of the physical attributes of animals, as this may be an important factor for the producer(s) involved.

Incorporation of feed efficiency into breeding objectives would increase the genetic potential for animals to have lower feed intake while maintaining the same production levels. It has been demonstrated that more efficient cattle have multiple benefits such as lower dry matter intake, less manure production as well as lower emission of methane (Okine et al., 2001; Basarab et al., 2001; Nkrumah et al., 2005). However, the main barrier to adoption of selection strategies based on RFI is the technical difficulty and expense warranted to obtain individual animal feed intake. Because of this, various indicator traits that could be used in place of RFI have been sought, but so far results have been disappointing. The prospect of using genetic markers that are predictive of RFI offers an attractive alternative to direct measurement of individual feed intake on large numbers of animals. This would allow not only increased accuracy in the genetic evaluation of RFI but also provide a means for effective marker assisted selection (MAS) of young animals before collection of their own phenotypic information. Such a scheme allows selection decision to be made early in the life of the animal, with more resources directed towards maintaining the more efficient and therefore more valuable animals. Consequently, young bulls may be sold off at a higher premium because of their potential cumulative benefits as sires of more efficient cattle.

1.1.1 Measuring feed efficiency

It is apparent that a large portion (70-75%) of the metabolizable energy (ME) of any ration is used for maintenance (Ferrell and Jenkins, 1985). Given that there is individual animal variation in maintenance requirements, there is considerable advantage in improving the efficiency of energy utilization in livestock species.

Over the years, various measures of feed efficiency have been used. Traditionally, efficiency has been defined as a ratio of feed to gain or gain to feed (Koch et al., 1963; Archer at al., 1999). Some of these ratio traits, such as partial efficiency of growth (PEG), feed conversion ratio (FCR) and maintenance efficiency have been characterized genetically (Archer et al., 1999). However, despite widespread use, these measures are undesirable because they are often correlated to growth (average daily gain, ADG) or other production traits such as mature weight (Koots et al., 1994). Also, since selective pressure on the components of a ratio trait is not predictable given that more intensity is usually placed on the component with higher variation (Gunsett, 1984), unit improvement in a ratio trait does not imply an improvement in overall efficiency, such that responses are unpredictable (Crews, 2005).

Koch et al. (1963) suggested an alternative measure that avoids many of the problems listed above, while taking advantage of individual animal variation in maintenance requirements. Residual feed intake (RFI) was originally defined as the difference obtained when an animal's actual feed intake is adjusted for growth

and maintenance requirements (Koch et al., 1963). Presently, RFI has become an even more desirable measure for characterizing feed efficiency because its definition implicitly allows inclusion of more 'energy sinks' besides growth and maintenance, such that comparisons between animals can be made across different segments of production and different stages of development while at the same time still describing individual animal differences (Crews, 2006). This is coupled with the fact that the measure is devoid of any phenotypic correlations with the measurable traits used to estimate it (Basarab et al., 2003). However, it has been shown that though RFI may be phenotypically uncorrelated with ADG and mid weight (MWT), genetically it is not (Kennedy et al., 1993). To remove such correlations, genetic RFI is often calculated. In many studies utilizing RFI in beef cattle, the correlation between genetic and phenotypic RFI is generally very high (Hoque et al., 2006; Nkrumah et al., 2007a).

Efficient animals consume less feed than expected based on their growth and maintenance requirements such that more efficient animals have a negative RFI value while inefficient animals have a positive RFI value. The mean of the trait is null within the cohort it is estimated and animals with such a value are considered to be of average efficiency.

1.1.2 Estimation of phenotypic (RFI) and genetic (RFI_G) residual feed intake

In the preceding discussion and throughout this thesis, the term "RFI" refers to phenotypic RFI, unless otherwise stated. Generally, RFI is a linear

function of feed intake, body weight and growth rate as first suggested by Koch et al. (1963). However, there is no universal mathematical formula that is currently in use, since various studies have included varied forms of 'energy sinks' while estimating RFI (eq.1, 2 and 3 below). Accurate measurements of growth (ADG) and maintenance requirements (estimated using the metabolic weight, $MWT^{0.75}$, which is initial weight plus half of gain on test) are obtained from repeated measurements of weights during a feeding trial. The estimation of maintenance requirements is thought to be best captured by using metabolic mid weight, which is a fractional power of shrunk body weight, adjusted to the three quarters power (NRC, 1996). It has previously been shown that $BWT^{0.75}$ is proportional to fasting energy expenditure such that metabolic requirements scale with body weight. Optimal feeding durations for RFI characterization have been estimated to range between 63 – 84 days depending on number of days between weights (Archer et al., 1997; Archer and Berg, 2000; Wang et al., 2006). Repeated measurement of weight reduces measurement error when estimating gain as suggested by Koch et al. (1963).

The mathematical formulae that have been used to estimate RFI are represented below as equations eq. 1 (Koch et al., 1963), eq. 2 (Archer et al., 1997) and eq. 3 (Basarab et al., 2003).

$$RFI = DMI - (\beta_0 + \beta_1 ADG + \beta_2 MWT) \qquad \text{eq. 1}$$

$$RFI = DMI - (\beta_0 + \beta_1 ADG + \beta_2 MMWT) \qquad \text{eq. 2}$$

$$RFI = DMI - (\beta_0 + \beta_1 ADG + \beta_2 MMWT + \beta_3 BF) \quad \text{eq. 3}$$

where β_1, β_2, β_3 are partial regression coefficients and β_0 the intercept; ADG is the average daily gain, BF is the end of test ultrasound back fat thickness, MWT the mid weight and MMWT is the metabolic mid weight. Feed intake is represented as daily dry matter intake (DMI) standardized to 10MJ of ME/kg DM.

Phenotypic RFI is expected to be uncorrelated with the traits used to calculate it. However, despite the lack of phenotypic correlations, RFI may still be genetically correlated with its component traits. To avoid such correlations, genetic RFI (RFI_G) is often used. Genetic RFI can be calculated using a genetic regression as

$$RFI_G = u - u^* = u - UG^{-1}k,$$

where u* is a vector containing EBV for expected feed intake from genetic regression, with dimension equal to number of animals, with u being the feed intake EBV from mixed model equations. The matrices **U**, **G** and **k** are a n x t matrix of MMWT and ADG EBV, a t x t matrix of genetic (co)variances for MMWT and ADG, and a t x 1 matrix of genetic co-variances of feed intake with MMWT and ADG, respectively. This may be extended to include any other production traits.

Typically, through multiple regression approaches, ADG and MMWT explain over 60% of the total phenotypic variation in feed intake (Basarab et al., 2003; Carstens and Tedeschi, 2006). However, other body composition traits,

such as ultrasound back fat have been incorporated in the calculation of RFI to account for the energy channeled towards fat deposition and muscle production (Basarab et al., 2003; Crews, 2006). In sheep, ultrasound muscle depth has also been included as an extra trait (François et al., 2002). However, it is presently unclear whether incorporation of body composition traits in the models for RFI estimation should be a routine measure or be data driven. It is generally agreed that ADG and MWT must be included in the estimation of RFI for growing animals. However, because of the low correlations between RFI and body composition traits, many studies have not included these traits in RFI estimation models. The disparity between data sets in the size of the correlations between body composition traits and RFI (most of the estimates of genetic correlations between back fat thickness and RFI have been small) have allowed the discordant development of the 'extended' RFI estimation models. There is increasing support in North America for the inclusion of back fat thickness in equations used to estimate RFI. However, the validity of such an exercise where no 'significant' correlation exists is in question. It remains to be determined what magnitude of a correlation is large enough to warrant inclusion of fatness traits in RFI estimation equations as a routine exercise.

1.1.3 Economic implications of residual feed intake (RFI) estimation

For accurate estimation of RFI, individual animal feed intake data has to be obtained, and this is only possible through use of expensive equipment. Estimation of pen efficiencies for group-fed animals has been attempted, and

several schemes of estimating individual animal efficiency from such intakes have been reported (Guiroy et al., 2001; Williams et al., 2006, Tedeschi et al., 2006). These systems use mathematical models to predict an animal's feed efficiency from the dry matter required based on the animal's weight and gain as well as the feed composition. However, it is only by recording individual animal feed intake that accurate estimation of RFI can be achieved without losing information on inherent differences between individuals.

Even though estimation of RFI is most often done in young growing cattle, the correlation between RFI in growing cattle and in mature cows is high (Archer et al., 2002). This is important because up to 75% of total feed costs are associated with the maintenance of the breeding cow herd. None the less, most research on RFI has been focused on young growing steers or bulls. One reason for this may be because it is typically easier to define maintenance requirements of bulls and steers as a function of body weight, given that the maintenance requirements of cows are dependent on their current position in the reproductive cycle. Also, since most cows are mostly fed forage based diets, it would be more complicated to facilitate large-scale measurement of forage intake. Further, current selection strategies are geared towards improving efficiencies of breeding sires given that a very high proportion of the genetic improvement of the cattle herd is obtained when sires pass on their characteristics to their offspring. This is because sires are mated to large numbers of dams and are subject to very high selection pressure, such that only the best sires are retained in the breeding population. Only a small proportion of cows are culled at each round of selection,

such that sire selection often drives trait improvement. Also, since a cow can only produce one calf per season, and a bull can potentially have tens of offspring every season, a breeding bull contributes a lot to the genetic makeup of the herd than a cow, despite passing only half his genetic makeup to every calf. However, given that cows stay longer in a herd, an optimal selection strategy would be one that ensures that replacement heifers are potentially daughter of efficient bulls, with the desired performance in terms of feed efficiency.

The total savings from increasing animal efficiency can be considerable especially for replacement heifers which stay longer in the herd. Selection for higher feed efficiency could potentially result in a reduction of 9-10% in maintenance costs for the cow herd, a 10-12% reduction in feed intake, reduction in methane emissions by 25-30% and manure production by 15–20% without affecting average daily gain or mature cow size (Basarab et al., 2002). The economic benefits of selecting for improved efficiency are thus sizeable.

1.1.4 Genetic evaluation of residual feed intake (RFI)

The genetic evaluation of RFI has resulted in estimates of genetic parameters and variance components comparable to those of more regularly measured traits such as growth traits. Estimates of RFI heritability have varied considerably from 0.16 (Herd and Bishop, 2000) to 0.58 (Crews et al., 2003) and considerable variation has been reported within groups of cattle tested for RFI (Herd and Bishop, 2000; Basarab et al., 2003). This large range of heritability estimates for RFI reflects the inadequacy of characterizing genetic parameters for

a relatively new trait such as RFI. Given that only a few animals (beef cattle) worldwide have been tested for individual feed intake, sample sizes used to estimate these parameters have been invariably small compared to other more regularly measured traits. It is to be expected that as sample sizes increase, the heritability will converge to a more narrow range of values. However, from these estimates, it is apparent that polygenic selection can lead to significant gain in efficiency as demonstrated by divergent selection studies in Australian cattle (Richardson et al., 1998; Arthur et al., 2001c). These studies reported that from 5 years (2 generations) of divergent selection in Angus cattle, more efficient animals (low RFI) consumed 1.2kg DM less than inefficient animals (high RFI).

One of the reasons why RFI is deemed a more appropriate measure of efficiency is its lack of correlation with growth rate, maturity patterns, and body weight. This lack of correlation implies that selection for RFI will result in minimal correlated response in other traits of interest. This is important because if such correlated traits are not included in the selection index used for RFI improvement, the projected targets for these traits, as enumerated in their selection objectives may not be achieved.

Significant correlations between RFI and FCR, DMI and fat depth have been described (Arthur et al., 2001b; Basarab et al., 2003; Robinson and Oddy, 2004; Nkrumah et al., 2007b). Other studies have indicated associations between RFI with carcass leanness, with more efficient animals having leaner carcasses (Herd and Bishop, 2000). The suggested incorporation of back fat thickness in the

estimation of RFI is informed by such correlations, and would enable obtaining RFI measurements that are net of any differences in body composition. Richardson et al. (2001) describe gains in efficiency after one generation of divergent selection, which were above and beyond differences in body composition, suggesting that the bulk of differences in efficiency are due to differences in maintenance requirements, probably as a result of inherent differences in the metabolic processes that underlie efficiency (Korver, 1988).

Breeding values (EBV) for RFI have not routinely been calculated because there have been only a small number of industry animals tested for individual feed intake. Because of the lower density of phenotypic data available, EBV for RFI will typically have low accuracies and several strategies may be needed to increase the accuracy before adoption of RFI EBV for selection purposes. So far, a viable indicator trait that may be used for genetic evaluation of RFI in a multivariate framework has been elusive. Multivariate analyses have been successfully utilized for genetic evaluation of hard to measure traits such are reproductive traits (fertility and calving ease) so as to increase the accuracy of the EBV obtained. Such a framework for RFI would require an easily measured trait with medium to high heritability and an equally high correlation with RFI.

The development of IGF-I as a possible indicator trait for RFI has yielded inconsistent results and may need more research. However, due to the rapid advancement of DNA marker technology after the mapping (and more recently the sequencing) of the bovine genome it is envisaged that various DNA based

tools that rely on genetic polymorphisms associated with RFI may be developed to aid in obtaining accurate estimates of genetic merit by way of molecular breeding values (MBV). Alternatively, these may be used to augment available phenotypic records in a marker assisted genetic evaluation process that yields marker-assisted breeding values (MEBV).

However, it has been variously estimated that at least 2,000 records are required for accurate estimation of marker assisted EBV (Meuwissen et al., 2001; De Roos et al, 2007; Hayes et al., 2009). This estimation has been done in relation to genomic selection in dairy cattle, where typically half-sib families are rather large and the 'phenotypes' used are sire proofs of high heritability and accuracy. In the beef cattle scenario, because of the relatively small half-sib families, and little or no progeny testing schemes, many more records may be required before accurate estimates of MEBV are obtained.

1.1.5 Prospects for genetic selection of residual feed intake (RFI)

Residual feed intake (RFI) is moderately heritable (Arthur et al., 2001b) with heritability ranging from 0.16 to 0.58 (Herd and Bishop, 2000; Crews et al., 2003). Considerable genetic variation has been demonstrated within populations and across different breeds of cattle tested for RFI (Herd and Bishop, 2000; Archer and Berg, 2000; Basarab et al., 2003). This demonstrates that selection for RFI is possible and benefits of reduced feed intake can be passed on between generations. However, single trait selection for RFI, a component trait whose underlying economic trait is feed intake is generally not recommended. This has

led to an increased need to define genetic correlations between RFI and other economic traits. Arthur et al. (2001b) reported strong genetic correlations between RFI, feed conversion ratio (FCR) and feed intake, and a weak correlation of RFI with subcutaneous fat (Table 1.1). Other studies have also associated lower RFI with a leaner carcass (Schenkel et al., 2004; Basarab et al., 2003). Given these correlations and because there is no association between RFI and growth, it would appear that variation in RFI is a reflection of between-animal differences in biological systems related to efficient feed utilization that are still largely unknown (Crews, 2006).

Richardson et al. (1998) and Arthur et al. (2001a) demonstrated that selection for RFI was effective and the benefits of improved feed efficiency can be achieved in a beef operation. Due to the minimal correlations between RFI and body composition traits, multi-trait selection can be undertaken without risk of unfavorable correlated response. Such a selection strategy would be important to ensure that appropriate economic weights are placed on the several component traits in the breeding objective thereby maximizing the benefits obtainable from selecting for increased feed efficiency. Crews et al. (2006) developed a multi-trait economic index that incorporates bull average daily gain, RFI and yearling weight. In a bid to relate biological efficiency to feedlot profitability, Carsten and Tedeschi (2006) used this index to rank market progeny of bulls tested for RFI and observed that index values ranged between 80 and 120. In their study, they observed +17% and -9% gains in ADG and feed intake respectively for the more efficient bulls (ranking higher than 105) compared to the low efficient bulls

(ranking below 95). These two classes of animals had similar yearling weights. This demonstrates that profitability can be maximized at all levels and segments of production, if industry adoption of such an index is expedited. However, measurement of the trait requires expensive and specialized equipment and this has been the major factor hindering wide-scale adoption of feed efficiency as an economically relevant trait and its inclusion in breeding programs. Effective selection could be enhanced if marker assisted evaluation tools were used. Consequently, there have been concerted efforts to develop genetic and molecular tools which indirectly measure RFI.

1.1.6 Indicator traits for residual feed intake (RFI)

Due to the expense involved in measuring individual animal feed intake, various physiological parameters have been examined as possible indicator traits for RFI. These include the measurement of the levels of insulin-like growth factor I (IGF-I) and leptin in blood samples. Even though serum leptin concentration has been shown to be associated with RFI in cattle and pigs (Nkrumah et al., 2007a; Hoque et al., 2009), its use as a possible indicator trait has not seen widespread adoption. By far, IGF-I showed the most promise as a useful indicator and has received considerable research attention. Insulin-like growth factor, IGF-I, is a hormone that regulates growth and cellular metabolism, and is secreted in response to growth hormone. Circulating levels of IGF-I have been shown to be associated with increased feed efficiency (Bishop et al., 1989; Stick et al., 1998).

The use of this physiologic marker as an indirect selection criterion for RFI has been demonstrated (Davis and Simmen, 2006).

However, even though lower IGF-I concentrations are associated with improved efficiency (r_g = 0.6), and has high heritability of 0.4 (Moore et al., 2005), IGF-I is correlated with some growth traits (Davis and Simmen, 2006) and carcass measures. To obtain a highly accurate EBV from IGF-I measures alone, much more testing would be required. The use of IGF-I in feed efficiency selection will likely be more useful where RFI data is available, where its incorporation in RFI evaluations will increase accuracy of the EBV obtained. Kahi and Hirooka (2007) used IGF-I and RFI in a selection strategy resulting in higher accuracy and profitability for Japanese black cattle. However, results from recent studies (Carstens et al., 2007; Lancaster et al., 2008) have cast doubt as to the usefulness of IGF-I as a physiologic indicator of RFI and its suitability has increasingly fallen into question. The effect of IGF-I has proven to be breed specific, with consistent correlations with RFI observed for Taurine breeds. However, inconsistent results have been obtained for Indicine and cross-bred cattle. The correlation between RFI and IGF-I has also proven to be dependent on the age of animal at the time of blood sample collection such that different collection times (e.g. pre-weaning and post-weaning) result in different correlations. Other results have also shown an unfavorable correlation between IGF-I with reproductive traits (Carstens, 2007). Echternkamp et al. (2004) and Basarab et al. (2007) have shown that high serum IGF-I levels are associated with increased twinning rate. IGF-I is thought to have a role in follicular stimulation,

proliferation, differentiation and steroidogenesis with associated inhibition of follicular apoptosis thereby leading to multiple recruitment of follicles during ovulation. Consequently, high RFI cows had higher serum IGF-I levels, increased twinning rates, low calf weights, and increased calf death. On the other hand more efficient (low RFI) cows calved 5 days later (Basarab et al., 2007). Also, because IGF-I levels are associated with fertility, very low values may lead to reproductive problems, such that selecting heavily for increased efficiency (low RFI, low IGF-I) may lead to reduced fertility in the long term. In view of these results, further studies will be needed before IGF-I can be widely applied as an indicator for RFI.

1.1.7 The molecular basis for residual feed intake (RFI)

Considerable research has been undertaken to determine the genetic basis of RFI with varying degrees of success with only a few studies having been published (Moore et al., 2006; Arthur and Herd, 2006; Nkrumah et al., 2007b; Sherman et al., 2008a,b). Nkrumah et al. (2007b) performed a primary genome scan to identify quantitative trait loci (QTL) that underlie variation in RFI in young growing steers sired by Angus, Charolais or Alberta Hybrid bulls. In this study, eight QTL for RFI, located on 8 different chromosomes and significant at the 5% chromosome-wise threshold were identified in an across-family analysis. Some of these QTL were in the same regions as those identified for traits related to RFI such as ADG, FCR and DMI suggesting shared genetic components among these traits. This is expected due to the strong and positive genetic

correlations between RFI, FCR and DMI. In a bid to narrow the confidence intervals for the detected QTL, Sherman et al. (2008b) performed a fine mapping study by increasing the number of markers around the relevant regions on four select chromosomes. This resulted in a substantial decrease in the confidence intervals of these QTL from an average of 30cM to 18.25cM. Such a narrowing of the confidence region enhances considerably the chances of finding the causative genes.

In a whole-genome association study of a population consisting of various breeds of cattle with extreme RFI values, Barendse et al., (2007) obtained 161 SNPs significantly ($P < 0.01$) associated with RFI. Of the 161 SNPs, 90 contained mi-RNA motifs while 86 contained promoter elements in the sequence flanking the SNPs. Sherman et al. (2008a,b) identified various polymorphisms associated with RFI among which was one within an intronic region of the growth hormone receptor (GHR). However, no gene governing a specific process known to have a huge impact in feed efficiency has been identified to date. These results indicate that finding a set of genes responsible for feed efficiency is still a formidable challenge, and a practical solution may be to identify a set of SNP in linkage disequilibrium (LD) with putative genes underlying the various metabolic pathways that underpin variation in RFI. These may then be combined into a panel that will be useful for marker assisted selection (MAS) and marker assisted genetic evaluation of RFI.

The transition from discovery of significantly associated polymorphisms to a viable genetic test that is commercially applicable requires that such associations undergo third party validation in independent populations to ensure consistent and repeatable results. So far two commercial gene tests for RFI (GeneStar feed efficiency from Pfizer animal health and Igenity feed efficiency from Merial Igenity) are available. However, the proportion of RFI genetic variance accounted for by these marker panels is not known. It has been suggested that for marker panels to be useful for genetic selection and evaluation purposes, they must account for over 10% of the genetic variance of RFI (Crews et al., 2008).

1.2 OVERALL OBJECTIVES

The overall objective of this research was to demonstrate the use of molecular markers for the genetic evaluation of residual feed intake (RFI).

Specific objectives were as follows

1. To assess the effect of climate parameters on feed intake and efficiency for steers tested in fall and winter seasons.
2. Estimate variance components and genetic parameters for RFI.
3. To assess the utility of SNPs preselected for association with RFI using single marker association analysis in predicting phenotypes for RFI, DMI and ADG.

4. To compare the accuracy of prediction of genomic breeding values (GEBV) derived from three genomic selection methods with RFI, DMI and ADG.

Table 1.1 Genetic correlations between residual feed intake (RFI) and production traits

Trait	R_g	Source
Back Fat	0.16 – 0.17	Arthur et al., 2001a; Schenkel et al., 2004.
FCR	0.66 – 0.85	Arthur et al., 2001a,b ; Schenkel et al., 2004 ; Herd and Bishop, 2000.
FI	0.64 – 0.81	Arthur et al., 2001a,b ; Schenkel et al., 2004 ; Herd and Bishop, 2000.
IMF/Marbling Score	-0.44	Crews et al., 2003.
REA	-0.17	Schenkel et al., 2004.
Methane	0.44	Nkrumah et al., 2006.
Feeding duration	0.43	Lancaster et al., 2005.
Heat production	0.68	Nkrumah et al., 2006.

R_g – genetic correlation

1.3 LITERATURE CITED

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CHAPTER 2 : Season of testing and its effect on feed intake and efficiency in growing beef cattle[1]

2.1 INTRODUCTION

Residual feed intake (RFI) is increasingly becoming the standard measure for evaluating feed efficiency. The trait is typically a linear function of feed intake, live weight and weight gain (Koch et al., 1963; Arthur et al., 2001) and any other measurable "energy sinks" (Crews, 2005), such as body composition, and lactational performance (Veerkamp, 1995; Montanholi et al., 2009). The intention of having RFI net of correlated traits is such that differences in efficiency between animals are due to differences in metabolic efficiency rather than in production (Crews, 2005).

Variations in animal performance occasioned by seasonal changes in environmental and climatic conditions are known to occur (Birkelo et al., 1991). Such variations are thought to be due to differences in adaptation and efficiency of energy utilization in response to the requisite energy demands. The effects of ambient temperature on animal performance have also been widely studied in beef cattle. Exposure to extended periods of cold can lead to cold stress, invoking various thermoregulatory mechanisms such that maintenance requirements remain unchanged until a critical temperature is surpassed (Young, 1983). Metabolic acclimatization due to exposure to cold temperatures has been thought to reduce performance and efficiency in animals compared to those not exposed to such

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conditions at the same level of feed intake (Young, 1981). Residual feed intake (RFI) measures individual animal differences in maintenance requirements after adjusting for growth. Consequently, due to the increased physiological load in cold conditions, RFI estimated in winter periods may represent a different trait to that obtained in warmer seasons. This study sought to compare if there were significant differences in the performance and efficiency of groups of steers tested for feed intake in two periods (Fall-Winter and Winter-Spring seasons) over 3 successive years.

2.2 MATERIALS AND METHODS

2.2.1 Animal resource and data collection

The data consisted of 378 beef steers, offspring of a cross between a composite dam line, generated as an experimental dam population after 30 yrs of selection and Angus, Charolais or University of Alberta hybrid bulls. The dams used were produced from crosses among 3 composite cattle lines, namely beef synthetic 1, beef synthetic 2, and dairy x beef synthetic (**DBS**). Beef synthetic 1 was composed of 33% Angus, 33% Charolais, and about 20% Galloway, among other beef breeds while beef synthetic 2 comprised 60% Hereford with the remaining 40% being other beef breeds. The dairy x beef synthetic was composed of approximately 60% dairy breeds (Holstein, Brown Swiss, or Simmental) and 40% beef breeds, mostly Angus and Charolais (Goonewardene et al., 2003). Sire and breed distributions for fall tested and winter tested groups are shown in Table 2.1. Feed intake data was collected using the GrowSafe automated feeding system

(GrowSafe Systems Ltd) over a period of three years with two cohorts of animals tested for feed efficiency in each year, except in year 1 where one cohort was included in the analysis (Table 2.1). Feeding behavior data (number of feeding events, feeding duration and head-down time) was also collected from the GrowSafe system and summed to obtain daily counts following similar methods as those in Basarab et al. (2003).

The test diets consisted of standard high energy feedlot diets as shown in Table 2.2 (Nkrumah et al., 2007). Each formulation of the test diet was sampled every two weeks and stored for future analysis (samples were pooled prior to analysis) to ascertain nutrient and dry matter content as described by Nkrumah et al. (2006). The testing periods lasted approximately 90 days and animals had free-choice access to feed and drinking water. Body weight (BW) data were recorded every two weeks, with the first weight obtained on the day preceding the test. The exception was for year 1 where weights were recorded weekly. The last weight was obtained as close to the end of test as possible, generally within 2 – 3 d. Ultrasound back fat thickness, measured between the 12 – 13th rib, was obtained at the end of the feed intake test using an ultrasound transducer as described by Basarab et al., (2003). All animals were cared for following the protocols and guidelines outlined by the Canadian Council on Animal Care, CCAC (1993).

Climate data (average, minimum and maximum air temperature, average relative humidity, average solar radiation and wind speed) for the years 2003-2004 (designated year 2004) and 2004-2005 (2005) was obtained from the

University of Alberta Kinsella meteorological station. The Kinsella station was installed in October 2003, such that data for 2002-2003 (2003) was obtained from the Vikings AGCM, the weather station closest to Kinsella (about 20km away).

2.2.2 Trait derivations

Each animal's average daily gain (ADG) was obtained as the slope of the regression of body weight (BW) on test days, with the intercept being the weight at start of test (SWT). Metabolic mid-weight (MMWT) was calculated as the mid-weight on test raised to 0.75 ($MW^{0.75}$). Average daily feed intake was converted into daily dry matter intake (DMI) by multiplying intake with the dry matter content of the diet. The DMI of the diet was then standardized across the different years to 10 MJ of ME/kg of DMI by multiplying intake with diet metabolizable energy (ME) content then dividing by 10 (Basarab et al., 2003). All animals tested between Sept and Jan belonged to the Fall-Winter (Season 1) test group, while those tested between Jan and May were assigned to the Winter-Spring (Season 2) test group. Individual animal RFI was calculated as the difference between an animal's average daily dry matter intake (DMI) and its expected feed intake (EFI), using one of 3 methods;

1. By fitting a regression model (eq. 1), $RFI_C = DMI - (\beta_0 + \beta_1 ADG + \beta_3 MWT)$ to each test group (cohort) separately as in Basarab et al. (2003).

2. By fitting a regression model (eq. 2), RFI_O = DMI – (β_0 +β_1Cohort + β_2ADG + β_3MWT) to pooled data (overall) consisting of all tests groups but including test group as a fixed effect (Arthur et al., 2001).

3. Or by fitting a regression model (eq. 3), RFI_S = DMI – (β_0 +β_1Cohort + β_2ADG + β_3MWT) to pooled data with test group as a fixed effect but within seasonal (Fall-Winter (1) or Winter-Spring (2)) groups.

where, β_0 is the intercept and β_1, β_2, β_3 are partial regression coefficients, and Cohort is a group of steers tested together for feed intake. Models 2 and 3 assume that regressions of DMI on ADG and MWT are the same across groups, with Model 3 allowing for separate regressions within season, while model 1 considers regression within group thus allowing for different residual variances between groups. Other traits evaluated included ultrasound back fat (UBF), measured at the end of test, body weight at start of test (SWT), and body weight at slaughter (SLTWT), measured one day before animals were shipped to slaughter.

2.2.3 Statistical analysis

Least square means and differences between seasons and cohorts for climate as well as performance data were obtained using the MIXED procedure of SAS (SAS Inst. Inc., Cary, NC). Because there were differences in the weight and age (at start of test) of the animals between the 2 seasons at the start of the test, start weight was included as a covariate in the model used to compare the means between the two seasonal groups. The model used was defined as follows:

$$y_{ijk} = \mu + SWT_k + Season_j + e_{ijk} \quad \text{eq. 4}$$

where y_{ijk} represent various traits to be evaluated, **μ** is the overall mean, SWT_k the weight of k-th animal at start of test, season of test (j = 1 or 2) and $\mathbf{e}_{ijk}$ random residual associated with each record.

Phenotypic correlations between feed intake, efficiency and body composition traits were calculated using the CORR procedure of SAS while regression parameters were estimated using the REG procedure. Average air temperature, average relative humidity and wind speed were regressed on feed intake to assess where these parameters influenced the amount of feed consumed within each season. However, wind speed was found to only have a significant effect on DMI in the winter cohort and the final model used was as follows:

$$DMI_{ijk} = \beta_0 + \beta_1 Temp + \beta_2 RH + \beta_3 Season + e_{ijk} \quad \text{eq. 5}$$

Where, DMI is the average daily dry matter intake, RH, the relative humidity, TEMP the average daily temperature, **Season**, the season when the test was performed (1 or 2) and $\mathbf{e}_{ijk}$ the random residual associated with each record.

Two different forms of animal model were used to estimate variance components, genetic parameters and breeding values using the ASREML program (Gilmour et al., 1998). The models were defined as follows:

$$y_{ijk} = \mu + age_k + Breed_i + Cohort_j + a_k + e_{ijk} \quad \text{M1}$$

$$y_{ijk} = \mu + age_k + Breed_i + Season_j + a_k + e_{ijk} \quad \text{M2}$$

where **y** is any one of RFI_C, RFI_O or RFI_S, **μ** is the overall mean, **age** is the age of the k-th animal at start of test and is used as a covariate, **Breed** is the breed of the sire (i = Angus, Charolais, or Hybrid), Cohort is the test group (j = 2–6), **season** is the season in which the feed intake test was performed (j = 1-2), **a** is the random genetic effect of the k-th animal (**a**~N(0, $\mathbf{A}\sigma^2_{\mathbf{a}}$)), and **e** is the random residual (**e**~N(0, $\mathbf{I}\sigma^2_{\mathbf{e}}$)) with **A** being the numerator relationship matrix of all animals and **I** an identity matrix with order equal to the number of animals with records.

Estimated breeding value (EBV) accuracies were calculated using elements of the inverse coefficient matrix as accuracy = $\sqrt{(1-s_k^2/(1+f_k)\sigma_a^2)}$, where s^2_k is the prediction error variance associated with the BLUP for the k^{th} animal, f_k the inbreeding coefficient for the k^{th} animal and σ_a^2 the additive genetic variance (Gilmour et al., 1998). The effect of year within season was not included in the final model because it neither changed the model likelihood nor was it significant. The interaction of year by season was equivalent to fitting a fixed effect of cohort. Genetic correlations between traits were obtained from a bivariate analysis based on model M1.

2.3 RESULTS

The distribution of steers within sire breeds is shown in Table 2.1. There was more Angus type steers than Charolais or Hybrid type steers. The number of steers per sire ranged between 1 and 28, with an average of about 10 steers per sire, when considering sires with more than 1 offspring. Of the 89 sires in the

pedigree, 57 had a single offspring (Table 2.1). Table 2.2 details the ingredients and nutrient composition of the diets fed. The diets were typically high energy rations with similar energy density for the 3 years spanning the tests.

The integrity of the feed intake data used to calculate RFI is important so that parameter estimates are comparable across test conditions, regions and breeds. Often, there is a need to discard data for a number of days due to system malfunction and data collection problems. In this study, a relatively small amount of data, up to 2%, was lost in this way. Also, the proportion of DMI variance accounted for by ADG and MWT should be sufficiently large. Usually, between 30% and 45% of DMI variance is available as RFI (Basarab et al., 2003; Crews, 2005). Cohort specific values for expected feed intake prediction equations ranged between 54.12% to 76.93% (data not provided). On average, ADG and MWT accounted for 60% of the variation in DMI. Additionally, RFI is not expected to have phenotypic correlations with its component traits, ADG and MWT, as seen in this analysis. To remove genetic correlations between RFI and its component traits, genetic RFI is often calculated (Kennedy et al., 1993). However, because of the high correlation between phenotypic and genetic RFI (typically 0.9 or higher; Hoque et al., 2006; Nkrumah et al., 2007), only phenotypic RFI was used in this study.

Average values for climate parameters in the two seasons are given in Table 2.3. As expected, season 1 temperatures were much lower on average than season 2 temperatures. Similarly, solar radiation and wind speed were lower in season 1

than season 2. On the other hand, relative humidity was higher in season 1 than season 2. A similar trend was seen on a year to year basis, with season 1 temperatures being lower than season 2 temperatures. The average temperatures for cohorts 2, 3, 4, 5 and 6 were -5.13, -11.05, 3.51, -8.71 and 0.32, respectively.

Table 2.4 provides means and adjusted means for feed intake and efficiency, feeding behavior and performance traits. Season 2 animals started the feed intake test approximately 80 days later than the season 1 group and were subsequently older and heavier (by about 92 kg) at the beginning of the test. Consequently, season 2 animals had a higher feed intake (DMI), and metabolic mid weight (MWT) compared to the season 1 group. The feed intake per metabolic weight (DMI/MWT) of season 1 animals was higher compared to that of season 2 animals (124.6 vs. 113 g DMI d^{-1} /kg MWT, respectively). Additionally, the season 2 group had lower ultrasound back fat thickness, lower feeding duration (5.19 vs. 7.83 min/kg DMI), lower number of visits to the feeding bunk (0.48 vs. 2.98 events/kg DMI), and a shorter "head down" time (2.89 vs. 3.83 min/kg DMI). Even though ADG was not significantly different between the fall and winter groups, after adjusting for differences in start weight, season 1 animals had comparatively higher growth rates than season 2 animals. As shown in Table 2.5, the difference between ADG regression coefficients for the two seasonal groups is not significant (P = 0.0808) until a start weight (SWT) adjustment is applied (P = 0.0444).

The correlation between air temperature and DMI was moderate and negative in season 1, while moderate and positive in season 2 (Table 2.6). The trends between air temperature and feed intake are illustrated in Figures 2.1 to 2.5. Feed intake seemed to drop after sharp decreases in ambient temperature (Figure 2.3, 2.5, 2.6). Feed intake (DMI) for animals tested in season 1 was correlated with the minimum and average measures of relative humidity (RH), while season 2 animals did not show significant correlations between DMI and any measurement of RH. There were significant correlations between DMI and minimum, average and maximum solar radiation for season 1 while for season 2, significant correlations were only observed between DMI and maximum solar radiation. Wind speed was significantly correlated with DMI in season 2.

Regression of mean climate parameters on DMI indicated that air temperature and RH had a significant joint effect on DMI in season 1 but not season 2. For season 1, average air temperature accounted for 5% of the variation in DMI, while average RH accounted for 3.3% (Table 2.7).

Genetic and phenotypic correlations between the different measures of RFI, performance and behavior traits are shown in Table 2.8. Genetic correlations between RFI_S, RFI_C and ADG were not significant given the large standard errors observed. However, there was significant correlation between RFI_O and ADG. The correlations between RFI_C or RFI_S and DMI were moderate and within the range observed by other studies, while the correlation for RFI_O was slightly higher. Feeding duration was not genetically correlated with RFI, number of visits

showed a high correlation with RFI, while Hdown time was moderately correlated with RFI. Ultrasound back fat (UBF) did not have a significant correlation with RFI. Phenotypic correlations between RFI, UBF and feeding duration were significant in contrast to genetic correlations. On average, ADG and MWT accounted for 60% of the variation in DMI.

Estimates of variance components, heritability and EBV accuracy are shown in Table 2.9. Irrespective of the model used to evaluate RFI, RFI_C had a better model fit, while RFI_O had the least favorable fit, based on the model LogL. Single trait direct heritability and EBV accuracy were highest for RFI_C and lowest for RFI_O. In all instances evaluation of the various RFI derivations with models M1 and M2 led to higher residual variance estimates for RFI_O.

2.4 DISCUSSION

Table 2.3 gives mean values for climate parameters and the p-values associated with differences between season 1 and season 2 groups. In this study as expected, season 1 temperatures were lower than season 2 temperatures, because the Fall-Winter feed intake tests ended in Jan or Feb, and thus span the coldest months (Nov, Dec and Jan) in Alberta.

The average minimum air temperature in season 1 was close to the proposed critical body temperature (-20^{o}C) for cattle (NRC, 1996; Young, 1981). Under thermo-neutral conditions, the core body temperature, (temperature of the inner body of the animal) is between 38 and 38.5^{o}C (Sjaastad et al., 2003). Exposure to cold conditions below the critical body temperature has been associated with

metabolic cold acclimatization, which results in elevated levels of resting heat production (Young, 1983). Lefcourt and Adams (1998) found that ambient temperature affected body temperature when a certain low threshold was attained. In a separate study, Berman (2004) estimated significant increases in metabolic heat production as well as increased maintenance requirements due to exposure to cold at -10^{o}C using published experimental data. Similar results were observed by several other studies reviewed by Young (1983) which attribute increased energy requirements in winter to enhanced resting heat production (RHP) brought about by the effects of cold climates on body core temperature. However, Kennedy et al. (2005) found no relationship between exposures to cold with metabolic acclimatization in crossbred beef heifers exposed for as much as 10h d^{-1} to -20^{o}C conditions. Similarly, Birkelo et al. (1991) found no effect of season on maintenance requirements in Hereford steers. None-the-less, various studies provide evidence suggesting that lower temperatures results in poor performance in terms of feed efficiency (Delfino and Mathison, 1991) and ADG (Birkelo et al., 1991).

In this study, the animals tested in season 2 were older and heavier at the start of the feed intake test, while ADG was not significantly different between the groups. In order to remove differences attributable to body size, the weight at start of test was used to adjust growth and performance traits using eq. 4. Feeding behavior for season 1 animals (increased feeding duration, feeding events and visits to the feed bunk) suggests increased feed intake, and less efficiency. This group also had longer meal durations, and visited the feed bunk more than

animals tested in season 2. More energy was required for the more feeding events especially because the animal would be more exposed to the elements, increasing the chances of heat loss. On a weight to weight basis, and considering the adjusted DMI estimates and intake per MWT, season 1 animals consumed more feed than season 2 animals, even though animals that are larger in size are expected to consume more feed. Given that this 'higher' intake did not translate into faster growth rates (unadjusted ADG is the same for both groups), feed energy may have been allocated to mitigate the effects of harsh weather conditions, such as increasing heat production or accumulation of body fat to aid in insulation against heat loss. As shown in Table 2.4, season 1 animals had on average higher ultrasound back fat thickness compared to season 2 animals.

The trend of increased feed intake with reducing air temperature is further supported by the negative correlations between DMI and air temperature (Table 2.6). Correlations between DMI and solar radiation (Table 2.6) also suggest that feed intake increased with higher levels of solar radiation. The magnitude of this correlation was higher for season 1 compared to season 2, suggesting that the prospect of reduced heat loss may have encouraged animals to venture out to the feed bunks, as opposed to huddling together in order to conserve heat. Young (1981) suggests that the lower critical temperature of a group of animals is much more reduced compared to that of a single animal. In their simulation study, Keren and Olson (2006) showed that in cold conditions, solar radiation is important in lowering the effects of extreme weather on metabolic requirements. On the other hand, wind velocity increases metabolic requirements due to the

“chill” factor, such that ambient temperature feels much colder with higher wind speed. The negative correlations for season 1 suggest that days with higher wind speed accompanied by typically low temperatures in that season may have led to a reduction in feed intake, by necessitating increased huddling behavior or restricted movement by the animals so as to conserve body heat. Similarly, higher humidity levels may often result into wet hair coat for the animals thus reducing insulation capabilities. For season 1, days with lower humidity showed increased feed intake (Table 2.6). On the whole, air temperature and relative humidity had the biggest impact on feed intake in season 1 (Table 2.7). Regression of DMI on climate parameters did not yield any detectable effects for season 2 despite the correlations observed between DMI and climate parameters for this group.

Metabolic acclimatization to cold may possibly be a response to changes in the core body temperature and such changes affect energy partitioning. Individual animals are bound to show differences in metabolic adaptation to these changes. Given the differences in the correlation and regression parameter estimates for feed intake and climate parameters in the two seasons, these results suggest possible differences in energy partitioning, adaptation and hence efficiency of energy utilization in the two seasons. Consequently, RFI calculated in these two seasons may actually be indicative of 2 different traits, each capturing different components of energetic efficiency. However, because of the confounding brought about by animals in the two seasons being at different age and weight levels, it is impossible to specify a cause and effect relationship between climate parameters and feed intake.

None-the-less, having observed differences in DMI, MWT and UBF for the two groups, and possible individual animal differences in metabolic adaptation to cold conditions, it seems appropriate to group the cohorts into season 1 and season 2 for genetic evaluation purposes. Further, it also becomes necessary to assess how effective the various methods used to calculate RFI perform, with respect to these groups. Normally, RFI is calculated as the differences between observed feed intake and expected feed intake (EFI). Typically, EFI is predicted by regressing DMI on ADG, MMWT and any other "energy sinks" (Crews, 2005) that show a correlation with RFI either within (Basarab et al., 2003) or across test groups (Arthur et al., 2001; Hoque et al., 2006). Some body composition traits such as ultrasound and carcass back fat (Arthur et al., 2001; Robinson and Oddy, 2004) and rib eye area (Hoque et al., 2005) have been shown to be associated with RFI. However, these correlations as reported in the literature are small in magnitude with large standard errors. A third way of deriving RFI is used here following the method of Arthur et al., (2001), but the regression is performed separately in each seasonal group. The reason for such an approach is to try and account for season specific influences on DMI.

Estimates of least square means for the different RFI derivations are provided in Table 2.4. Within seasonal groups, both RFI_C and RFI_S sum to 0 while RFI_O does not. This is to be expected based on the methods applied, where RFI will average zero in the group (or across the groups) it is estimated. Table 2.8 provides estimates of genetic and phenotypic correlations between RFI and growth, feed behavior and body composition traits. The genetic correlations between RFI_C,

RFI_S and ADG, MWT were not significant. On the contrary, there was a significant correlation between RFI_O and ADG. Even though RFI may be genetically correlated with ADG and MWT, the fact that RFI_C and RFI_S did not show this correlation and RFI_O did, points to reduced efficiency in minimizing the correlation between RFI and its component traits. Similarly, RFI_O has a higher correlation with head down time, and lower correlation with number of visits to the feeding bunk compared to RFI_S and RFI_C.

The high genetic correlations between RFI and number of visits or head down time would imply reduced feed efficiency for animals tested in season 1, given that this group had a higher number of visits to the feeding bunk. Even though the magnitude of the differences between the correlations for the three measures of RFI is well within the range of the S.E., there seems to be a trend that suggests that RFI_O performs differently from the other two measures of RFI. Estimates of variance components (Table 2.9) using either model (M1 or M2) resulted in RFI_C having the smallest residual variance, and highest estimates of heritability and EBV accuracy. Given the LogL, model M2 was best for evaluating RFI_C and RFI_O while model M1 was suitable for evaluating RFI_S. For RFI_C, the results suggest that seasonal effects can be partly accounted for by including a season effect in the evaluation model (M2). However, for RFI_O trying to account for seasonal effects in the evaluation model results in the worst fit. These results suggest that the method of Basarab et al., (2003) leading to RFI_C is the most suitable for evaluating RFI in animals tested in the two seasons. No matter what evaluation model was used, estimation of RFI by fitting a separate regression for

each test group (RFI_C) seems to be more robust than when done within seasonal groups (RFI_S). However, the method of Basarab et al., (2003) would fail when the intention is to assess gain in efficiency due to RFI selection. Typically, a single regression would need to be applied to all selection groups so that the progressive change in mean EBV with successive generations of selection is assessed. The method of Basarab et al. (2003) ensures that each group tested has a mean of null while for the Arthur et al. (2001) method, each group will have a different mean allowing for changes in mean RFI value to be easily quantified as selection proceeds. Where selection has been undertaken, and the population under study is tested for feed intake in different seasons, it is envisaged that the season specific adjustments suggested in this study would become useful, given no confounding factors.

The results in this study are suggestive of seasonal effects on feed intake and RFI estimation. However, because the two groups of animals started the tests at different ages, there is confounding of age with season and it is hard to separate these two such that the differences in intake observed be wholly attributed to seasonal influences. The inclusion of age as a covariate in the evaluation model only allows a mathematical equalization to a common age (given that animals started the test at different ages) but does little to adjust for the real metabolic differences caused by the animals being at different physiological stages. Even though the differences in the estimated parameters cannot be wholly attributed to seasonal influences, it is apparent that feed intake measured in the two seasons relates differently to climate parameters, and the manner in which RFI is derived

impacts variance component estimation. However, as the drive to obtain more efficient cattle using RFI becomes intensified, more studies need to be conducted to understand how animals respond to environmental perturbations in situations of cold stress and how this may impact selection for net energy efficiency.

2.5 CONCLUSIONS

This study sought to assess the influence of climate parameters on feed intake and whether residual feed intake (RFI) calculated by regressing feed intake (DMI) on growth rate (ADG) and metabolic weight (MWT) in 3 different ways led to similar estimates of genetic parameters and variance components for young growing cattle tested for feed intake. There was a significant difference between Fall-Winter (season 1) and Winter-Spring (season 2) in mean climate parameters to warrant separation of the tested cohorts into seasonal groupings. For season 1 animals, feeding behavior observed was indicative of increased intake although unadjusted DMI was lower than for season 2 animals. Correlation between climate parameters and feed intake showed increased feeding with reducing temperature for season 1. Results obtained suggest that given no selection for RFI in previous generations, RFI is best estimated by regressing DMI on ADG and MWT for each test group separately, followed by genetic evaluation using a model that includes season as a fixed effect. However, confounding in terms of age and weight of animals in the two seasons affected the results observed.

Table 2.1. Summary of the number of steers per sire, within test group and sire breed

Year	Cohorts (Season1, Seaon2)	Steers (Season1)	Steers (Season2)
2003	Cohort 1, 2	NA	64
2004	Cohort 3, 4	80	76
2005	Cohort 5, 6	80	78
Breed			
Angus		70	93
Charolais		53	44
Hybrid		37	81
Sires			
Total number of sires		34	55
Average number of offspring per sire		4.7	3.96
No of sires with single offspring		19	38
Average number of offspring per sire[a]		9.4	10.59

[a] Averaged for sires with more than one offspring; Season1 – Fall-Winter; Season2 – Winter-Spring; NA – Not included.

Table 2.2. Nutrient composition and ingredients of experimental diets for the years tested

Diet ingredient (% as fed basis)	2003	2004	2005
Dry-rolled corn	80.00	--	--
Barley grain	--	64.50	64.50
Oat grain	--	20.00	20.00
Alfalfa hay	13.50	9.00	9.00
Beef feedlot supplement[1]	5.00	5.00	5.00
Canola oil	1.50	1.50	1.50
DM, %	90.50	88.90	88.90
Nutrient Composition, DM basis[2]			
ME, Mcal/kg	2.90	2.91	2.91
CP, %	12.50	14.00	14.00
CF, %	--	--	--
NDF, %	18.30	21.49	21.49
ADF, %	5.61	9.50	9.50

[1]Contained 440 mg/kg of monensin, 5.5% Ca, 568 0.28% P, 0.64% K, 1.98% Na, 0.15% S, 0.31% Mg, 16 mg/kg I, 28 mg/kg Fe, 1.6 mg/kg Se, 160 mg/kg Cu, 432 mg/kg Mn, 432 mg/kg Zn, 4.2 mg/kg Co, as well as a minimum of 80,000 IU /kg vitamin A, 8,000 IU/kg vitamin D, and 1,111 IU/kg Vitamin E.

[2] Obtained from digestibility trials and subsequent proximate analysis as described by Nkrumah et al. (2006).

ME – metabolizable energy; CP, - Crude protein; CF – Crude fat; NDF – Neutral detergent fiber; ADF – Acid detergent fiber

Table 2.3 Means (± S.E.) and significance levels for Climate parameters for fall and winter tested groups

	Season1	Season2	
Parameter	Mean ± SE	Mean ± SE	P-value
Min Air Temperature(^{o}C)	-14.58 ± 0.74	-6.72 ± 0.62	***
Max Air Temperature(^{o}C)	-4.95 ± 0.81	5.20 ± 0.63	***
Average Air Temperature (^{o}C)	-9.7 ± 0.75	-0.72 ± 0.63	***
Average Relative Humidity (%)	78.59 ± 1.0	64.56 ± 1.03	***
Average Solar Radiation (W/m^2)	43.18 ± 3.55	161.85 ± 3.65	***
Wind speed scalar (m/s)	3.37 ± 0.11	3.92 ± 0.11	**

***P-value < 0.0001, **P-value < 0.01; Season1 – Fall-Winter; Season2 – Winter-Spring.

Table 2.4. Adjusted and unadjusted least squares means (± S.E.) for various feed intake and performance traits evaluated on steers tested in fall and winter

Trait	Season1 Mean ± S.E.	Season2 Mean ± S.E.	Season1 Adj Mean ± S.E.	Season2 Adj Mean ± S.E.
ADG (kg d^{-1})	1.49[1] ± 0.02	1.48[1] ± 0.02	1.55* ± 0.03	1.44* ± 0.02
Age (d)	211.72 ± 1.39	293.91 ± 1.19	--	--
DMI (kg DM d^{-1})	10.43 ± 0.11	11.14 ± 0.09	11.58 ± 0.12	10.31 ± 0.10
Duration (min d^{-1})	81.70 ± 1.23	57.84 ± 1.06	84.36 ± 1.68	56.02 ± 1.35
HDown (min d^{-1})	39.95 ± 0.90	32.25 ± 0.77	39.84 ± 1.23	32.48 ± 0.99
MWT (kg)	83.70 ± 0.52	98.77 ± 0.45	92.74 ± 0.18*	92.12 ± 0.14*
RFI_C	0.00[1] ± 0.06	0.00[1] ± 0.05	--	--
RFI_O	0.21 ± 0.07	-0.15 ± 0.06	--	--
RFI_S	0.00[1] ± 0.07	0.00[1] ± 0.06	--	--
SLTWT (kg)	561.20 ± 4.67	524.42 ± 4.01	616.55 ± 4.74	483.49 ± 3.82
SWT (kg)	311.67 ± 3.00	404.42 ± 2.58	--	--
UBF (mm)	10.77 ± 0.27	9.02 ± 0.23	12.06 ± 0.36	8.10 ± 0.29
Visits (events d^{-1})	31.12 ± 0.51	23.02 ± 0.44	26.93[1] ± 0.62	26.18[1] ± 0.50
WWT (kg)	241.22 ± 2.81	182.48 ± 2.42	--	--

[1]Means for fall and winter do not significantly differ; -- No adjustment done; Season1 – Fall-Winter; Season2 – Winter-Spring;

*P-value < 0.05. All other P-values < 0.001; Season1 – Fall-Winter; Season2 – Winter-Spring;

Adjmean – Adjustment mean; Adjustment obtained by including weight at start of test (SWT) as a covariate.

ADG – Average daily gain; DMI – standardized dry matter intake; HDown – Head down time; MWT – Metabolic mid-weight; SWT – Weight at start of test; SLTWT – Weight at slaughter; UBF – Ultrasound back fat; Age – represents the age at the beginning of test; Visits – number of visits to the feeding bunk; WWT – Weaning weight. RFI_C – RFI obtained by regressing ADG and MWT on DMI for each cohort separately; RFI_O - RFI obtained by regressing ADG and MWT on DMI over pooled data, with test group as a fixed effect; RFI_S - RFI obtained by regressing ADG and MWT on DMI, with test group as a fixed effect but within seasonal (fall, winter) groups.

Table 2.5. Differences between estimated regression coefficients for Fall and Winter test groups based on different models for estimated expected feed intake (EFI)

Model Parameter	Season1	Season2	Difference	p-value
Model: DMI = GROUP + ADG + MWT + ADG*GROUP + MWT*GROUP				
Intercept	-3.14 ± 0.94	-2.25 ± 0.92	-0.89 ± 1.41	0.5312
ADG	2.05 ± 0.24	1.38 ± 0.28	0.67 ± 0.38	0.0808
MWT	0.13 ± 0.01	0.12 ± 0.01	0.01 ± 0.02	0.5379
Model: DMI = STWT + GROUP + ADG + MWT + ADG*GROUP + MWT*GROUP				
Intercept	-7.36 ± 3.17	28.98 ± 8.78	-1.09 ± 1.43	0.4460
SWT	-0.03 ± 0.02	0.21 ± 0.06	--	0.5272
ADG	0.86 ± 0.88	8.63 ± 2.07	0.80 ± 0.40	0.0444
MWT	0.31 ± 0.13	-1.15 ± 0.36	0.01 ± 0.02	0.5372

ADG – Average daily gain; MWT – Metabolic mid weight; SWT – Weight at start of test; -- parameter not estimated; RSQ for both models is 60%; Season1 – Fall-Winter; Season2 – Winter-Spring.

Table 2.6. Estimates of correlation coefficients and associated significance levels for the correlation between daily measures of climate parameters and feed intake (DMI) data for fall and winter seasons

	Season1		Season2	
	†Estimate	p-value	†Estimate	p-value
Max Air Temperature (^{o}C)	-0.26	0.001	0.27	<.0001
Min Air Temperature (^{o}C)	-0.26	0.0008	0.33	<.0001
Average Air Temperature (^{o}C)	-0.26	0.0011	0.31	<.0001
Max Relative Humidity (%)	0.00	0.9526	0.14	0.0949
Min Relative Humidity (%)	0.32	<.0001	-0.08	0.3161
Average Relative Humidity (%)	0.23	0.0034	-0.04	0.6598
Max Solar Radiation (W/m^2)	0.19	0.0134	0.21	0.0109
Average Solar radiation (W/m^2)	0.30	0.0001	0.14	0.0957
Total Solar radiation (W/m^2)	0.30	0.0001	0.14	0.096
Wind Speed (m/s)	-0.14	0.0712	0.16	0.0495

†Estimate obtained by correlating each of the climate parameters with daily DMI within season. Season1 – Fall-Winter; Season2 – Winter-Spring, DMI – Dry matter intake. Dry matter intake data used is the daily average for all animals in each season

Table 2.7. Parameter estimates (± S.E) obtained by the regression of weather parameters on feed intake for fall and winter tested groups.

	Season1 Estimate	Season2 Estimate
Intercept	8.89 ± 0.82	9.36 ± 0.82
Cohort	-0.42 ± 0.08	0.08 ± 0.011
Average air temp	-0.02 ± 0.01	0.05 ± 0.02
Average RH	0.03	0.01 ± 0.01
RSQ	0.23[a] ± 0.01	0.03
Model P-value	<0.0001	0.1584

[a]Average air temperature accounts for 5% of variation in DMI while average RH accounts for 3.3%; RH – Relative humidity, RSQ – coefficient of determination.; Season1 – Fall-Winter; Season2 – Winter-Spring.

Table 2.8. Genetic and phenotypic correlations (± S.E.) among various measures of RFI and feed intake, performance and behaviour traits

	Genetic correlations			Phenotypic correlations		
	RFI_C	**RFI_O**	**RFI_S**	**RFI_C**	**RFI_O**	**RFI_S**
ADG	0.21 ± 0.37	0.53 ± 0.46	0.31 ± 0.39	-0.00	0.00	0.00
DMI	0.45 ± 0.29	0.68 ± 0.24	0.51 ± 0.28	0.56	0.63	0.58
MWT	-0.33 ± 0.55	-0.32 ± 0.59	-0.27 ± 0.58	-0.00	-0.00	0.00
UBF	-0.92 ± 1.05	-0.79 ± 1.15	-0.99 ± 1.20	0.19	0.23	0.17
Duration	0.03 ± 0.45	0.29 ± 0.41	0.04 ± 0.47	0.36	0.46	0.36
Visits	0.95 ± 0.31	0.64 ± 0.50	0.94 ± 0.34	0.25	0.16	0.21
HDown	0.46 ± 0.38	0.74 ± 0.35	0.51 ± 0.39	0.41	0.49	0.45

ADG – Average daily gain; DMI – dry matter intake; Duration – length of time spent on a meal; HDown – head down time; MWT – metabolic mid – weight; UBF – ultrasound back fat; Visits – number of visit to the feed bunk;

RFI_C – RFI obtained by regressing ADG and MWT on DMI for each test group separately; RFI_O - RFI obtained by regressing ADG and MWT on DMI on all pooled data, with test group as a fixed effect; RFI_S - RFI obtained by regressing ADG and MWT on DMI, with test group as a fixed effect but within seasonal groups.

Table 2.9. Variance component and genetic parameter estimates obtained from the genetic evaluation of the three measures of RFI using two different evaluation models

	Model M1			Model M2		
	RFI_C	**RFI_O**	**RFI_S**	**RFI_C**	**RFI_O**	**RFI_S**
Direct genetic variance	0.15	0.12	0.13	0.13	0.14	0.14
Residual variance	0.47	0.56	0.50	0.48	0.61	0.53
Heritability, h^2_a	0.24 ± 0.17	0.18 ± 0.14	0.20 ± 0.16	0.22 ± 0.16	0.18 ± 0.14	0.21 ± 0.16
EBV accuracy	0.53	0.48	0.50	0.51	0.48	0.50
Model LogL	-113.01	-131.61	-116.51	-108.49	-144.71	-123.13

RFI_C – RFI obtained by regressing ADG and MWT on DMI for each test group separately; RFI_O - RFI obtained by regressing ADG and MWT on DMI on all pooled data, with test group as a fixed effect; RFI_S - RFI obtained by regressing ADG and MWT on DMI, with test group as a fixed effect but within seasonal groups.

Figure 2.1. Plots for trends of average air temperature and average daily dry matter intake (DMI) for animals tested in the Winter-Spring of 2002 – 2003.

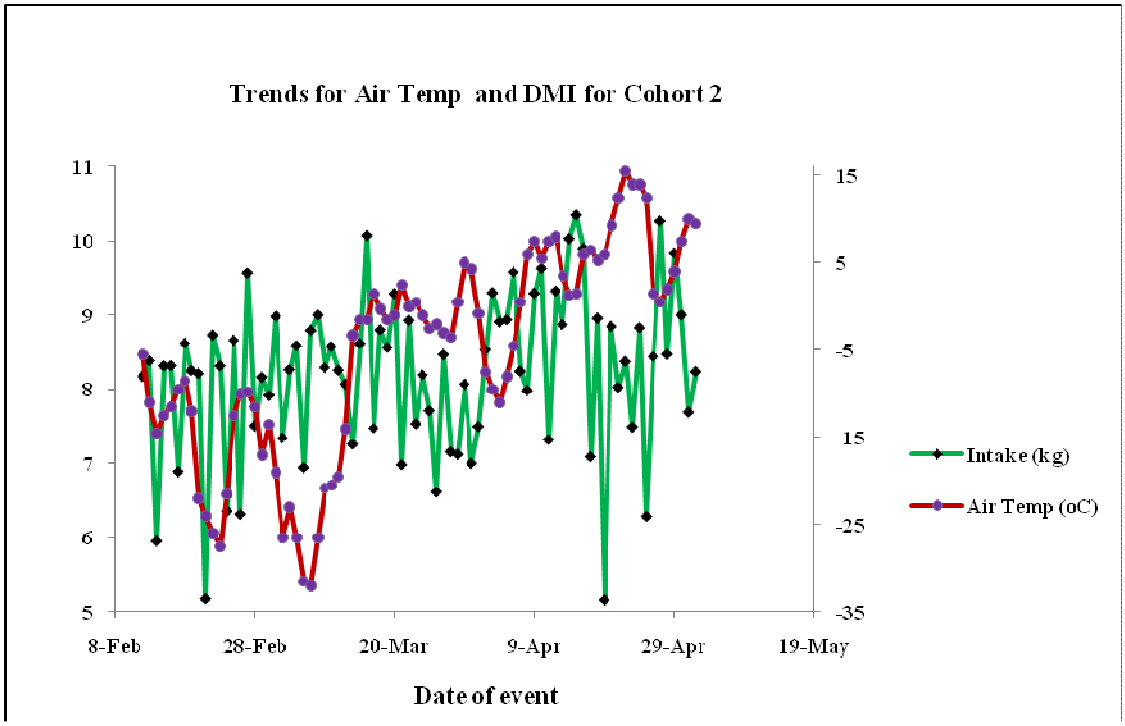


Figure 2.2. Plots for trends of average air temperature and average daily dry matter intake (DMI) for animals tested in the Fall-Winter of 2003 – 2004.

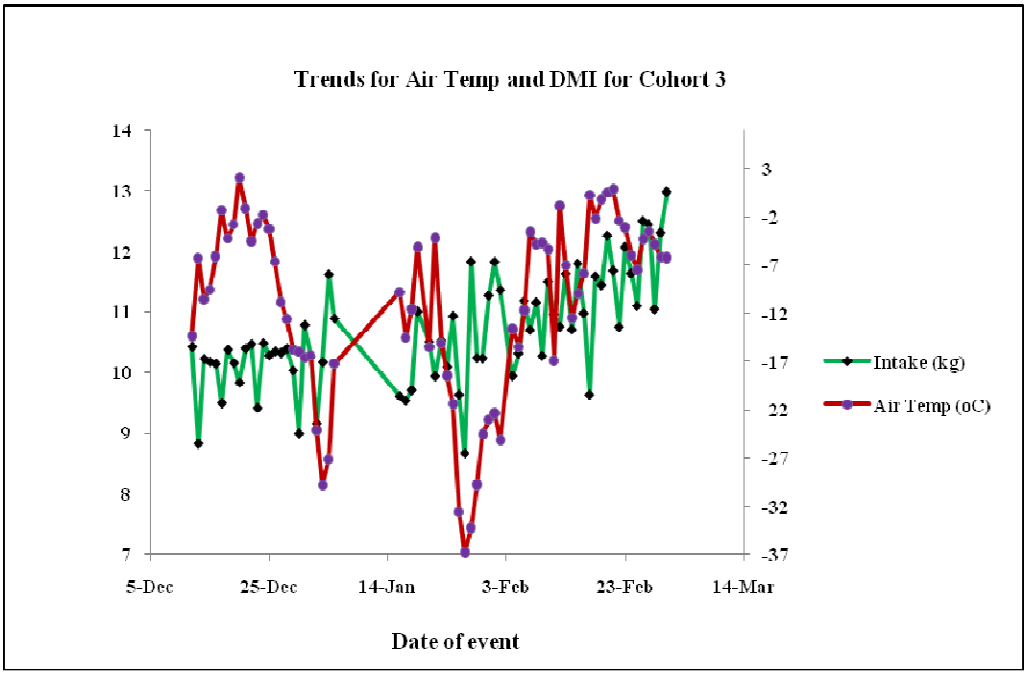


Figure 2.3. Plots for trends of average air temperature and average daily dry matter intake (DMI) for animals tested in the Winter-Spring of 2003 – 2004.

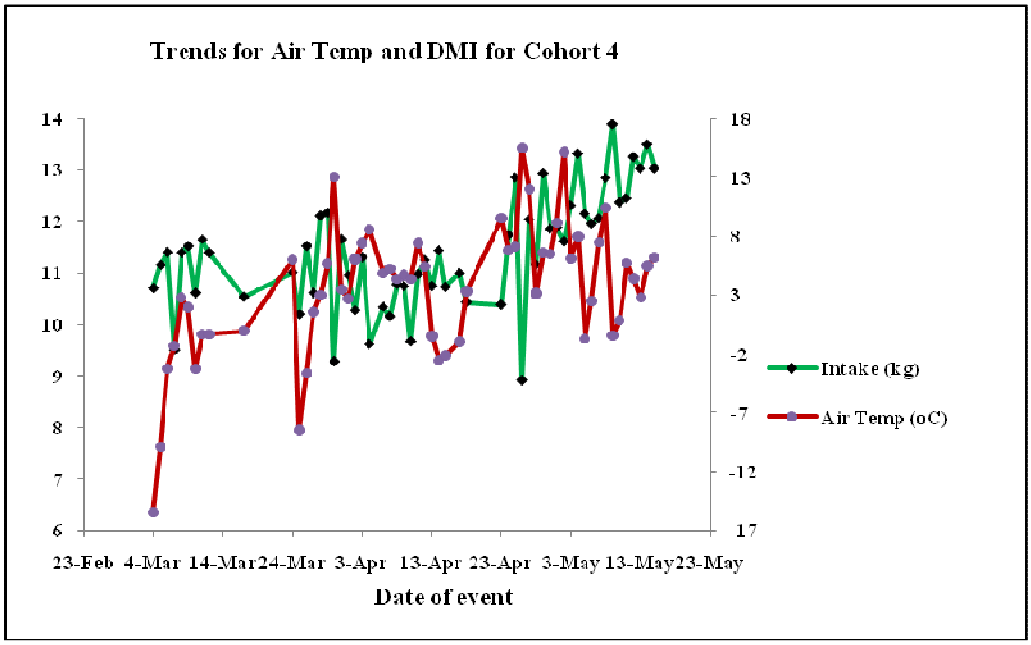


Figure 2.4. Plots for trends of average air temperature and average daily dry matter intake (DMI) for animals tested in the Fall-Winter of 2004 – 2005.

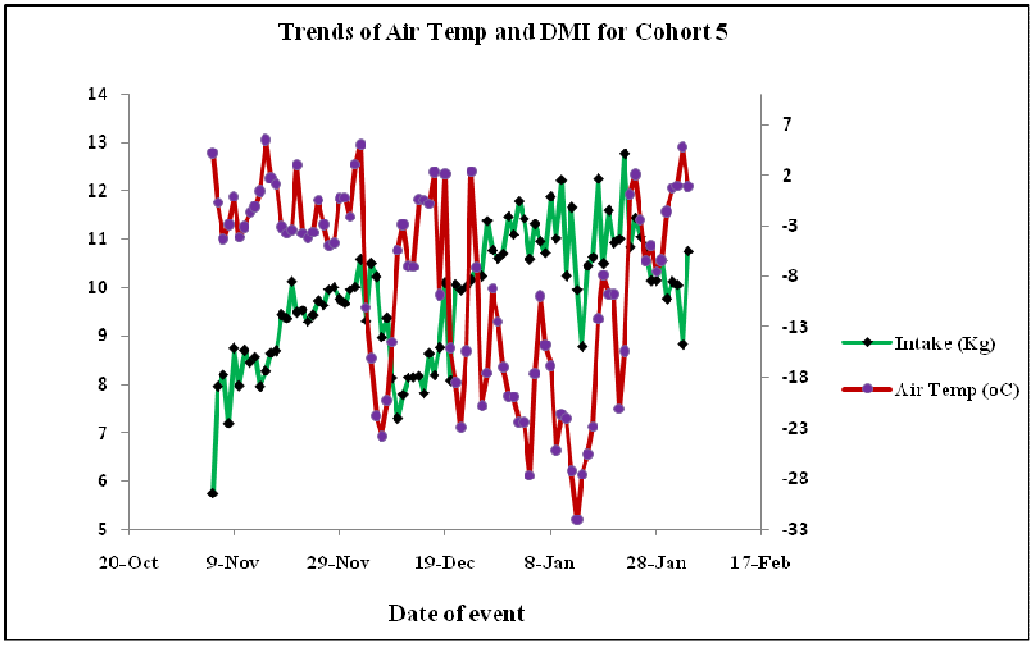
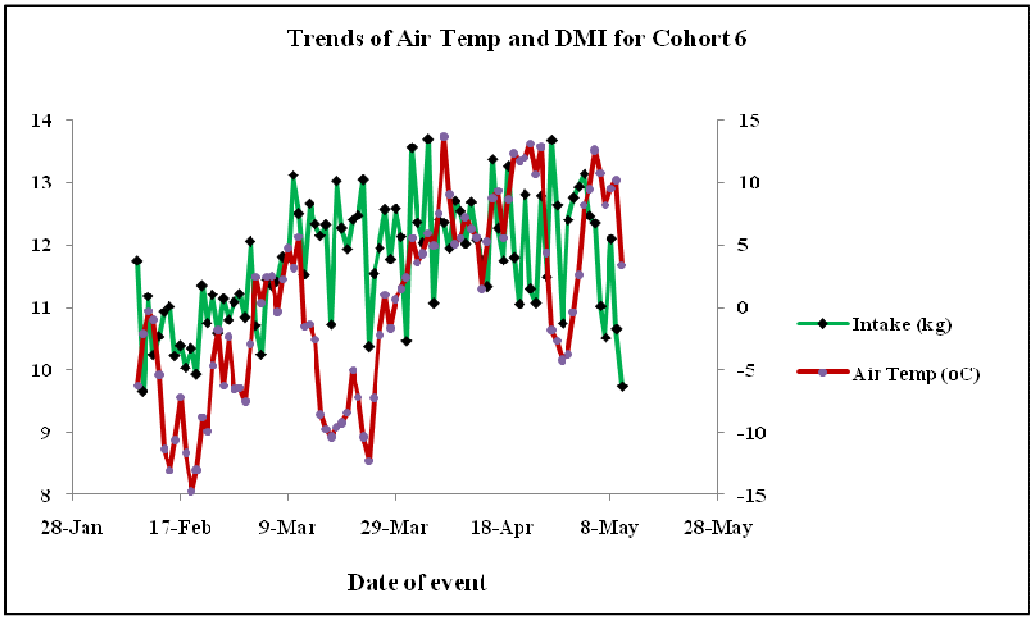


Figure 2.5. Plots for trends of average air temperature and average daily dry matter intake (DMI) for animals tested in the Winter-Spring of 2004 – 2005.



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CHAPTER 3 : Associations of marker panel scores with feed intake and efficiency traits in beef cattle using pre-selected SNPs

3.1 INTRODUCTION

Feed efficiency is often measured as residual feed intake (RFI), the difference between an animal's actual feed intake and its expected requirement for growth and maintenance of body weight over a specified period (Koch et al., 1963). The trait is moderately heritable (Arthur et al., 2001b) with estimates ranging from 0.16 to 0.58 (Herd and Bishop, 2000; Crews et al., 2003) and considerable variation has been reported within groups of cattle tested for RFI (Herd and Bishop, 2000; Basarab et al., 2003). Richardson et al. (1998) and Arthur et al. (2001c) demonstrated that selection for RFI was effective and the benefits of improved feed efficiency can be achieved in a beef operation. However, the collection of individual feed intake data that is required for implementation of selection in breeding programs has been hindered by the need for expensive and specialized equipment. On top of that, there are other hidden costs associated with data collection, such as transportation of test animals to a centralized testing facility, the cost of feed and yardage, estimated at about $250 - 350/hd (John Basarab, personal communication) and the cost of the actual feed intake test ($1-1.25/hd/day). Given that results from feed intake tests can only be obtained after at least one year from birth, selection could be enhanced if DNA markers associated with RFI were used in the management and selection of animals early in life as well as in the genetic evaluation of RFI.

Recent advances in marker technology have led to the development of various DNA based selection tools (Van Eenenaam et al., 2007a, b; Johnston et al., 2008). These tools are useful not only for pre-selection of superior animals without own records, but also for increasing the accuracy of breeding value estimation for traits that are difficult or expensive to measure such as RFI. Such selection tools would serve to augment the national database supporting traditional polygenic EPD selection. In the absence of phenotypic measurements, DNA tools may still be used to estimate EBV as well as predict future performance for a particular trait, especially for young unproven sires. This however, is contingent on the structure of the reference population used to estimate marker effects. Such a population should have both genotypes and phenotypes, and potentially large numbers of individuals for low heritability traits.

The usefulness of DNA selection tools depend on the proportion of the true genetic variance accounted for by the marker panels selected. Crews et al. (2008) suggested that for marker panels to be useful, they would need to account for 10-15% of the genetic variance in the trait of interest. In this chapter, the utility of marker panels in the prediction of ADG, DMI and RFI was evaluated for a group of crossbred beef steers. The marker panels were derived from SNPs preselected for association with the various traits. Despite the relatively small number of individuals in the dataset, the potential usefulness of genetic markers as an additional tool for the selection of RFI was demonstrated.

3.2 MATERIALS AND METHODS

3.2.1 Animal resource, data collection and study design

The data consisted of 721 spring born beef steers, offspring of a cross between a composite dam line and Angus, Charolais or University of Alberta hybrid bulls. The 3 composite dam lines used consisted of beef synthetic 1 (BS1), beef synthetic 2 (BS2) and dairy beef synthetic (DBS). The breed composition of BS1 included Angus and Charolais (each approximately 33%), Galloway (20%) and other beef breeds (approximately 14%). The BS2 synthetic consisted of Hereford (60%) and other beef breeds (40%), while the DBS synthetic was made up of 60% dairy breeds (Holstein, Simmental, or brown Swiss) and 40% beef breeds (Goonewardene et al., 2003).

Feed intake data was collected over a 5 year period with two groups (Fall-Winter and Winter-Spring, also referred to as period 1 and 2, respectively) tested every year for the first three years. The data for the Fall-Winter period in year 1 was not included in the analysis due to inconsistent feed intake records occasioned by a drought in that year. In year 4, one group of animals was tested for two consecutive periods (Fall-Winter then Winter-Spring), first on a low energy feedlot diet in period 1 then a high energy feedlot diet in period 2. In year 5, two groups of animals were tested in two consecutive periods as follows: The first group was put on a high energy feedlot diet for both periods 1 and 2, while

the second group was first tested on a lower energy diet in period 1 then switched to a high energy diet in period 2 as shown in Table 3.1.

The consequence of feeding a low energy diet in the first testing period implies potential carry over effects of diet on the Winter-Spring test results, thus making it necessary for animals thus treated to be grouped separately (Table 3.1). However, despite the separate grouping, period 1 test data for the diet switch group was not included in the analysis, so that only data obtained from high energy feedlot diets was included. Animals had free-choice access to feed and water. In total, 9 batches of animals were available for analysis, a batch being a combination of year and period of testing. These were organized into 3 groups namely, the Fall-Winter, Winter-Spring, and diet switch groups (Table 3.1). Table 3.2 gives the number of animals in each of the test groups.

Animal body weight data was collected every two weeks for the duration of the test, except in year 1 when weights were recorded weekly. The test periods lasted approximately 90 days or until 70 days of useful data was available. The Canadian Council on Animal Care, CCAC (1993) protocols and guidelines were followed when caring for the animals.

3.2.2 Diets and feed composition

Test diet composition and associated nutritional data (Table 3.3) were obtained after digestibility trials and proximate analyses as described by Nkrumah et al. (2006). All the diets were barley based high energy feedlot rations, except in

year 1 where a shortage of feed barley led to use of corn. In typical feedlot practice, a mineral supplement was also offered as part of the diet. Animals were tested for feed intake using the respective test diets following a 2 week adjustment period to familiarize the animals with the test environment and feeding bunks. All diets for periods 1 and 2 within each year were the same except where diet switching from a low energy to a high energy density diet occurred.

3.2.3 Trait derivation

Individual animal feed intake and feeding behavior data was collected using the GrowSafe automated feeding system (GrowSafe Systems, Ltd., Airdrie, AB) at the University of Alberta Kinsella ranch. Daily feed intake was converted into daily dry matter intake (DMI) by multiplying intake by the dry matter content of the diet. Daily DMI was then standardized across the different years to 10 MJ ME/kg DM by multiplying daily DMI with the diet metabolizable energy (ME) content then dividing by 10 (Basarab et al., 2003). Average daily gain (ADG) was calculated as the slope from the regression of body weight on test day. Metabolic mid weight (MMWT) was obtained as the mid-weight on test raised to the power of 0.75.

RFI was calculated within group using the following formula

$$RFI = DMI - (\beta_0 + \beta_1 Batch + \beta_2 ADG + \beta_3 MMWT),$$

where β_1, β_2, β_3 are partial regression coefficients and β_0 the intercept.

Training and validation data sets were obtained by splitting the data into two distinct sets as follows:

i) by randomly splitting the data into a training set (2/3, n=490) and a testing set (1/3, n=203) based on sire family so that there was no overlap of sires in the two sets. This was designated as split 1 (Table 3.2). This strategy reduces the relatedness between individuals in the training and testing set, which relatedness could inflate the accuracy of prediction (Habier et al., 2007). This random split was replicated 5 times.

ii) by retaining all animals with no known pedigree relationships as the validation set. The validation set had a total of 148 individuals that did not have apparent relationships with any of the sires or any other animal in the training dataset. This was determined using a custom script and approx. 96 select SNPs specifically chosen for parentage assignment. This was designated as split 2 (Table 3.2). Because of a lack of relationship between training and testing datasets, the prediction observed will be truly due to LD between SNPs and QTL underlying the trait.

All association analyses were performed in the 5 training sets, while the ability of selected markers to predict the phenotype was explored in the 5 testing

set. The final estimates were obtained as the average of the results from the 5 testing data sets.

3.2.4 Genetic data

More than 50,000 SNP, part of the Illumina Infinium BovineSNP50 bead chip (Illumina, San Diego, CA) were genotyped for 745 beef steers (some sires were included in the genotyping) using the Illumina Infinium II platform. The 50K chip was designed such that markers were uniformly distributed across all chromosomes (Van Tassell et al., 2008; Matukumalli et al., 2009) as well as being polymorphic in the various breeds used in the International Bovine HapMap Project. The selection criteria applied to obtain SNPs for further analysis was performed using the Rosetta Syllego data management system (Rosetta Biosoftware, Seattle, WA, USA) where SNPs were tested for Hardy-Weinberg Equilibrium ($P > 0.05$), minor allele frequency (> 5%) and SNP Call frequency (> 88%). Consequently, 38,158 SNPs met the test criteria and were selected for further analysis. Genotypes were coded as 0, 1 and 2 with 0 being the SNP allele with the lower frequency and 1 the allele with higher frequency, such that the two homozygotes were represented as 0 and 2, and 1 was the heterozygote. Missing genotypes (about 1% of all genotypes) were imputed by submitting SNP genotype calls as well as missing genotype information to fastPHASE (Scheet and Stephens, 2006) chromosome by chromosome, the SNPs having been ordered according to their chromosomal position. The parameters used were as follows: Ten (10) random starts of the EM algorithm (T), 30 iterations of the EM

algorithm (C), 15 cross-validation clusters (K), and no sampling of haplotypes from the posterior distribution of each random start of the EM algorithm (H). The most probable genotype imputed by fastPHASE was considered the true genotype. All SNPs with unknown chromosomal positions were discarded. A final 37,959 SNPs were included in the analysis.

3.2.5 Polygenic breeding value estimation

The following animal model was used in the whole data set to estimate polygenic breeding values, variance components and genetic parameters using ASReml (Gilmour et al., 1998). The model (eq. 1) included fixed effects of breed of sire, test group and batch, with age at start of test as a covariate:

$$\mathbf{y}_1 = \mathbf{X}_1\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{a} + \mathbf{e}, \quad (1)$$

where, the design matrices $\mathbf{X}_1$, and $\mathbf{Z}_1$ relate phenotypic observations in the vector $\mathbf{y}_1$ to fixed ($\boldsymbol{\beta}$), and polygenic ($\boldsymbol{a}$) effects, respectively. The vector *e* contains random residual terms specific to animals. The parameters *a* and *e* were assumed to be normally distributed with a mean of 0, and variances $\boldsymbol{A}\sigma_a^2$ and $\boldsymbol{I}_n\sigma_e^2$, respectively. The matrix $\boldsymbol{I}_n$ is an identity matrix of order equal to the number of animals with RFI observations, while **A** is the additive relationship matrix, σ_a^2 is the random polygenic effect variance, and σ_e^2 the residual variance.

Accuracy was calculated using the formula $\boldsymbol{accuracy} = \sqrt{1 - \frac{se^2}{a^2}}$, with se^2 being

the prediction error variance and $\boldsymbol{a}^2$ the additive genetic variance (Gilmour et al., 2008).

3.2.6 Pre-selection of SNPs

In order to reduce the available SNPs to a more tractable number, the effect of each SNP on RFI, DMI and ADG was assessed individually using single marker association analysis. The model applied extended eq. (1) to include SNP data as follows:

$$\mathbf{y}_1 = \mathbf{X_1\beta} + \mathbf{X_2g} + \mathbf{Z_1}\boldsymbol{a} + \mathbf{e}, \quad (2)$$

where, $\mathbf{X}_2$ relates phenotypic observations in the vector y_1 to SNP effects (g), with elements $\mathbf{X}_{2ij} = 0$, 1, or 2, corresponding to the genotype of animal *i*, with the parameter **g** being the allele substitution effect. All other parameters were as previously described. Only SNPs with associations significant at $P \leq 0.05$ in the pre-selection analysis were retained for further analysis.

3.2.7 Selection of the final SNP panel

Of the SNPs retained from pre-selection, the top 100 SNPs, corresponding to a significant value of $P < 0.002$ were chosen for each trait and fit simultaneously using a random regression BLUP (RR-BLUP) model. The SNPs were assumed to be random to allow for shrinkage of the estimates while assuming a constant variance of $\boldsymbol{\sigma^2 g}_j$ for all instances of *j*, as follows:

$$\mathbf{y_1} = \mathbf{X_1\beta} + \mathbf{Z_1}\boldsymbol{a} + \mathbf{Z_2g} + \boldsymbol{e}, \quad (3)$$

where, $\mathbf{Z}_2$ relates phenotypic observations in the vector $\mathbf{y}_1$ to SNP effects (g), with elements $\mathbf{Z}_{2ij}$ = 0, 1, or 2, corresponding to the genotype of animal *i* and **g** normally distributed with mean 0, and variance $\boldsymbol{\sigma^2 g}_j$. The solutions for $\boldsymbol{g}$ were obtained by solving the normal mixed model equations with SNP variance $\boldsymbol{\sigma^2 g}_j = \boldsymbol{\sigma}_a^2 / \boldsymbol{n}$, *n* being the number of SNPs jointly fitted in the model. The estimates g_j obtained differed in the level of shrinkage due to differences in allele frequency between SNPs (Moser et al., 2009). Only SNPs that were jointly significant were retained in the model (eq. 3) so as to maximize the correlation between the panel of SNPs selected and the trait. Significance was assessed by running a model equivalent to eq. (3) where SNPs are fitted as fixed effects and sequentially discarding any SNP that was not significant at $P < 0.05$. The remaining SNPs were then re-run using eq. (3) and the prior estimate of SNP variance adjusted accordingly using the new *n*.

3.2.8 Estimation of marker effects

For split 1, the SNP pre-selection and creation of panels was done using one of the 5 replicates for split 1. The final panels of SNP markers selected from the above process were then used to re-estimate allelic substitution effects in the remaining 4 replicates such that each of the selected SNP had an estimated effect for each of the replicate data sets. For split 2, there was only one estimate for the selected SNPs, given that there was no replication. These final estimates of $\boldsymbol{g}$ were obtained using model eq. 3, with SNPs fitted as fixed effects.

3.2.9 Cumulative marker phenotype (CMP) estimation

The marker panels obtained from the analysis above were used to calculate marker scores (MS). These MS were calculated for all animals in the testing data as a weighted sum of the number of copies of the more frequent allele at each SNP locus, with the weights being the allele substitution effects (β) obtained from the RR-BLUP. The summation of all MS for each individual yielded a cumulative marker phenotype (CMP, Johnston et al., 2008):

$$\boldsymbol{CMP} = \sum_{j=1}^{N_m} \boldsymbol{X}_{ij} \hat{\boldsymbol{g}}_j \,, \qquad (4)$$

where, X_{ij} represents the marker genotype of animal i at SNP j, coded 0, 1, 2 as previously described in the training data, $\hat{g}_j$ is the allele substitution effect estimate of SNP j, and N_m is the number of SNPs. The CMP nomenclature was adopted since the model fitted a small number of markers, as opposed to molecular breeding values and genomic breeding values obtained from whole genome analyses. The trait specific CMP were designated CMP^{RFI}, CMP^{DMI}, and CMP^{ADG}, for RFI, DMI and ADG marker panels, respectively.

3.2.10 Genomic predictions

The predictive ability of the marker panels was assessed as the correlation between CMP and the phenotype (also called accuracy of prediction), within and across traits. Comparisons in accuracy of prediction were also made within sire

breeds. For split 1, mean accuracies were obtained as the average of the correlations observed in the 5 replicates of the testing data.

3.3 RESULTS

Table 3.5 gives a summary of the descriptive statistics for RFI, DMI and ADG. On average, the diet switch group exhibited higher feed intake and gain compared to Fall-Winter and Winter-Spring groups. The estimated RFI mean was null for all groups, given that RFI was calculated within group. The distributions of the resulting F statistic from the single marker regression analysis for all SNPs in both splits 1 and 2 was as expected, with a large number of SNPs with small F values and a small number of SNPs with large F values (Appendix 3, Figures 1 to 6).

For split 1, the single marker association analysis yielded 2,242, 2,158 and 2,587 SNPs that were significantly associated with DMI, ADG and RFI, respectively, at an F statistic value of 3.84 (P = 0.052). The top 100 SNPs were selected for each trait to run the RR-BLUP analysis, and these corresponded to F statistic values of 10.14 (P = 0.002), 9.8 (P = 0.002) and 10.38 (P = 0.001) for DMI, ADG and RFI, respectively. In split 2, a total of 2,409, 2,380 and 2,196 SNPs were significant for DMI, ADG and RFI, respectively, at an F value of 3.84 (P = 0.052). The distribution of the test statistic from these analyses is shown in Appendix 3, Figures 1 to 6, and was as expected with a large number of SNPs having small F-values while a small number of SNPs had large F-values.

From these SNPs, the top 100 SNPs were chosen with the significance threshold corresponding to F statistic values of 10.04 (P = 0.002), 10.45 (P = 0.001) and 9.38 (P = 0.002) for DMI, ADG and RFI, respectively. The final marker panels selected for DMI, ADG and RFI had different numbers of SNPs, ranging between 34 and 44 as shown in Table 3.6.

Correlations between traits and CMP were used to assess the ability of the selected marker panels in the two data splits to predict phenotypes for animals in the testing dataset. Table 3.6 provides trait specific correlations between CMP and ADG, DMI and RFI phenotypes. For split 1, the correlations between CMP and traits were low, ranging between 0.27 for DMI trained panels to 0.414 for ADG trained panels, given that the polygenic EBV accuracy for all animals in the data before the split was 0.575, 0.504 and 0.602 for ADG, DMI and RFI, respectively. For split 2, correlations between CMP^{RFI} and CMP^{ADG} with their respective traits were practically null.

Results of CMP by trait correlations within sire breed in split 1 are shown in Tables 3.7. For DMI and RFI, the correlations for the Charolais breed tended to be lower than those observed for Angus and Hybrid sire breeds. Generally, there was similar predictive ability within and across sire breeds. The proportion of phenotypic variance attributable to SNPs was obtained as a product of the prediction accuracy in the testing data. The proportion of total variance attributable to SNPs can also be found by comparing residual variances when the analysis model contains or excludes the SNPs. The difference between these two

variances gives the SNP variance (Appendix 4, Table 1). For both testing and validation data, a larger proportion of phenotypic variances could be explained for RFI while the lowest was for DMI.

An attempt to run a bivariate analysis between CMP and the traits in the testing data to assess the gain in EBV accuracy occasioned by inclusion of the CMP in the trait evaluation failed because the estimates of variance components obtained for the various traits in the bivariate analysis, (particularly genetic variance estimates) were too small in the test dataset, to the point of causing model convergence problems.

3.4 DISCUSSION

3.4.1 Intake data integrity check

In this study, the test length for feed intake data collection averaged 80 days, well within the range for similar studies. Wang et al. (2006) and Archer and Bergh (2000) suggest that test period for feed intake measurements intended for RFI calculation last between 63 to 84 days, when BW is measured weekly, while Archer et al. (1997) estimate a 70d test period when BW data is collected every two weeks. The test period target for this study was approximately 90 days or until 70 days of usable data were obtained. To ensure that the feed intake data used for RFI calculation was not erroneous, a series of audits and checks were instituted as detailed in Table 3.4. The quality of the feed intake data is monitored by the “Check Audit Data” routine of the GrowSafe System, and is considered

acceptable when the average of all feeding nodes within pen and day have an "Assigned Feed Disappearance" (AFD) ≥ 95%. In addition, no feeding node within pen or day can have an ADF value less than 90%. This limits the inclusion of unaccounted feed disappearances, which may bias intake estimations. The AFD values for the last two years of the study are provided in Table 3.4 and only days with acceptable AFD values were used to calculate feed intake. However, in year 5, additional days were removed from the analysis if system problems caused the feeding bunks to go offline or if there was lack of data recording due to power failure. For years 1, 2 and 3, this information was not available at the time of analysis.

The percentage of DMI variance accounted for by ADG and MWT is important in assessing the integrity of the data. Typically, these two traits account for 60% or more of the DMI variation (Basarab et al., 2003) even though lower values have been reported (Crews, 2005). Values significantly lower than 60% may indicate a problem with the data. In this study, ADG and MWT accounted for 61.2% of the variation in DMI.

3.4.2 Parameter estimates for RFI and feed intake traits

Table 3.4 gives summary statistics for the traits evaluated. There was considerable variation in RFI and DMI (SD ranged between 1.27 to 1.65 for DMI and 0.73 to 1.05 for RFI), at levels slightly higher than those observed by similar studies (Archer and Berg, 2000; Archer et al., 1997; Arthur et al., 2001a).

However, this may be attributed to larger families in those studies compared to the current study. In this study, there were on average 4 offspring per sire (Table 3.2). Animals in the diet switch group were first tested on a lower energy diet in period 1 then a high energy diet in period 2. Based on the groups' mean ADG observed for the period 2, there was compensatory growth during this period, given the significantly higher ($P < 0.0001$) growth rate compared to the Fall-Winter and Winter-Spring groups. This group also had a significantly higher ($P < 0.001$) DMI compared to the other two groups, which may have further accelerated their growth rate. The difference in intake between Fall-Winter and Winter-Spring groups would mostly be due to the fact that animals tested in period 2 were older and larger in size than those tested in period 1, and as such are expected to have a higher intake to meet their metabolic requirements. However, seasonal effects unique to each period are likely to further confound differences between these groups, especially where feed intake is concerned. Variation in ambient temperature, solar radiation and photoperiod are known to affect feed intake and efficiency in animals (Young 1983; Delfino and Mathison, 1991).

Single trait heritability estimates (Table 3.5) observed for all traits are within the range observed by similar studies (Koch et al, 1963; Crews et al., 2003) suggesting that polygenic selection can result in significant genetic improvement for RFI, given adequate data and selection intensity as evidenced by studies by Richardson et al. (1998) and Arthur et al. (2001c). The emphasis on RFI is

because it is a newer trait, with potentially large economic benefits for feedlot producers.

3.4.3 An LD-MAS approach for RFI selection

Following the observations of Kizilkaya et al. (2010), the strategy employed in this study was such that marker panels selected for each of the traits consisted of SNPs highly associated with the trait thereby maximizing the possibility of capturing as many QTL underlying the trait as possible. In this way, CMP derived from such panels would possibly be highly correlated with the trait and offer a better prospect as indicator traits especially where RFI is concerned. Given the inconsistent results observed for IGF-1, which had previously shown promise as a viable proxy for RFI (Kahi et al., 2003; Wood et al., 2004; Moore et al., 2005; Carstens et al., 2007; Lancaster et al., 2008), it has become of immense importance to access a panel of SNPs with such capabilities, given the cost of feed intake testing is still high.

3.4.4 Correlations between CMP and phenotypes

Different strategies have been used to create so called training and validation (testing) data sets. Random splits (Luan et al., 2009), splits made based on sire family or generation number in a population (Hayes et al., 2009; Moser et al., 2009) or use of other independent dataset (Kizilkaya et al., 2010) have all been employed to this end. All the strategies seek to minimize as much as possible, an overlap of related individuals in the training and testing data sets such

that correlations between CMP and phenotypes are mostly based on LD between markers and causative mutations, and not genetic relationships between individuals. Genetic markers have been shown to capture relationship between individuals and thus have the potential to confound estimates of correlations between observed merit and marker predicted merit (Habier et al., 2007). However, in practice such confounding may be difficult to remove in any population.

Two different data splits were used in this study. Analysis using split 2 was similar to a situation where SNPs were trained in one crossbred population and the resulting CMP used for prediction in a different crossbred population. It is important to note that the training dataset used was an admixed population consisting of steer offspring of a cross between Angus, Charolais, or University of Alberta hybrid bulls and a composite dam line consisting of various beef and dairy breeds (Goonewardene et al., 2003). The validation dataset in split 2 consisted of offspring from U of A hybrid bulls. All the offspring were therefore crossbred, but the composition of the validation set was quite different from that of the training set.

In split 1, the pattern of the correlations observed between the traits and CMP reflected the magnitude of trait variances, with DMI, which had the largest genetic variance and thus heritability estimate, having the smallest correlation. This is a reflection of the number of polymorphisms required to explain the phenotypic variation in a trait, and given that DMI had a larger phenotypic

variance, a larger marker panel would be necessary to account for a substantial proportion of the trait variance.

The results in Table 3.6 also exemplify the folly of training SNPs in a population with a very different breed composition compared to the validation population. In split 2, correlations between CMP and traits performed poorly, except for DMI whose correlation was close to half what was obtained in split 1. Correlations for RFI and ADG were practically null. These results suggest that the genetic composition of animals borne of hybrid sires in the validation set is very different from that of steers from Angus and Charolais sires. De Roos et al., 2008 have shown that LD between breeds extends to shorter distances such that QTL captured by the training set may not reflect any one breed satisfactorily. Such factors as differences in allele frequencies between breeds, differences in LD phase as well as potential instances of differential epistatic interactions between QTL in different breeds may contribute to low prediction accuracy. Even though hybrid animals were included in the training dataset used for split 2, prediction in the validation data (composed solely of the hybrid type) seemed to fail for traits with low variation (ADG and RFI). It is also possible that the lack of substantial correlations for this split may also be due to a sample size problem rather than a lack of congruency in the genetic composition between training and testing data such that increasing the number of individuals in the training set would improve accuracy. In their simulation, Toosi et al. (2010) found that increasing the percent contribution of a certain breed in an admixed population used for training leads to

an increase in accuracy of prediction when validating in the single breed. One possible explanation is that for a SNP to be selected in a multi-breed scenario, it has to be in LD with QTL in all breeds or most of the breeds. This scenario is further complicated by the fact that the hybrid population is a mixture of many other breeds. However, given that the number of animals in the validation dataset for split 1 and 2 is not markedly different (Table 3.2), sample size is possibly not the biggest driver of the reduced correlations observed in split 2. Perhaps of greater importance in the results obtained for split 2, is the fact that there were no known pedigree relationships between the animals in the validation set. This low information density would likely be the greatest cause of reduced predictive ability.

The study by Kizilkaya et al. (2010) showed that across breed predictions are possible if a substantial number of causative mutations are captured in the prediction panel. Increasing the number of markers in strong association with the traits in the SNP panel would have possibly increased the extent of the correlations observed (de Roos et al., 2009).

3.4.5 Within sire breed correlations

The results in Table 3.7 show breed specific correlations in the validation set for CMP selected using the admixed training population in split 1. The interpretations offered from this analysis are to be viewed with caution due to the small number of individuals within each sire breed. The within breed results

illustrate similar prediction for the sire breeds, even though predictions for the Charolais breed tend to be lower compared to the other breeds. A similar correlation pattern is seen within breed as across breed, with DMI having the lowest prediction accuracy.

Other studies such as Dunner et al. (2003), have shown that functional mutations can be breed specific thereby limiting the usefulness of the marker panels to breeds in the discovery data. However, when the validation population is admixed, another level of complexity is introduced, limiting prediction accuracy. It is thus important that marker panels be tested in different breeds and environments, but in a manner congruent to the reference population used for training.

The small number of animals in this study notwithstanding, the results obtained point to a lack of significant differences in accuracy of prediction between the breeds studied, such that the prediction accuracy obtained for this analysis is likely due to LD between QTL and trait phenotypes and not because the SNPs trace breed differences. This may further suggest that the composite population used can serve as a useful resource for testing of the SNP panels selected here in other populations with breeds of similar genetic background as the component breeds in our population.

For most practical purposes, gene tests that constitute only a small subset of markers, especially those in high LD with putative causative mutations are

desirable. Even though significance testing in association analyses limits the proportion of genetic variance accounted for by the selected SNPs because the estimates are inflated and have a positive error variance (Beavis, 1994; Lynch and Walsh, 1998), marker panels derived from SNPs associated with the trait allow gene tests on fewer polymorphisms, reducing the cost of tests, while still integrating genetic marker information into existing genetic evaluations through BLUP or selection index methodology, to facilitate an efficient LD-MAS scheme.

The proportion of genetic variance that SNP markers should explain to be useful in a MAS scheme is a subject of current research. Crews et al. (2008) suggests that markers need to explain at least 10-15% of the genetic variance in RFI or feed intake to be useful. So far in the literature, there is no genetic test that accounts for such variability for RFI. In this study, the genetic polymorphisms identified account for about 17.1%, 7.29% and 16.1% of the phenotypic variance in ADG, DMI and RFI, respectively, obtained as r^2, r being the average accuracy of prediction in the 5 replicate validation data sets for split 1. Appendix 4, Table 1 gives estimates of variance component observed in the training data sets, as well as the proportion of the phenotypic variance that can be attributed to SNPs (9%, 6% and 10% for ADG, DMI and RFI, respectively) in those data. These results follow the same trends as those seen in the validation data. However, the higher prediction accuracies in the testing data may be a function of the small number of individuals in the testing data, and validation in larger populations would be necessary.

3.5 CONCLUSION

Several marker panels predictive of RFI, DMI and ADG were developed from a small number of genetic markers pre-selected for high association with the traits. These marker panels were able to predict a small proportion of the trait phenotypic variance. However, the correlations observed were still low for all traits compared to polygenic EBV accuracies. Results obtained from split 1 suggest that the breed composition of the training data did not have significant effect on the within sire-breed predictions. Given the results from split 2, using an admixed training population to select SNPs followed by prediction in another crossbred population, whose type was also included in the training population yielded very low correlations for traits with low variation (ADG and DMI), and this strategy is not recommended. However, a leading cause of this may be due to a lower information density in the validation dataset for split 2 since no pedigree relationships between individuals in this data were known. The results from this study suggest that the composite breed used in this study may be a useful resource for assessing prediction accuracy in similar breeds as those in this population. Ultimately, the utility of the panels will be determined if validated in an independent population.

Table 3.1 Summary of the testing groups, study design and number of animals used

Year	Year No.	Batch	Season[a]	Group	No.
2002/3	1	1	1[‡]	-	86
		2	2	Group 2	64
2003/4	2	3	1	Group 1	80
		4	2	Group 2	76
2004/5	3	5	1	Group 1	80
		6	2	Group 2	78
2005/6	4	7	2*	Group 3	176
2006/7	5	8	2	Group 1	88
		9	2*	Group 3	87

[‡] This batch was removed from analysis due to problems identified with the phenotypes.

[a]Season 1 = Fall-Winter, Season 2 = Winter-Spring; Group 1 = Fall-Winter tested; Group 2 = Winter-Spring tested; Group 3 = Diet switch.

* These batches were also tested in the fall, but only winter values were included in the analysis

NB: The term batch is used to refer to a cohort of animals tested in the same period. It is synonymous in its use here to a contemporary group.

Table 3.2 Summary of the number of steers per sire, within test group and sire breed

Item	†Split 1		Split 2	
Sire Breed	Train	Test	Train	Test
Angus	177	42	219	
Charolais	48	49	97	
Hybrid	168	61	229	
Unassigned	97	51	0	148
Totals	490	203	545	148
Sires				
Total number of sires	197			
Average number of offspring per sire	3.5			
No of sires with single offspring	161			
Range of number of offspring	1 – 51			
Average number of offspring per sire[a]	14.77			

[a] Averaged for sires with more than one offspring; 12 sires had offspring ranging from 3 to 48 and 53 sires had 1 offspring each for split 1

†Some animals were removed in split 1 because they had missing genotypes

Table 3.3 Composition of experimental diets for the different years tested[†].

Diet ingredient	2002-3	2003-4	2004-5	2005-6	2006-7
	(% as-fed basis)				
Dry-rolled corn	80.00	--	--	--	--
Barley grain	--	64.50	64.50	56.70	56.70
Oat grain	--	20.00	20.00	28.30	28.30
Alfalfa hay	13.50	9.00	9.00	10.00	10.00
Beef feedlot supplement[1]	5.00	5.00	5.00	5.00	5.00
Canola oil	1.50	1.50	1.50	--	--
DM, %	90.50	88.90	88.90	87.00	87.00
Nutrient Composition, DM basis[2]					
ME, Mcal/kg	2.90	2.91	2.91	2.90	2.90
CP, %	12.50	14.00	14.00	13.50	13.50
CF, %	--	--	--	3.29	3.29
NDF, %	18.30	21.49	21.49	29.51	29.51
ADF, %	5.61	9.50	9.50	10.28	10.28

[1]Contained 440 mg/kg of monensin, 5.5% Ca, 568 0.28% P, 0.64% K, 1.98% Na, 0.15% S, 0.31% Mg, 16 mg/kg I, 28 mg/kg Fe, 1.6 mg/kg Se, 160 mg/kg Cu, 432 mg/kg Mn, 432 mg/kg Zn, 4.2 mg/kg Co, as well as a minimum of 80,000 IU /kg vitamin A, 8,000 IU/kg vitamin D, and 1,111 IU/kg Vitamin E. 1Mcal = 4.185 MJ.

[2] Obtained from digestibility trials and subsequent proximate analysis as described by Nkrumah et al. (2006). ME – metabolizable energy; CP, - Crude protein; CF – Crude fat; NDF – Neutral detergent fiber; ADF – Acid detergent fiber.

[†]Only the periods of high energy diet were used for analysis, so the diets presented are only the high energy rations for the 5 years tested. The low energy diets for 2005/6 and 2006/7 are not included in the table.

Table 3.4 Details of some parameters associated with feed intake data used to calculate RFI

Years	2002-3,2003-4, 2004-5	2005-6, 2006-7
Days on test, d	84	92, 74
Days deleted, d	1-2%[a]	16, 23
Average AFD (%)	--[b]	94.8, 97.7
Days used to calculate RFI, d	~80	76, 51
Days with acceptable feed disappearance (95%), d	--[b]	76, 62

[a]Percentage of total number of days, Nkrumah et al. (2007)

[b]Information not available

AFD – Average feed disappearance; ADG – Average daily gain; DMI – Dry matter intake; MWT – Metabolic midweight; RFI – residual feed intake

Table 3.5 Descriptive statistics and heritability estimates for traits analysed

	Group 1	Group 2	Group 3*	Overall	
Trait	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Heritability
RFI, $Kg.d^{-1}$	-0.00 ± 0.73	-0.00 ± 0.88	0.02 ± 1.05	0.01 ± 0.92	0.29 ± 0.12
ADG, $Kg.d^{-1}$	1.49 ± 0.27	1.53 ± 0.28	1.82 ± 0.28	1.62 ± 0.31	0.28 ± 0.11
DMI, Kg	10.43 ± 1.27	11.45 ± 1.45	12.59 ± 1.65	11.63± 1.70	0.41 ± 0.12

ADG – average daily gain; DMI – dry matter intake; RFI – residual feed intake; Group1 = Fall-Winter; Group 2 = Winter-Spring tested; Group3 = Diet Switch; overall = across all groups.

*This group was tested on a low energy diet in the fall then a high energy diet in the winter. Only winter data is analysed for this group.

Table 3.6. Correlations (± SE) between CMP and trait phenotypes in the validation data for the two data splits used in the analysis, with number of SNPs in the panel for Split 1 and 2, respectively in brackets

Split	ADG (35/35)	DMI (44/34)	RFI (35/34)
‡Split 1	0.414 ± 0.051	0.270 ± 0.066	0.402 ± 0.065
Split 2	0.007	0.156	-0.042

‡Average from 5 replicates. Split 1 = validation dataset obtained from a random split of the data (1:2) based on sire family; Split 2 = validation data obtained by using animals with undetermined parentage, thus with undefined relationship to those in the training set. ADG –Average daily gain; DMI – dry matter intake; RFI – residual feed intake.

Table 3.7 Correlations (obtained as the average of 5 replications, ± SE) between CMP and trait phenotypes by sire breed in the split 1 validation dataset

Breed	ADG	DMI	RFI
Across Breed	0.414 ± 0.051	0.270 ± 0.066	0.402 ± 0.065
Angus	0.440 ± 0.060	0.314 ± 0.045	0.462 ± 0.010
Charolais	0.368 ± 0.051	0.249 ± 0.128	0.295 ± 0.099
Hybrid	0.387 ± 0.057	0.429 ± 0.068	0.465 ± 0.106
†Undefined	0.298 ± 0.069	0.381 ± 0.081	0.414 ± 0.109

†Sire breed not known.
ADG –Average daily gain; DMI – dry matter intake; RFI – residual feed intake.

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CHAPTER 4 : Accuracy of genomic breeding values for residual feed intake in crossbred beef cattle

4.1 INTRODUCTION

A large number of genomic tools have become available due to the rapid advancement of DNA marker technology after the mapping (and more recently the sequencing) of the bovine genome. This has led to increasing interest in inclusion of DNA marker tools into traditional evaluation systems, which typically combine pedigree and phenotypic data to form an estimated breeding value (EBV) which is then used in some form of index for selection purposes. Incorporation of DNA marker tools in a marker assisted evaluation system results in marker assisted EBVs (MEBV), often with higher accuracy compared to traditional EBVs. Such increase in accuracy will be highest for traits which are difficult or expensive to measure, such as residual feed intake (RFI). The DNA marker tools can also be used to predict future phenotypes as well as predict EBV where there is little or no phenotypic data.

Various strategies have been suggested for inclusion of marker information into genetic evaluations. Results from a DNA test can be used to create a molecular score (MS) or a molecular breeding value (MBV), which are a weighted sum of the number of copies of the frequent alleles of several polymorphisms with the weights being allele substitution effects estimated in a reference dataset (Kachman, 2008). Because the MS or MBV is derived from a

marker genotype related to the genotype associated with the economically relevant trait (ERT) of interest, it may be regarded as a separate and correlated trait to the ERT. Selection of SNPs with high association with the economically relevant trait can lead to greater correlation between the trait and the MS or MBV.

Given that MS will likely only account for a small portion of the total genetic variance, it will be necessary to combine polygenic and molecular breeding values into a single selection tool. Several strategies have been advanced to this effect. Selection index methodologies have been shown in simulation and with real data to be useful in combining polygenic and molecular/genomic breeding values (Dekkers, 2007; Crews, 2008; Moser et al., 2009). A strategy that makes use of multi-variate analyses of MS and economically relevant traits has also been proposed, and benefits from a familiarity with the current EPD selection framework, by taking advantage of the genetic correlation between the MS and the trait (Johnston et al., 2008; Kachman, 2008). Molecular markers have also been shown to accurately approximate the genetic relationships between individuals, such that the numerator relationship matrix could be replaced with a genomic relationship matrix, in what has been referred to as genomic BLUP (Habier et al., 2007; Van Raden, 2008; Hayes et al., 2009).

Perhaps the greatest development has been in the use of genomic selection to predict future performance of individuals (Meuwissen et al., 2001). In this technique, selection decisions are based solely on genomic breeding values obtained by estimating marker effects in the whole genome. The technique makes

assumptions about sufficient linkage between genetic markers and genes underlying the trait, such that marker effects can be used to estimate breeding values for animals, especially in situations where the selection candidates have no performance records of their own.

Recently, Bayesian estimation has emerged as the method of choice for genomic selection because it allows different variances to be fitted to each SNP as opposed to BLUP estimation, which assumes a homogeneous variance for all loci. Newer methods for efficient implementation of genomic selection continue to be developed (Legarra and Misztal, 2008; VanRaden, 2008) and it may soon be that genomic selection becomes the method of choice for marker assisted selection. Genomic selection proceeds in two steps:

i) A training dataset is used to estimate the effect of all markers. The individuals in this set typically have both phenotypes and genotypes. Care is taken so that there is minimal overlap of related individuals between the training data set and the testing or validation data set. The reason for this is that genetic markers are able to capture relationship information thereby biasing upwards the accuracy of prediction (Habier et al., 2007).

ii) The estimates obtained in the training data are combined with the genotypes of individuals in the testing (validation) data set (as a weighted sum) to obtain a genomic breeding value (GEBV) which

is then compared to a realized breeding value if present or used to predict the phenotype of animals in the testing data.

The predictive ability of the GEBV is usually higher if individuals in the training and testing data sets are related or of the same genetic base.

In this Chapter, Bayesian based methods and the theory underlying genomic selection were used to select a subset of markers, and ultimately derive GEBV to predict RFI, DMI and ADG for a group of steers tested for feed intake.

4.2 MATERIALS AND METHODS

4.2.1 Animal resource and study design

Data consisted of 721 crossbred steers sired by Angus, Charolais or University of Alberta Hybrid Bulls with a composite dam line. The composition of the damline is described in detail by Goonewardene et al. (2003). Feed intake data was collected over a 5 year period with two groups (Fall-Winter and Winter-Spring) tested every year for the first three years. In year 4, one group of animals was tested for two consecutive periods (Fall-Winter then Winter-Spring), first on a low energy feedlot diet in period 1 (Fall-Winter) then a high energy feedlot diet in period 2 (Winter-Spring). In year 5, two groups of animals were tested in two consecutive periods as follows: The first group was put on a high energy feedlot diet for both periods, while the second group was first tested on a lower energy diet and then switched to a high energy diet in period 2 as shown in Table 4.1. Animals had free-choice access to feed and water. In total, 9 batches of animals

were available for analysis, a batch being a combination of year and season of testing (Table 4.1). All batches were placed into three groups as follows: Fall-Winter tested animals were in Group 1, Winter-Spring test animals in Group 2, and diet switch animals in Group 3. Phenotypic records for average daily gain (ADG), daily dry matter intake (DMI) and residual feed intake (RFI) were available for analysis.

Training and validation data sets were defined by randomly splitting the data into a training set (2/3, n = 485) and a testing set (1/3, n = 243) based on sire family so that there was no overlap of sires in the two sets. This random split was replicated 5 times such that there were 5 training and 5 testing data sets. Random splitting by sire family reduces the ability of genetic markers to approximate the relationship between individuals in the training and testing data, thereby minimizing chances of an inflated correlation of GEBV and trait phenotype in the prediction process (Habier et al., 2007). The first replicate of the training data was used for SNP pre-selection, and the selected SNPs were then re-analysed in all replicates of the training data. The association between genotypes and phenotypes was tested in the training set, while the accuracy of prediction of the marker derived breeding value explored in the testing set, as the correlation between GEBV and phenotypes.

4.2.2 Genetic data

Approximately 50,000 SNP were genotyped for 745 beef steers using the Illumina Infinium II platform. These SNPs were tested for Hardy-Weinberg Equilibrium ($P > 0.05$), minor allele frequency (> 5%) and SNP Call frequency (> 88%) with non qualifying SNPs being discarded. Ultimately a total of 38,158 SNPs were selected for further analysis. Genotypes were coded as 0, 1 and 2 with 0 being the SNP allele with the lower frequency and 1 the allele with higher frequency, respectively, such that the two homozygotes were represented as 0 and 2, and 1 was the heterozygote. Missing genotypes (about 1% of all genotypes) were imputed by submitting SNP genotype calls as well as missing genotype information to fastPHASE (Scheet and Stephens, 2006) chromosome by chromosome, the SNPs having been ordered according to their chromosomal position. The parameters used were as follows: Ten (10) random starts of the EM algorithm (T), 30 iterations of the EM algorithm (C), 15 cross-validation clusters (K), and no sampling of haplotypes from the posterior distribution of each random start of the EM algorithm (H). The most probable genotype imputed by fastPHASE was considered the true genotype. All SNPs with unknown chromosomal positions were discarded. A final 37,959 SNPs were included in the analysis.

The following animal model was used in the whole data set to estimate polygenic breeding values, variance components and genetic parameters using ASReml (Gilmour et al., 1998). The model included fixed effects of

contemporary group (breed, batch, and test group combinations) with age at start of test as a covariate:

$$\mathbf{y}_1 = \mathbf{X}_1\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{a} + \mathbf{e}, \quad (1)$$

where, the design matrices $\mathbf{X}_1$, and $\mathbf{Z}_1$ relate phenotypic observations in the vector y_1 to fixed (β), and polygenic (*a*) effects, respectively. The vector **e** contains random residual terms specific to animals. The parameters *a* and *e* were assumed to be normally distributed with a mean of 0, and variances $\boldsymbol{A}\sigma_a^2$ and $\boldsymbol{I}_n\sigma_e^2$ respectively. The matrix $\boldsymbol{I}_n$ is an identity matrix of order equal to the number of animals with RFI observations, while **A** is the additive relationship matrix, σ_a^2 is the random polygenic effect variance, and σ_e^2 the residual variance, respectively. Accuracy was calculated using the formula $\boldsymbol{accuracy} = \sqrt{1 - \frac{se^2}{a^2}}$, with se^2 being the prediction error variance and a^2 the additive genetic variance (Gilmour et al., 2008). A bivariate model was used to compute genetic correlations between the traits by extending eq. (1) to include a second trait.

4.2.3 Bayesian estimation of marker effects

Estimation of marker effects was performed using two models

i) Random regression BLUP (RR-BLUP), which assumes the same prior variance for all random SNPs as described by Meuwissen et al. (2001).

ii) BayesB, where a locus specific variance is estimated, but the loci are divided into two groups: a group of relatively small number of SNPs with large effects that contribute to the genetic variance with probability (1 – $\boldsymbol{\pi}$), and a second group of large number of SNPs with no effect, with probability $\boldsymbol{\pi}$ (Meuwissen et al., 2001). The BayesB model used was similar to Meuwissen et al., (2001), except that effects of SNP genotypes and not haplotype were fit. Also the polygenic and residual variances were sampled using a Gibbs algorithm.

BayesB makes strong assumptions about the prior distribution of marker effects, namely a large proportion of SNPs have no effect. The BayesB and RR-BLUP models used are implemented in the AlphaBayes software (Hickey and Tier, 2009), which utilizes a modified version of the Gibbs sampling algorithm to solve for model effects. The SnpBlup and BayesBFast implementations in AlphaBayes were used for RR-BLUP and BayesB analyses, respectively. Even though the real value of $\boldsymbol{\pi}$ was unknown for this dataset, $\boldsymbol{\pi}$ was set at 0.95 for all analyses, such that 5% of SNPs were fitted simultaneously in each cycle of the Gibbs chain.

The model of analysis used for RR-BLUP and BayesB was as follows:

$$\mathbf{y}_1 = \mathbf{X}_1\boldsymbol{\beta} + \mathbf{Z}_1\boldsymbol{a}^* + \mathbf{Z}_2\boldsymbol{g} + \boldsymbol{e}, \qquad (1)$$

where, the design matrices $\mathbf{X}_1$, $\mathbf{Z}_1$ and $\mathbf{Z}_2$ relate phenotypic observations in the vector $\mathbf{y}_1$ to fixed ($\boldsymbol{\beta}$), residual polygenic ($\boldsymbol{a}^*$) and SNP ($\boldsymbol{g}$) effects, with

elements $\mathbf{Z}_{2ij}$ = 0, 1, or 2, corresponding to the genotype of animal *i* at locus *j*, with $\boldsymbol{g}$ normally distributed with mean 0, and variance $\boldsymbol{\sigma}^2_{gj}$, for RR-BLUP, and drawn from an inverse chi-squared distribution with probability $\boldsymbol{\pi}$ in BayesB. The variance $\boldsymbol{\sigma}^2_{gj} = \boldsymbol{\sigma}^2_a / \boldsymbol{n}$ in RR-BLUP, and was estimated for each instance of *j* in BayesB. The vector $\boldsymbol{e}$ contains random residual terms specific to animals. The parameters *a** and *e* were treated as random. The matrix $\boldsymbol{I}_n$ is an identity matrix of order equal to the number of animals with trait observations, while **A** is the additive relationship matrix, $\boldsymbol{\sigma}^2_{a*}$ is the random residual polygenic effect variance, and $\boldsymbol{\sigma}^2_e$ the residual variance. Fixed effects fitted included contemporary group (breed-batch-test group combinations) while age at start of test was used as a covariate.

The first 20,000 iterations from the total 100,000 iterations were discarded as burn-in. Mean SNP substitution effects were obtained from the posterior samples for each trait and SNPs ranked from highest to lowest based on the magnitude of the allele substitution effect. From this ranking, the top 200 SNPs were selected for further analysis. Allele substitution effects for the selected SNPs were re-estimated in each of the 5 replicates of the training data, with the first 5,000 iterations of the total of 20,000 discarded as burn in. For this analysis, $\boldsymbol{\pi}$ was set to 0.0005 so that estimates for all 200 SNPs could be obtained.

4.2.4 Genomic value estimation

Trait specific marker panels were obtained from analysis using the various methods outlined above. The SNPs were subsequently used to derive marker scores. Marker scores (MS) were calculated as a weighted sum of the number of copies of the more frequent allele at each SNP locus, with the weights being the allele substitution effects (β) estimated. The summation of all MS for each individual yielded a genomic estimated breeding value (GEBV):

$$GEBV = \sum_{j=1}^{N_m} X_{ij} \hat{g}_j ,$$

where, X_{ij} represents the marker genotype of animal i at SNP j, coded 0, 1, 2 as previously described, $\hat{g}_j$ is the estimate of SNP effect j, and N_m is the number of SNPs. The following nomenclature $GEBV_{No.SNPs}^{Trait}$ was used for clarity. GEBV were derived for panels with all 37,959 markers as well as the top 200 SNPs for each trait.

4.2.5 Genomic predictions

The accuracy of prediction for the GEBV was assessed as the correlation between GEBV and the phenotype both within and across sire breeds.

4.2.6 Candidate gene analysis for RFI

For the trait of RFI, the 1:2 ratio of validation to training records was randomly replicated 5 times, and each replicate analysed using both RR-BLUP and BayesB methods so as to obtain SNPs that consistently ranked within the top

200, as these were likely viable candidate genes for RFI. The number of times that a SNP was ranked within the top 200 after the 5 analyses yielded the 'detection' frequency, expressed as a percentage. The positions of SNPs with the highest detection frequency were used to search for gene annotations and associated publications in Entrez Gene, HomoloGene, and PubMed, using a custom Perl script.

4.3 RESULTS

4.3.1 Genetic parameters and variance components

Phenotypic and genetic correlations between the 3 traits analyzed are shown in Table 4.1. Correlations were highest between ADG and DMI and lowest between ADG and RFI. There were significantly high phenotypic and genetic correlations for DMI with both RFI and ADG.

Table 4.2 gives variance components and genetic parameters for the traits evaluated. Estimates of phenotypic and genetic variance were highest for DMI and lowest for ADG. Subsequently, single trait heritability estimates for RFI and ADG were moderate to low, while DMI heritability was in the medium range.

4.3.2 Accuracy of GEBV prediction

Table 4.3 shows trait specific as well as between trait correlations for GEBV with RFI, DMI and ADG. For both BayesB and RR-BLUP with the 200 SNP panel, the highest correlation was observed between RFI and $\boldsymbol{GEBV}_{\mathbf{200}}^{\boldsymbol{RFI}}$

while the lowest correlation was observed between DMI and $\boldsymbol{GEBV}_{200}^{DMI}$. Accuracies between ADG with $\boldsymbol{GEBV}_{200}^{RFI*}$ (GEBV obtained from estimates for association with ADG but using SNPs identified by training on RFI) were very low, while association between DMI and $\boldsymbol{GEBV}_{200}^{RFI**}$ (GEBV obtained from estimates for association with DMI but using SNPs identified by training on RFI) yielded higher correlations than trait specific values. Correlations between traits and GEBV with all the markers included yielded lower correlations than using only a subset of the top 200 SNPs for both BayesB and RR-BLUP (Table 4.3). Generally, the RRBLUP method yielded higher prediction accuracies than BayesB, while prediction accuracy for RFI was higher than for DMI and ADG.

In Table 4.4, trait specific correlations for different sire breeds are shown, for panels trained using BayesB and RR-BLUP. For both BayesB and RR-BLUP, the correlation of GEBV and RFI was slightly different within sire breed compared to the value obtained in across-breed comparisons. Further, for RR-BLUP, there is a pattern of differential accuracy within sire breed, where the correlations between sire breed tended to differ depending on what trait was being evaluated. For ADG, the Hybrid and Angus breeds tended to be different, while for RFI, the Charolais sire breed tended to have a distinct correlation pattern from the others (Table 4.4).

4.3.3 Candidate genes for RFI

Eleven (11) SNPs associated with RFI were consistently ranked within the top 200 in 3 of 5 replicates (detection frequency of 60%) when the training data was analysed using the RR-BLUP model. The highest detection frequency obtained using the BayesB method was 40% with a total of 28 SNPs having been detected, while 92 SNPs had a detection frequency of 40% or higher with the RR-BLUP method. Seven of the 11 SNPs with detection frequency 60% were either located within a gene or close to a gene whose function could affect feed intake or feed efficiency (Table 4.5). Further, 4 of the 11 SNPs were also identified with a 40% detection frequency using the BayesB method, while all 92 SNPs from RR-BLUP had a detection frequency of at least 20% with the BayesB method. A total of 6 SNPs were common between the 92 from RR-BLUP and 28 from BayesB.

4.4 DISCUSSION

The strategy employed in this analysis, to limit the number of SNPs used for GEBV estimation to the top 200, was to maximize the chance of capturing a large number of SNPs in high LD with underlying QTL as well as reduce the number of redundant markers. Studies by Kizilkaya et al. (2010) and Zhong et al. (2009) have shown that panels that include QTL or markers in high LD with QTL perform better when predicting across breeds or across multiple generations. The foregoing assumption is that markers with large effect signify markers in high LD with the trait, and thus account for a larger portion of the trait variance. This strategy in itself has a practical implication in that by using a subset of SNPs

instead of the whole range of markers available in the analysis, equivalent levels of prediction accuracy can be achieved without incurring the costs of genotyping associated with high density SNP chips when used in a commercial application. In any case, it is very probable that for the 50K bovine SNP chip, only a subset of markers are useful for prediction purposes for various traits, and inclusion of additional SNPs increases 'noise' without a substantial change in prediction accuracy. This has been demonstrated in several studies (Luan et al., 2009; Kizilkaya et al., 2010) where smaller subsets of markers have achieved equivalent or higher accuracies as larger sets.

In this study, for all traits with 200 SNP markers, the BayesB method performed marginally lower than the RR-BLUP method. When allele substitution effects of SNPs selected using RFI were re-estimated using ADG as the training phenotype, the resulting GEBV ($\boldsymbol{GEBV}_{200}^{RFI*}$) could not predict ADG for both BayesB and RR-BLUP. However, process with DMI resulted in higher predictive accuracy for than trait specific GEBV ($\boldsymbol{GEBV}_{200}^{DMI}$) as shown in Table 4.3. The RFI SNP panel was able to achieve higher accuracies with DMI than using the within trait panel. This offers the prospect of a multi-trait panel, which can be used for both DMI and RFI. When using all available SNPs (37,959), the predictive accuracy was much lower than that seen with a smaller subset of 200 SNPs.

4.4.1 Differences between methods

The performance of BayesB and RR-BLUP were quite varied, given the differences in assumptions for the Bayesian and BLUP methods. In the Bayesian methods, posterior estimates are influenced to a large extent by the choice of parameters given by the prior distribution. On the other hand, parameters utilized in the RR-BLUP analysis are optimized by minimizing the prediction error. The biggest difference between the methods is in the assumptions associated with SNP variances. Typically, the genetic variance associated with each SNP in RR-BLUP is assumed to be small, and a uniform value of $\sigma_g^2 = \frac{\sigma_a^2}{n}$, is often used (as in this study), where σ_a^2 is the total genetic variance estimated by REML, σ_g^2 the variance associated with each SNP and *n* is the number of loci. This SNP variance structure has been deemed unrealistic since many of the SNPs are believed to have small or no effect on trait variance, and many effects are fitted compared to number of records present (Xu, 2003). An alternative definition, $\sigma_g^2 = \frac{\sigma_a^2}{2\sum_j p_j(1-p_j)}$ has been proposed (with p_j being the frequency of an allele at locus *j*), under assumptions of Hardy-Weinberg equilibrium and linkage equilibrium between QTL (Fernando et al., 2007).

Given that RR-BLUP fits all marker effects in the model, with marker variances obtained as a fraction of the total genetic variance, a larger number of markers would be needed to account for substantial genetic variance, especially

for traits with low genetic variance. This means that for the RR-BLUP method, to achieve equivalent levels of prediction accuracy compared to the Bayesian methods, larger SNP panels would be necessary, especially for ADG and RFI, whose trait variance is small compare to DMI. Therefore the results obtained in this study run contrary to that expectation. Such a result may be possible if the SNPs selected actually capture a reasonable proportion of QTL underlying the traits. This can only be tested by validating in an independent population.

Further, based on the suggestion by Meuwissen et al., (2001) that large QTL are heavily regressed back to the mean in RR-BLUP, the effects estimated by RR-BLUP will typically be small in comparison to those from Bayesian analyses, which only fit a fraction $(1-\pi)$ of the total numbers of SNPs available. This means that given the SNP selection was accomplished by ranking SNPs from highest to lowest in order of effect magnitude, such regression would lower the rank of erstwhile larger QTL.

The use of a Bayesian model that includes a polygenic effect is expected to aid in effect estimation by properly partitioning the phenotypic variance to the various components. However, some studies such as (Calus and VeerKamp, 2007) have alluded to minimal influence of including polygenic effects on accuracy in genomic selection analyses

In all instances, the RR-BLUP method obtained higher correlations than BayesB. This difference may be related to the underlying genetic architecture of

the traits. The infinitesimal model applied by RR-BLUP may fit the RFI and DMI data quite well compared to the notion of a few key QTL underlying the traits, as implemented in BayesB. Given that the range of metabolic processes that underlie RFI is quite large (Richardson and herd, 2004) and recent discoveries suggesting that many putative genes may be associated with feed intake (Barendse et al., 2007; Chen et al., 2009), there is increasing evidence to suggest that a larger portion of the trait variance is under influence of many QTL of small effect. This lends support to assertions that the assumptions underpinning RR-BLUP may closely approximate the genetic architecture for RFI and DMI compared to Bayesian models. Still, there may be a substantial number of QTL of large effect affecting these two traits.

On the other hand, given that there is typically little variation in ADG between animals both in this study as well as in similar studies, it is logical to assume that the genic contribution towards this trait may be limited to a smaller number of QTL compared to RFI and DMI. Thus, the assumptions of the Bayesian model would be expected to favor a trait like ADG. It is not immediately clear why this isn't the case in this study and further analysis with a larger dataset will be necessary to verify this result. Estimates of variance components obtained from the 5 replicates of the training data are shown in Appendix 4, Tables 2 and 3. Estimates obtained with the BayesB method were substantially higher than those obtained for RR-BLUP and the proportion of the variance attributable to the SNPs in BayesB was quite high (Appendix 4: Tables 2, 3). However, the correlations

observed using both BayesB and RR-BLUP were lower that those observed for the polygenic EBV (0.575, 0.504, and 0.602 for ADG, DMI and RFI, respectively).

4.4.2 Within breed correlations

The admixed population of cross bred animals used in this analysis consisted of steers sired by bulls of various breeds. Accuracy of prediction within sire breed showed greater variation between breeds using the RR-BLUP method that with the BayesB method. There was also higher prediction accuracy within breed than across breed.

This pattern of higher within breed accuracy with RR-BLUP was clearly different than that observed using BayesB, where the within breed correlations were closer to the across breed estimates. A possible reason for this may be due to the possibility that SNPs selected using RR-BLUP may trace breed differences (SNPs are optimized to capture breed differences), such that the accuracy observed across breeds is confounded and not purely due to LD between SNP and underlying QTL.

Given that varying amounts of shrinkage are applied to SNPs based on differences in allele frequencies (the shrinkage term is the same for all SNPs for the RR-BLUP method), any differences in allele frequencies between breeds for any locus will impact the size of the allele substitution effect and by extension the prediction accuracy. Habier et al. (2007) showed that for RR-BLUP, genetic

relationships captured by the genetic markers affect prediction accuracy to a larger extent than in Bayesian methods, since more markers are fit in the model. The consequence of this is that there would be an increase in prediction accuracy if validation animals become more related to training animals, especially if the markers are able to resolve relatedness more than the average relationship matrix.

A key issue in genomic selection of RFI is the utility of GEBV in selection of un-phenotyped animals. In this study, the accuracies obtained were low, compared to those seen in studies using dairy breeds where more accurate phenotypes are used to train SNPs. A framework that allows incorporation of EPD and GEBV into a single unit of merit after appropriate weighting will be useful. The weights used could be derived from the reliability of the polygenic EBV and the percentage of genetic variance accounted for by the marker panels (VanRaden, 2001; Dekkers, 2007; Cerón-Rojas et al., 2008; Moser et al., 2009). A framework that utilizes BLUP (Kachman, 2008) has also been proposed. Such a combined index for selection seems to be the best option, especially for beef cattle until such a time when large populations of animals have been tested for feed intake and GEBV accuracies are higher than the EBV accuracies obtained using traditional BLUP evaluations.

The number of animals in the training set also has a bearing on the accuracy of GEBV (Hayes et al., 2009). For RFI, there is therefore a need for increased testing of feed intake, despite the cost associated with such an undertaking. This is a priority for several Canadian collaborations involving the

Universities of Alberta and Guelph, Alberta Agriculture and Rural Development (AARD) and Agriculture and Agri-Food Canada (AAFC).

4.4.3 Candidate genes for RFI

Several studies have attempted to characterize the molecular basis of RFI. Barendse et al. (2007) and Sherman et al. (2008, 2010) describe a series of polymorphisms associated with RFI, but the usefulness of these SNP and associated genes in explaining the total RFI variance is yet to be determined. In this study several SNPs with a high detection frequency were in close proximity of genes that may be useful in controlling feed efficiency (Table 4.10). Other SNPs that were detected in the top 100 in only a single replicate were also located within other useful genes (Appendix 2). Despite the fact that these SNPs are associated with some genes of interest, their individual contribution was small. So far, no study involving RFI has shown a gene(s) with a significantly large effect, such that a candidate gene approach may not be the best strategy in characterizing the molecular basis of RFI. The SNPs identified in this study may be more useful when seen as key elements of a gene network controlling RFI, as the contribution of individual genes is likely to be small. Further research and analysis of gene networks for RFI is therefore warranted.

4.5 CONCLUSION

In this study, accuracy of prediction, defined as the correlation between ADG, DMI and RFI and trait specific GEBV was compared between SNP panels

derived using two genomic selection methods, namely BayesB and RR-BLUP. The accuracies obtained for all 3 traits were low, signaling a need for continued feed intake testing to acquire a large number of phenotyped animals. RR-BLUP derived GEBV achieved higher correlations with trait phenotypes with accuracy being highest for RFI. Differences in accuracy between sire breeds were observed with the RR-BLUP method. This may imply that there may be significant differences between the component breeds used in the study population and the SNPs selected are consensus SNPs that wouldn't work equally well for all breed and trait combinations evaluated.

Table 4.1.Genetic (below diagonal) and phenotypic (above diagonal) correlations between feed intake and efficiency traits

	RFI	ADG	DMI
RFI		0.01*	0.55
ADG	-0.03 ± 0.30		0.64
DMI	0.51 ± 0.18	0.53 ± 0.18	

*Not significantly different from zero; all other phenotypic correlations significant (P<0.001). ADG – average daily gain; DMI – dry matter intake; RFI – residual feed intake; MWT – metabolic body weight.

Table 4.2 Variance components and parameter estimates for feed intake and efficiency traits

Model Item [a]	ADG	DMI	RFI
Variance component			
Var(P)	0.08	2.09	0.85
Var(G)	0.02	0.86	0.25
Var(E)	0.05	1.23	0.61
Parameter			
h^2	0.28 ± 0.11	0.41 ± 0.12	0.29 ± 0.12

[a]Var (P) = phenotypic variance; Var (G) = direct genetic variance; Var (E) = residual variance; h^2 = direct heritability.

Table 4.3 Correlations between $GEBV_{200}$ and $GEBV_{37959}$ with trait phenotypes for BayesB and RR-BLUP analyses

Trait	GEBV	Method	Replication					Average
			1 (n = 203)	2 (n = 194)	3 (n = 255)	4 (n = 203)	5 (n = 198)	
ADG	$GEBV_{200}^{ADG}$	BAYESB200	0.119	0.344	0.255	0.116	0.284	0.223 ± 0.05
		RRBLUP200	-0.003	0.517	0.459	0.421	0.462	0.371 ± 0.09
	$GEBV_{37959}^{ADG}$	BAYESB37959	0.149					
		RRBLUP37959	0.126					
DMI	$GEBV_{200}^{DMI}$	BAYESB200	-0.030	0.287	0.289	0.081	0.352	0.196 ± 0.07
		RRBLUP200	0.267	0.383	0.351	0.382	0.545	0.385 ± 0.05
	$GEBV_{37959}^{DMI}$	BAYESB37959	0.239					
		RRBLUP37959	0.246					
RFI	$GEBV_{200}^{RFI}$	BAYESB200	0.153	0.566	0.472	0.446	0.526	0.433 ± 0.07
		RRBLUP200	0.184	0.574	0.499	0.611	0.526	0.479 ± 0.08
	$GEBV_{37959}^{RFI}$	BAYESB37959	0.117					
		RRBLUP37959	0.114					
ADG	$GEBV_{200}^{RFI*}$	BAYESB_RFI200	0.055	0.062	-0.003	0.062	-0.023	0.030 ± 0.02
		RRBLUP_RFI200	-0.021	0.074	-0.064	-0.222	-0.119	-0.070 ± 0.05
DMI	$GEBV_{200}^{RFI**}$	BAYESB_RFI200	0.293	0.471	0.308	0.327	0.222	0.324 ± 0.04
		RRBLUP_RFI200	0.406	0.424	0.245	0.430	0.476	0.396 ± 0.04

ADG – Average daily gain; DMI – Dry matter intake; RFI – residual feed intake; BAYESB – Bayesian estimation using an algorithm called BayesBFast implemented in AlphaBayes; RR-BLUP – Random regression BLUP; GEBV – Genomic breeding value. Standard errors for the average calculated as $SD/\sqrt{5}$, where SD = standard deviation. $GEBV_{200}^{RFI*}$ - GEBV obtained from ADG effects, with SNPs selected using RFI.

$GEBV_{200}^{RFI**}$ - GEBV obtained from DMI effects, with SNPs selected using RFI.

Table 4.4 Correlations (± SE, as the average of 5 replications) between $GEBV_{200}$ and trait phenotypes by sire breed for GEBV trained using BayesB and RR-BLUP

Methods	Breed	ADG	DMI	RFI
Bayes	Across	0.223 ± 0.046	0.196 ± 0.073	0.433 ± 0.073
	Angus	0.252 ± 0.051	0.333 ± 0.068	0.550 ± 0.040
	Charolais	0.280 ± 0.132	0.200 ± 0.098	0.304 ± 0.120
	Hybrid	0.352 ± 0.097	0.261 ± 0.078	0.454 ± 0.076
	†Undefined	0.168 ± 0.062	0.291 ± 0.075	0.312 ± 0.143
RR-BLUP	Across	0.371 ± 0.095	0.385 ± 0.045	0.479 ± 0.076
	Angus	0.359 ± 0.112	0.514 ± 0.037	0.542 ± 0.042
	Charolais	0.445 ± 0.133	0.319 ± 0.171	0.314 ± 0.083
	Hybrid	0.510 ± 0.078	0.495 ± 0.075	0.533 ± 0.089
	†Undefined	0.386 ± 0.115	0.362 ± 0.105	0.435 ± 0.128

†Sire breed not known. ADG – Average daily gain; DMI – Dry matter intake; RFI – residual feed intake; RR-BLUP – Random regression BLUP

Table 4.5. Locations, closest genes and associated gene functions for SNPs that ranked within the top 200 in 3 of 5 replicates of the training data analysed using the RR-BLUP method.

SNPID	Detection Freq (%)	Position (bp)	BTA	Distance to Gene†	Gene name	Gene function
ss86322201	60	147355780	1	21,611	ES 1 protein	Inhibition of cellular growth
ss86274038	60	45908516	24	51,911	SET binding protein 1	SET binding protein
ss86285204	60‡	14738309	19	121,112	Chaperonin containing TCP1, subunit 6B	Mediates protein folding in the cytosol; Folding of actin and tubulin
rs41641502	60‡	14541593	19	5,326	Caspase regulator (CARP2)	Ubiquitin ligase/protein metabolism
rs42316404	60‡	8899286	17	179,149	Endonuclease reverse transcriptase	Endonuclease reverse transcriptase
rs43557189	60	53208327	8	0	Trancient receptor potential cation subfamily M, member 6 (TRPM6)	Ion exchange/Mg++ transport
rs42142693	60‡	24107627	28	0	Bovine homolog of	Binding in trans-membrane

					SLC25A16 solute carrier family (Mitochondrial solute carrier)	transport
rs41636768	60	55150035	18	n/a	No gene annotation found	
ss105256889	60	44671099	21	n/a	No gene annotation found	
rs41579807	60	14667205	19	n/a	No gene annotation found	
rs41663853	60	14379998	28	n/a	No gene annotation found	

†Distance to closest gene (bases); n/a – No genes identified; Detection Freq1 – detection frequency: number of times a SNP ranks in the top 200 in 5 replicates for the RR-BLUP method.

‡SNP also detected using the BayesB method with frequency 40%. SNPID – NCBI rsSNP ID; BTA – Chromosome number.

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CHAPTER 5 : General discussion

5.1 INTRODUCTION

Residual feed intake (RFI) continues to be the subject of tremendous interest and research, given that it is a relatively newer metric for assessing feed efficiency. Given the considerable gap that still exists in the knowledge surrounding this trait, characterization of its genetic nature is essential in order to understand the full impact of its selection on other traits.

There are lingering fears as to the effect that long term selection for RFI may have on other reproductive and fitness traits. This is driven by the observation in various studies that more efficient cattle tend to have greater carcass leanness. Many producers fear that increased leanness in animals may have a negative impact on reproductive fitness, especially in breeding cows. Generally, leaner cattle experience problems getting into calve year after year. However, based on results from Basarab et al. (2007) who examined maternal productivity in 10 production cycles as well as divergent selection experiments in Australia (Arthur and Herd, 2008), there seems to be little evidence to associates cows that calve efficient animals with lower reproductive capacity.

Refinement of models that are used for RFI estimation as well as for genetic evaluation in presence of molecular markers is still ongoing, and will be necessary if genetic gain in true metabolic efficiency is to be achieved. The question of whether to include body composition traits in RFI estimation models

is still unresolved and for all purposes ought to be population driven. Different breeds will have different carcass characteristics, and the magnitude of the correlations between these traits and RFI will vary accordingly. At present, there is little evidence to warrant inclusion of such effects in most populations analysed so far, given that the correlations observed between RFI and carcass traits are small and the datasets used to estimate them are suboptimal in terms of accuracy of feed intake measurements and sample size.

5.1.1 The effect of season on RFI

Being a relatively new trait, RFI has seen concerted efforts to characterize its genetic properties. However questions abound as to the effect of RFI selection on fitness and reproductive traits, the interplay of RFI with different environments and RFI repeatability at different stages of an animal's life cycle. It is apparent, however, that RFI selection can lead to considerable response in genetic gain as exemplified by divergent selection experiments in cattle and chickens (Bordas et al., 1992; Arthur et al., 2001). Kahi and Hirooka (2007), who did an economic analysis of a breeding strategy that included IGF-I and RFI in the selection index, showed higher accuracy of selection and increased profitability for Japanese black cattle.

Apart from genetic influences on RFI, environmental influences play an important role in the expression of the trait. Herd et al. (2004) and Richardson and Herd (2004) suggest five major processes that contribute to variability in

efficiency. These are heat increment due to feed intake, digestion, metabolism, physical activity and thermoregulation which together account for about 33% of variation in RFI. Any factor in the physical world that can affect any or a combination of these processes may affect efficiency. However, it is much more difficult to measure these parameters in beef cattle, and more studies are needed to further characterize the influence environmental factors have on overall efficiency.

In Chapter 2, we demonstrated that when feed intake is measured in different seasons defined largely by differences in ambient temperature, solar radiation and relative humidity, there was a correlation of feed intake with these weather parameters. Feed intake was correlated with air temperature, relative humidity, solar radiation and wind speed, but the nature and magnitude of the correlations were different for the two seasons (Fall-Winter, Winter-Spring). Despite the fact that the differences observed in feed intake and body composition may not wholly attributed to differences in the weather parameters in the two seasons due to age-weight-season interactions, the results in this chapter imply that feeding habits in the two periods of testing are not the same. This has a bearing on feed efficiency, depending on how prolonged adaptive measures necessitated by the changing climatic conditions are in effect. It also became apparent that inclusion of a season effect in the RFI evaluation model yielded similar results as current evaluation models that estimate RFI for each individual test group. However, such a scheme would fail if the intention is to assess genetic

gain due to RFI selection. In such a situation, a single regression model is applied to all test groups across multiple years as described by Arthur et al., (2001). This ensures that the mean for all the groups would be null, but within the different years (selection groups) the estimate of RFI mean will be different and will reflect the gain in efficiency resulting from RFI selection. No matter what evaluation method is used, it would appear there is a case to further study the effect of climate parameters on feed intake, with care being taken to minimize age-weight-season interactions. This would allow definition of season specific adjustments such that real metabolic efficiency is estimated. Preliminary results at the University of Alberta have shown that RFI repeatability is low (approx. 0.4), between successive feed tests (Durunna et al., 2010). Whether this is due to the influence of differential environmental adaptation, or effect of the animal being at different physiological stages in the testing periods, is unclear. Further studies into this subject are warranted.

The models used in the estimation of RFI in Chapter 2 did not include a body composition trait such as back fat depth. Typically, RFI is a function of live weight gain and metabolic weight as suggested by Koch et al. (1963). However, in North America, there has been a leaning towards inclusion of body composition traits, especially back fat depth. Currently, there is no universal model that is applied in the evaluation and estimation of RFI, with models including not only back fat thickness, but also ultrasound muscle depth as in the model used by François et al. (2002) for French sheep. Models in use for RFI

estimation will need refinement as more information regarding genetic correlations between RFI with various fitness, reproductive, fertility and body condition traits is obtained. So far, RFI has been shown to be correlated with only a limited number of traits (Table 1.1). Perhaps of utmost importance are studies supporting the fact that selection for RFI does not impact negatively on fitness and reproductive traits (Arthur et al., 2005; Basarab et al., 2007).

The standard tool for genetic selection for almost all economically important traits is the EBV (or EPD), which because of its success has seen wide application and acceptance. Selection for RFI would benefit if such a tool were developed. As more interest grows in selecting for increased feed efficiency, for the most part, most producers will be accessing EBV on first generational pedigree phenotypes, meaning that accuracies will be inevitably low because of the small numbers of animals with phenotypic data. These accuracies are bound to slowly increase as more animals are tested and several generations of data become available. As seen in Chapter 2, the average accuracy of EBV obtained in our study was 0.51. Such levels of accuracy may be way below acceptance levels for most producers when compared to traits that undergo routine evaluation. This may be a hard sell considering the level of investment required to access RFI technology. In order to maximize genetic gain in RFI selection, strategies to increase EBV accuracy will need to be implemented.

5.1.2 Molecular breeding values as correlated traits for RFI

The use of genetic markers to obtain tools useful in RFI selection is gaining increased interest. Genetic markers give rise to molecular or genomic breeding values (GEBV) which are weighted averages of the number of favourable alleles at a locus (with allele substitution effects as weights; Kachman, 2008) summed over a large number of loci. These GEBV, having been derived from marker genotypes related to the genotype associated with the economically relevant trait under evaluation, are often correlated with the trait of interest. These tools can then be used for genetic prediction either as correlated traits in a multivariate BLUP framework or incorporated into an index as a weighted sum of an animals EPD (EBV) and its GEBV, the weights being functions of the reliability of the EPD and proportion of variance explained by the GEBV (Moser et al., 2009). Of critical importance in the usefulness of such DNA based tools is the need for accurate estimation of marker effects.

Various strategies have been proposed for the estimation of SNP marker effects, ranging from single marker regressions to genomic selection. However, despite the differences in these methodologies, they all require that SNP effects be independently validated. This is most effective when undertaken as a third party validation using a group of animals that are as unrelated as possible, but biologically similar to the population used for SNP effect estimation. Such has been the framework adopted by the national beef cattle evaluation consortium with regards to commercially available marker tests (Van Eenenaam et al., 2007a,

b). This independent validation is important because it ensures that SNP effects are repeatable across multiple populations and management structures and are not fortuitous. Industry confidence in the technology is thus enhanced in such situations and adoption of the marker test for wide use may become much faster.

However, it is often necessary to do a within sample validation to estimate the predictive ability of the set of markers selected for further testing. This is mostly because for some traits such as RFI, only a relatively small number of individuals have feed intake records worldwide, and it may be necessary to pool together records from different sub-populations, so as to increase the accuracy of parameter estimation. In such situations, it may become difficult to have a set of unrelated animals with feed intake data to be used for independent validation. This problem is often mitigated by dividing the available dataset into a training set and a testing set (Whittaker et al., 1997; Osborne, 2000). SNP effects are estimated in the training set and the prediction equations generated evaluated in the testing set. This provides some sort of semi-independent validation of the estimated SNP effects, and reduces possibility of gross over-representation of the usefulness of selected panels. The selected panels can then be used in an independent validation. This strategy is common for most types of association analyses and genomic prediction studies. Such is the framework undertaken in the analyses carried out in Chapters 3 and 4.

5.1.3 Utilizing molecular data for prediction

One of the best ways to increase EBV accuracy for difficult to measure traits is to incorporate in their genetic evaluation traits that are easily measured, have moderate to high heritability and most importantly are correlated with the trait of interest. A multivariate BLUP model as defined by Kachman (2008) could then be used to incorporate GEBV into RFI genetic evaluations.

A similar strategy of multivariate analysis may be applied for RFI to specifically increase estimates of EBV accuracy. The challenge has been to identify traits correlated with RFI that may be used as indicators. Various studies have shown that RFI has some correlation with back fat thickness, although the magnitude of the correlation is often small. The most promising indicator trait studied so far is serum insulin-like growth factor I, (IGF-I), an endocrine hormone produced primarily in the liver in response to growth hormone stimulation and has effect on growth and metabolism (Wood et al., 2004). However, this physiological marker has proved to be inconsistent in terms of its correlation with RFI (Lancaster et al., 2008) and especially across different breeds. Preliminary data in Australia suggests that if blood sample collection is restricted to a certain age of animals (150 – 250 d) and collection is at weaning or just before weaning, a consistent heritability for the trait (serum IGF-I levels) is obtained, meaning that the same trait is measured each time. However, the correlations for post-weaning and finishing RFI with IGF-I are different and opposite in magnitude. This

complicates the use of IGF as an indicator trait for RFI. The National beef cattle evaluation consortium (NBCEC) has issued a position paper discouraging the use of IGF-I as an indicator trait for RFI (Carstens et al., 2007).

Since the genetic make-up of an individual is the same from birth throughout life, molecular markers offer the advantage of a consistent correlation between marker score and phenotype irrespective of stage of life, if polymorphisms associated with the trait are obtained. This has led to concerted efforts to identify polymorphisms associated with RFI for prediction purposes. A strategy that combined EBV and GEBV can then be applied to increase EBV accuracy. This has already been achieved for carcass traits (Johnston et al., 2008; MacNeil et al., 2009). In Chapters 3 and 4, marker panels that consisted of SNPs that account for a small proportion of RFI variation were developed. The strategy employed in Chapter 3 consisted of applying single marker regressions to identify SNPs highly associated with ADG, DMI and RFI followed by random regression BLUP of the top 100 SNPs for each trait, sequentially dropping out from the model SNPs that were not jointly significant. This strategy was in a bid to maximize the chances of capturing some QTL of large effect in the final marker panels developed. In Chapter 4, genomic selection methodology was used to estimate marker effects, and the top markers, based on SNP effect size chosen to define marker panels.

The cumulative marker phenotypes (CMP) and genomic breeding values (GEBV) obtained in Chapters 3 and 4 respectively, were then used to assess

accuracy of predicting phenotypes. This is an important exercise especially given the potential of predicting the performance of animals that have not been tested for feed intake. Interestingly, despite the varying number of SNPs identified as being associated with RFI, similar levels of genetic prediction were achieved despite the different strategies applied in Chapters 3 and 4 (Table 5.1).

The pre-selection of SNPs associated with RFI through single marker association (Chapter 3) followed by RR-BLUP did not seems to limit the capability of obtaining a SNP panel with similar predictive ability compared to genomic selection models applied in Chapter 4. In fact, it may be that the pre-selection process in Chapter 3 mimics the Bayesian models in that only a small fraction of markers are fitted in the final estimation model, the assumptions about SNP variance notwithstanding. Consequently, the pre-selection strategy in Chapter 3 was actually more effective for predicting ADG that the Bayesian methods. Studies by Kizilkaya et al. (2010) have shown that if QTL in high LD with the underlying trait are used to generate markers panels, the accuracy observed is equal or may be higher in comparison to panels with larger numbers of SNPs having SNPs in weaker LD with QTL. The results observed in this study seem to concur with that sentiment, even though no knowledge of QTL is claimed. However, the prospect that the marker panels fashioned after a pre-selection step may harbor some SNPs in high LD with underlying QTL is high, given only the top 100 (Chapter 3) SNPs were considered. Using all SNPs that

were available for analysis yielded lower correlations (except for DMI) and doesn't seems to be a good strategy with this dataset.

For all methods evaluated, RFI marker panel was able to predict DMI with greater accuracy than the trait specific panel. This increases the prospect of a multi-trait panel, which may be desirable in certain situations where individual feed intake data necessary for RFI estimation may be unavailable.

The results in Chapter 4 showed that the performance of Bayesian estimation methods was related to trait heritability as well as underlying genetic architecture of the trait. Accuracy for DMI was lower than for RFI and ADG, given that DMI had the highest phenotypic variance.

The folly of validating SNPs in a population inherently different than the reference population used to define the prediction equations can be deduced from Chapter 3. In split 2, the validation animals no known pedigree relationships with any individuals in the training data set, and likely had a genetic constitution much different from that of the admixed population used for training. Given that LD in different breeds extends to much shorter distances, and the large variety of breeds in the training data, it is possible that SNPs selected in the training data are a 'consensus' set that is a poor match to the genetic structure of animals in the validation set. This phenomenon was exacerbated for low heritability traits (RFI and ADG), where prediction accuracy was practically null. It is envisaged that increasing the sample size in the training data would help improve accuracy of

prediction. Generally, for low heritability traits, large numbers of individuals are required to achieve accuracy equivalent to high heritability traits (Daetwyler et al., 2008).

There were important differences in prediction accuracy between sire breeds with the differences being specific to the trait evaluated. This difference in accuracy by sire breed was most pronounced when the RR-BLUP model was used, especially for RFI. Possibly, this pattern of difference in accuracy may generally signify that the marker panels selected are tracing breed differences alongside the main purpose of predicting the phenotype using the LD between SNP and QTL. Lower correlations were observed using the BayesB method with estimates closer to those seen across breeds.

Predictive accuracy was generally higher for RFI both within and across breeds. This result indicates that RFI is not just an extension of DMI, but a distinctive trait whose selection may lead to a different response, despite the high correlation with DMI. However, the fact that RFI selected SNPs when used to estimate GEBV for DMI, gave higher prediction accuracies than when using DMI specific panels implies that RFI selection may also be used successfully to effect change in DMI much faster than when selecting directly for DMI. However, these result needs to be replicated in independent populations with larger animal resources.

In summary, the use of marker panels in phenotype prediction achieved low accuracy compared to polygenic EBV accuracy in this study population, requiring that continued and concerted efforts be put in phenotype collection to increase the sample size available for use as a reference population. Our purpose of demonstrating that genetic markers associated with RFI can be used as a correlated trait has shown promise despite the low accuracies observed. At the moment, it is envisaged that better utility of marker information may involve use of a selection index or BLUP framework to combine traditional BLUP EBV with GEBV such as described by Moser et al (2009). An attempt to use a bivariate model that fits RFI with CMP or GEBV in the testing data following Kachman et al. (2009) was not successful and suffered from model convergence problems. Consequently, given the results in this study and other efforts elsewhere, the prediction of RFI phenotypes using molecular data for untested individuals in beef cattle may take a while to be realised. However, a more objective conclusion may be obtained when a larger dataset is used for independent validation of the prediction equations derived in this study.

5.2 IMPORTANT CONSIDERATIONS FOR RFI SELECTION

At present, there are still many unknowns where RFI is concerned and there is need for continued research to fully characterise the trait. The fact that many metabolic mechanisms (such as feed intake, digestibility, physical activity, thermoregulation, body composition and respiration rate; Richardson and Herd, 2004) contribute to variation in RFI requires that the full consequence of

selection for this trait be well investigated. Whereas it is routine to rank animals for efficiency based on differences in feed intake (with or without including body composition), true metabolic efficiency may also necessitate expressing feed intake net of physical activity as well.

Physical activity is a seldom measured component in beef cattle that likely contributes more to variation in efficiency than body composition (Richardson et al., 1999; Basarab et al., 2003). The effect of such activity is even more pronounced in other species such as pig (De Haer et al., 1993) and chicken (Luiting et al., 1991). Yet, in North America, there seems to be a trend towards inclusion of body composition traits, especially ultrasound back fat thickness in RFI estimation protocols but not physical activity. This may be attributed to the fact that there is no simple measure that is representative of physical activity related to feeding with various parameters such as daily pedometer count, feeding frequency, feeding events and feeding time having been studied. Whether or not to include such measures in RFI estimation, or consider them as separate traits is subject to debate. One of the biggest issues is that because of the relatively small contribution of these traits to overall RFI variability in beef cattle, it is unclear whether adjusting for such effects to obtain a residual value, as necessitated by RFI calculation, is the best strategy, there being a potential that selection for RFI would lead to antagonistic outcomes for such traits.

An alternative approach would to incorporate all the traits correlated with RFI into one selection objective using selection index methodology. It is thus

imperative that both the physiological and molecular basis of RFI be well characterised to maximize the benefits of selection for feed efficiency. Ultimately, the magnitude of genetic change begins with a sound framework for genetic evaluation of RFI, which this thesis tries to define.

Preliminary results at the University of Alberta have shown that the correlation of post-weaning RFI measured at two consecutive test periods is moderate at best, often being below 60% for young growing steers. The re-ranking of animals in RFI hierarchy presents questions as to the best time to measure life-long efficiency. Archer et al. (2002) observed near unity correlations between heifer post-weaning RFI and mature cow RFI. However, more studies that relate growing RFI, finishing RFI and mature cow RFI are needed to validate results by Archer et al. (2002). Also, very few studies have related finishing RFI to mature cow RFI. This will also need to be characterised in view of different energy densities of the diets.

Although multiple genetic markers associated with RFI have been described in a number of studies, no major genes affecting metabolic processes underlying efficiency have been characterized. It may be worthwhile to expand this molecular exploration so that comparisons are made between gene networks and functional systems as opposed to single candidate genes. These will allow interactions between putative genes to be explored based on the observed expression patterns. Similarly, once important gene networks are identified, it

may be easier to have an overview of how selection for RFI will affect other related and economically important traits.

Ultimately however, the full potential for RFI in increasing production efficiency will only be realized if feed intake testing is undertaken on a large scale so that many animals with well characterized pedigrees are phenotyped in addition to having molecular data available. This will require substantial investments in data collection and associated technologies.

5.3 CONCLUSION

This thesis set about to demonstrate how genetic markers can be applied in the genetic evaluation of RFI so as to increase EBV accuracy. Chapter 1 gives an overview of the current state of knowledge on RFI research. Chapter 2 demonstrates the typical low accuracies associated with RFI evaluations and the potential influence of climate parameters on feed intake and feed efficiency. Chapters 3 and 4 describe a suite of genetic markers that are predictive of RFI and evaluate the value of marker panels to predict phenotypes for 3 feed intake and efficiency traits.

Much still remains that is unknown about RFI and more research in warranted. The quest for genes underlying RFI is ongoing and more efficient methodology both for gene discovery and marker assisted genetic evaluation are still being sought. Suggestions for future research are listed below.

1. Development of efficient algorithms necessary to select the most informative suite of genetic markers predictive of RFI.

2. Analysis of gene networks and expression patterns for animals with different efficiency profiles, in relation to fitness and reproductive traits.
3. Pursuit of indicator traits that may be used to rank animals in terms of RFI in a more cost effective manner.
4. Better characterization of the relationship between RFI measured in growing, finishing and mature stages of an animal's life cycle.
5. Characterization of the influence of environmental perturbations, such as weather and climatic changes on feed intake and feed efficiency.

Table 5.1. Accuracy of prediction for various traits obtained by using RFI panels derived from various methods.

Method	ADG	DMI	RFI
BLUP	0.414 ± 0.051	0.270 ± 0.066	0.402 ± 0.065
BAYESB200	0.223 ± 0.046	0.196 ± 0.073	0.433 ± 0.073
RRBLUP200	0.371 ± 0.095	0.385 ± 0.045	0.479 ± 0.076
BAYESB37959	0.149	0.239	0.117
RRBLUP37959	0.126	0.246	0.114

ADG – Average daily gain; DMI – Dry matter intake; RFI – residual feed intake; RR-BLUP – Random regression BLUP; PS RR-BLUP – Preselected RR-BLUP (Pre-selection using single marker analysis followed by RR-BLUP of the top 100 SNPs).

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CHAPTER 6 SUPPLEMENTARY WORK: Genetic parameters for calving ease, gestation length and birth weight in Charolais cattle[2]

6.1 INTRODUCTION

6.1.1 The accuracy problem for RFI EBV

As shown in Chapter 2, because of the few number of animals tested for feed intake, the accuracies of the RFI estimated breeding values are typically low. This implies that selection for RFI using such EBV will not result in the projected levels of efficiency for any specific sire, but rather exhibit wide variability with respect to the offspring obtained. For effective application of RFI EBV for selection purposes, the EBV accuracies need to be increased. The best option to do this would be to measure more individuals for the trait. Ideally we may want to measure many offspring from particular sires such that their EBV will be more accurate given the large families. However, due to the lack of widespread progeny testing schemes for beef cattle, and the relatively small half-sib families compared to dairy cattle, the utility of such a strategy is limited at present. Also, given the cost associated with measuring feed intake, this process would take a considerable amount of time, the expense notwithstanding. Alternatively, if we could find a trait that is relatively easy to measure, has medium to high heritability with a sizeable correlation with RFI, we could use a multivariate analysis strategy to increase the accuracy of the RFI EBV, by allowing a flowing of the information

[2] A version of this chapter has been published; Mujibi and Crews (2009); J. Anim Sci. 87:2759-2766.

between the traits by way of the genetic correlation between them. In this way, we mitigate to some extent the lack of data and use other trait values to increase the density of the information available for each individual, such that we can rank the animals accurately on the basis of their genetic merit. A highly predictive RFI panel, once identified, fits such a criterion and a BLUP based strategy as described by Kachman (2008) may be used to increase RFI accuracy.

Such multivariate analyses have been used for various difficult to measure traits to increase the accuracy of parameter estimation. An illustration of how this may be done is the subject of this chapter using calving ease as an example for a hard to measure trait.

6.1.2 Case study: Calving easy as a hard to measure trait

Calving difficulty (dystocia) is a significant cost to beef production. Dystocia has been associated with calf and cow mortality, increased postpartum interval, and increased veterinary labor costs (Meijering, 1984). Genetic improvement of calving ease has in some cases been based on the high and positive genetic correlation estimated between dystocia and birth weight (Koots et al., 1994b), but the use of bulls with low birth weight EPD is often associated with lower growth rates and lighter weights in progeny. Calving ease EPD directly predict the genetic potential for animals to produce calves without difficulty and typically include birth weight as an indicator trait, thereby increasing the evaluation accuracy and the numbers of sires evaluated.

The threshold model approach has been applied in many cases to evaluate calving ease phenotypes (e.g., Wang et al., 1997; Wiggans et al., 2003). However, a scale with four or more calving ease scores tends to rank animals similarly using linear and threshold models (Varona et al., 1999; Lee et al., 2002; Ramirez-Valverde et al., 2001). Snell (1964) suggested a scaling procedure for ordered categorical data such as calving ease score which make the use of a linear model more appealing, especially for large field data sets. Beginning in 2005, the Canadian Charolais Association (CCA) has published calving ease EPD from a three-trait model including birth weight and gestation length. In this system, inclusion of gestation length as another indicator for dystocia is desirable because of its relative ease of recording and higher heritability (Crews, 2006).

Complete genetic correlations among birth weight, transformed calving ease scores and gestation length have not been published with field data. This study sought to: 1) estimate genetic parameters required for genetic evaluation of transformed calving ease score, including birth weight and gestation length as indicators, and 2) estimate genetic trend in calving ease in the Canadian Charolais population.

6.2 MATERIALS AND METHODS

6.2.1 Data

A dataset (n = 40,420) consisting of birth weight, gestation length and calving ease records from first parity heifers was extracted from the Canadian

Charolais Association Charolais Herd and Record Management (CHARM) performance database which included artificial insemination (AI) and calving date records on animals born between 1979 and 2004. Birth weight (BWT) records were pre-adjusted for age of dam and sex of calf effects following procedures outlined by the Beef Improvement Federation (BIF, 2002). The reported breed average for birth weight in Canadian Charolais cattle is 46 ± 5 kg (Crews, 2006).Gestation length (GEST) was calculated as the number of days between AI mating and birth date and all GEST records were adjusted for age of dam and sex of calf using estimates reported by Crews (2006). Calving ease (CE) records were used for first parity heifers only and were scored as N, U, A, E, H, S, and M. The scores represented a normal or unassisted birth (N, U), assisted or easy pull birth (A, E), hard pull or mechanically assisted birth (H), surgical birth (S) and mal-presentation or dead calf (M). These scores were then converted into numerical scores 1, 2, 3, 4, and 5, respectively. Only animals with phenotypic data for at least two of the three traits were included in the study. Contemporary groups were constructed as a combination of herd of origin and year of birth subgroups. Groups with less than 10 animals were excluded from analysis since there were many groups with one or a few individuals and these mostly represented animals missing data for two of the three traits. A total of 1,664 groups were obtained, with all ancestral animals without birth date or herd information placed into one contemporary group. The dams were classified into 5 age classes, 2, 3, 4, 5-10 and 11 years or older, according to BIF guidelines (BIF, 2002). The final pedigree

included 69,118 animals (Table 3.1) with year of birth ranging from 1979 to 2004 that comprised at least two ancestral generations for animals with records.

6.2.2 Snell scores

In order to fit a three-trait linear model involving CE, BWT and GEST, 14,403 CE phenotypes, recorded as 5 categorical scores from first parity heifers, were transformed to a continuous scale (Snell, 1964). These scores reflect percent unassisted calving (SC). The basic premise is that there exists an underlying continuous distribution of calving ease scores of which the Snell scores represent class interval midpoints. Snell scores were constructed following the approximation procedure of Snell (1964), which uses a logistic model to obtain scores that can be generalized to a normal distribution. The procedure consists of three basic steps.

1. Estimation of class boundaries, x_i and class intervals midpoints (Snell scores, s_i).
2. Estimation of Snell score means for the various sex of calf x age of heifer groups
3. Scaling of raw Snell scores to range between 0 and 100%

There being five (k = 5) CE categories to be transformed into Snell scores s_j (j = 1 to 5), six class boundaries x_j (j = 0 to 5) were estimated. Four groups (m = 4) were constructed based on age of heifer and sex of calf combinations. There were two age classes (2 and 3 year old heifers) and two sexes (male and female).

Cumulative frequencies, $p_{ij,}$ were obtained for each group such that Snell score category 5 had a cumulative frequency of 1. Maximum likelihood estimates of the group intervals, x_i, were then obtained for $x_5 - x_4$ to $x_2 - x_1$ intervals using equation (5) of Snell (1964).

$$0= \frac{N_{k-1}}{[e^{x_{k-1}-x_{k-2}}-1]} + N_{k-1} - \sum_{i=1}^{m}(n_{i,k-1}+n_{i,k})\hat{p}_{i,k-1}$$

where N_k is the total number of animals in the Snell score category k, while j = k -1. $\hat{p}_{i,\,k-1}$ is the cumulative frequency for ease category j and group i. To obtain the value of the class boundaries, the origin, x_1 was arbitrarily set to 0. Snell scores were calculated as the midpoints of the class intervals. However for the extreme categories, Snell scores s_1 and s_5 were obtained from the relative proportion (Q) of CE score in that category using Snell's equations below:

$s_1 = x_1 - (-(\ln P_1)/Q_1)$

$s_5 = x_4 + (-(\ln P_5)/Q_5)$

where, P_j is the probability of a value less than x_j, while Q is the relative proportion of the calving ease scores in the Snell score category. Snell score means for each group were obtained as in section 7 of Snell (1964). The overall Snell score mean, was calculated as the average of the four Snell score group means. The difference between the group means and the overall mean, δ, was used to update the raw Snell scores, by subtraction, to the expected proportions. A scaling factor forced the Snell score to range between 0 and 100% such that a score of 0% indicated the lowest calving ease and 100% highest calving ease.

6.2.3 Variance Component Estimation Models

Univariate models were used to obtain starting values for each trait while bivariate models provided covariance parameters between the traits. A three-trait linear model was used for final estimation of variance components and to obtain BLUP of breeding values. Since birth weight and gestation length records were pre-adjusted for sex of calf and age of dam, only the contemporary group effects were treated as fixed for these traits. However, for calving ease, sex of calf, age of dam and contemporary group effects were treated as fixed, while direct genetic effects, maternal genetic effects and the residual were treated as random for all traits. Calving ease was treated as a trait of the calf. The three-trait model can be represented in matrix notation as:

$$\begin{bmatrix} y_1 \\ y_2 \\ y_3 \end{bmatrix} = \begin{bmatrix} X_1 & 0 & 0 \\ 0 & X_2 & 0 \\ 0 & 0 & X_3 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} + \begin{bmatrix} Z_1 & 0 & 0 \\ 0 & Z_2 & 0 \\ 0 & 0 & Z_3 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \\ a_3 \end{bmatrix} + \begin{bmatrix} Z_{m1} & 0 & 0 \\ 0 & Z_{m2} & 0 \\ 0 & 0 & Z_{m3} \end{bmatrix} \begin{bmatrix} a_{m1} \\ a_{m2} \\ a_{m3} \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \\ e_3 \end{bmatrix}$$

where X, Z, are Z_m are incidence matrices relating records with the fixed effects, direct genetic, and maternal genetic effects, respectively. The vectors y_1, y_2, y_3, contain the BWT (measured on the calf), SC and GEST (measured on the heifer but specific to the calf) phenotypes while b, a, a_m, and e contain fixed effects, direct genetic effects, maternal genetic effects, and the random residual, respectively. The expectations of the vectors and (co)variances of the random terms for the model used are as follows:-

$$\mathrm{E}\begin{bmatrix} y \\ a \\ a_m \\ e \end{bmatrix} = \begin{bmatrix} Xb \\ 0 \\ 0 \\ 0 \end{bmatrix}, \mathrm{Var}\begin{bmatrix} a \\ a_m \\ e \end{bmatrix} = \begin{bmatrix} A\sigma_a^2 & & Symmetric \\ A\sigma_{a,m}^2 & A\sigma_m^2 & \\ 0 & 0 & I_T\sigma_e^2 \end{bmatrix}$$

Direct genetic, maternal genetic and residual variances are represented by the terms σ^2_a, σ^2_m and σ^2_e respectively. A is the numerator relationship matrix of all animals, while I_T is an identity matrix with order equal to the number of animals with records for the particular trait. Variance components were estimated using ASREML (Gilmour et al., 2006) which uses an average information algorithm. The program also routinely reports log-likelihood statistics which were used for model comparison while variance components were used to estimate phenotypic and genetic parameters. The initial values of the variance and covariance parameters for BWT and GEST were fixed to values reported by Crews (2006). The animal variance component represented an estimate of the additive genetic variance (σ^2_a), while the phenotypic variance (σ^2_P) was obtained from the sum of all variance components. Heritability (h^2) was computed as the ratio between the additive genetic and phenotypic variances.

6.2.4 Genetic trends

Genetic trends were obtained by regressing average EBV obtained for the three traits from the three-trait analysis on year of birth of the animals, which ranged from 1979 to 2004. Trends were also obtained for all traits by regressing average EBV on year of birth for the period between 1990 and 2004. Further, the

animals were ranked based on their estimated breeding values (EBV), the ones with the highest EBV (negative values for BWT and GEST, and positive values for SC) having the best rank. Both spearman rank correlations and Pearson correlation analyses were performed.

6.3 RESULTS AND DISCUSSION

Three traits, BWT, GEST and CE, expressed as percent unassisted calving (SC) were evaluated. Table 3.1 gives summary statistics observed for these traits. Less than half of the animals evaluated had CE data. This number is small because of the imposed condition that allowed only animals with phenotypes for at least two traits to be included in the analysis. The mean percentage unassisted calving (SC) score was high, indicating that a large majority of first parity heifers (72%), calved without assistance (Table 3.2), similar to estimates obtained by Wang et al. (2005) and Basarab et al. (1993). Only a small proportion of heifers required surgical delivery or bore a dead calf (Table 3.2). The average GEST was 286.48 d, a result comparable to that observed (285.2 d) by Crews (2006) using a larger dataset from the same population. The average BWT was 46.54 kg.

6.3.1 Choice of models

It would appear that for parameter estimation with categorical traits, threshold traits perform better because linear models applied to an underlying scale seem to under-estimate the parameters (Abdel-Azim and Berger, 1999; Steinbock et al., 2003). However, for field data, the comparative advantages of

threshold models over linear models are small (Matilainen et al., 2008; Matos et al., 1997; Phocas and Laloë, 2003), in so far as EBV or EPD estimation is concerned. The ranking of animals using both models is mostly the same (Weller and Ron, 1992). None the less, the accuracy obtained from having 5 categories of calving ease is still high even where parameters are under-estimated. Further, implementation of threshold models is complicated and computationally expensive and not easily extended to multiple categorical traits within the same analysis (Misztal et al., 1989; Abdel-Azim and Berger, 1999; Ramirez-Valverde, 2001; Lee et al., 2002). Threshold animal models have been known to have problems with convergence leading to biased estimates (Luo et al., 2001). For these reasons, a multivariate linear animal model approach was used. A transformation to Snell scores provides desirable distributional properties ideal for fitting a linear model to CE data (Jamrozik et al., 2005).

Linear models have been routinely used to evaluate categorical traits using an animal model. Gutiérrez et al. (2007) used BWT, CE, calving interval and weaning weight data in their study, while Cole et al. (2007) evaluated two categorical traits, CE and still birth. The incorporation of correlated traits such as GEST in addition to BWT should lead to increases in the accuracy of predicted breeding values compared to those obtained through a BWT and CE bi-variate analysis.

6.3.2 Variance components and parameter estimates

The estimate of heritability obtained for GEST was similar to that reported by Crews (2006). However, a lower value was seen for BWT (Table 3.3). Heritability estimates for BWT and SC obtained are similar to those obtained by Wang et al. (2005) in their analysis of BWT and SC. The SC estimate was also equivalent to that obtained for French Charolais (0.14) as reported by Phocas and Laloë (2003). Maternal heritability estimates for BWT and SC are within the ranges observed in other studies (Koots et al., 1994a; Eriksson et al., 2004; Wang et al., 2005). Generally, reproductive traits such as CE are known to have lower heritabilities. These results suggest that response to selection for CE would be low, especially for the maternal component.

Table 3.4 gives variance components estimates for SC obtained from single trait and multitrait analyses. The multitrait analysis resulted in higher estimates of direct and maternal genetic components such that the corresponding direct and maternal heritability were higher compared to those in single trait analysis. The genetic correlation between direct and maternal effects saw the greatest change, with a substantial reduction in the standard error as well.

6.3.3 Genetic and residual correlations

A wide range of results has been obtained in different studies for genetic correlations, especially involving maternal and direct genetic effects for BWT and CE (or dystocia). The correlation obtained in this analysis (Table 3.5) was very

high but by no means unique. Correlations ranging from -0.60 to -0.98 have been reported (Koots et al., 1994b; Bennett and Gregory, 2001 and Gutiérrez et al., 2007). There was a smaller number of CE records available, compared to BWT records. Also, 74% of animals with CE records had a SC of 90% or higher, with a mean BWT of 44.33 compared to the herd average of 46.54. This contributed to the high correlation observed between BWT and SC. Wang et al. (2005) obtained a correlation of -0.67 between BWT and SC.

Even though the correlation observed between SC and GEST (-0.38 ± 0.08) direct genetic effects was smaller than that with BWT, the estimate obtained was higher than that observed by Jamrozik et al. (2005) and Lee et al. (2002), even though the former modeled CE as a trait of the heifer. These two studies obtained correlations of 0.19 and 0.22, respectively (the signs are different due to different CE definitions). The correlations between direct and maternal effects among the different traits were negligible to moderate, ranging from 0.01 between maternal GEST and direct SC to 0.26 between maternal SC and direct BWT (Table 3.5).

The correlation of maternal effects of SC and GEST was higher than that between direct effects. Similarly, the correlation between maternal effects of BWT and GEST were higher than those for direct effects. This implies an important maternal component in the association between these traits. The genetic correlation between maternal and direct genetic effects for BWT were smaller than those reported elsewhere (Phocas and Laloë, 2003; Crews, 2006) but similar

to Wang et al. (2005), while the GEST estimate obtained was within the range of that observed in related studies, such as Phocas and Laloë (2003), Eriksson et al. (2004) and Wang et al. (2005). However, differences in the magnitude of correlations observed between this study and the others referenced above can be attributed to the use of either a two trait model or inclusion of different traits in the analysis. Further, the initial variance and covariance parameters for BWT and GEST used for the three-trait analysis in this study were fixed to values reported by Crews (2006), since these are used for the national cattle evaluation. The negative genetic correlation between direct and maternal effects for SC (Table 3.5) is indicative of an antagonistic relationship, and can be attributed to physiological and biological factors of the heifer, such as size of pelvic opening (Bennett and Gregory, 2001; Phocas and Sapa, 2004). In their analysis of CE, Phocas and Sapa (2004) treated CE as a trait of the dam.

Estimates of residual correlations (Table 3.6) ranged from small to moderate. Residual correlations between SC and GEST were negligible (-0.04 ± 0.04), while a moderate negative correlation similar to that obtained by Wang et al. 2005 was observed between SC and BWT (-0.35 ± 0.05). The estimate of the correlation between GEST and BWT was small and positive (0.06 ± 0.04).

6.3.4 Gain in EBV accuracy for SC

One of the biggest advantages of using multivariate analyses is the gain in accuracy of the resulting evaluations, because these models reduce the prediction

error variance (Mrode, 2005). Further, missing-ness in the records can be handled if the animals have data for other traits. Similarly, selection or culling bias is accounted for supposing that any selection has been carried out indirectly for one trait based on another correlated trait included in the evaluation.

In this study, there was a significant increase in EBV accuracy for SC after the multivariate analysis, with the largest increase (64%) being for calves with CE records. Sires and dams of calves evaluated had increases of 51% and 39%, respectively (Table 3.7). One possible explanation for this increase is the large difference in the genetic and residual correlations between SC with BWT (-0.93 vs. -0.35) and GEST (-0.38 vs. -0.04). Schaefer (1984) suggests that larger differences between genetic and residual correlations between the traits yield greater increases in accuracy. Thompson and Meyer (1986) also contend that residual covariance between traits lead to better connections in the data, such that accuracy is increased.

6.3.5 Genetic trend

Regression of average EBV on year of birth from 1979 to 2004 yielded significant genetic trends for all traits. However, regression of average maternal EBV for BWT, GEST and SC on year of birth resulted in very small regression coefficients that were not significantly different from zero. There was a significant increase in the average birth weight EBV between 1990 and 2004 (Figure 3.1). All preceding years had an average EBV of zero. Regression of

direct EBV on year of birth for data excluding years prior to 1990 yielded significant genetic trends of similar magnitude for direct effects as those obtained using data from all years. The trends for BWT, GEST and SC had regression coefficients of magnitude -0.06, -0.08 and 0.17, respectively for 1990 to 2004 and -0.04, -0.08 and 0.10, respectively when all years were included. However, the changes in GEST and SC are due to a correlated response of selecting for lower birth weight, since the CCA had not published GEST or CE EPD prior to 2005. The trends observed for maternal effects for the period 1990 to 2004 were insignificant (Figure 3.2).

Average direct birth weight EBV showed the greatest change, from an average of 0 in 1989 to -2.15 in 2004. Direct gestation length and percent unassisted calving EBV followed the same pattern exhibited by direct BWT, (albeit in the opposite direction for SC) changing by approximately -1.25 and 2.66 units, respectively. There was no observable change in average maternal EBV as the birth weight became progressively lower. This is particularly important considering the antagonistic behavior of direct and maternal effects. For the population analyzed, there has neither been a preferred selection for direct effects over maternal effects nor use of an index to drive the trends to what is seen in Figure 3.1 and 3.2, other than selection using published EPD.

6.4 CONCLUSION

In summary, the genetic evaluation of calving ease, birth weight and gestation length yielded heritability and genetic correlation estimates that were comparable to most studies involving beef cattle breeds. The use of Snell scores expressed as percentage unassisted calving is a useful means of implementing an all-linear genetic evaluation of calving ease. The antagonistic effect between direct and maternal effects, especially for calving ease means that improvement of both effects at the same time could prove a challenge, and selection strategies need to have this in mind. It has been shown that a selection index that incorporates both direct and maternal CE EBV with subsequent assortative mating of sires having desirable direct CE EBV to first-parity heifers provides optimal results compared to using an index that only considers direct CE in Canadian Holsteins (Dekkers, 1994). Though small in magnitude, a genetic trend was observed for BWT and by correlated response for GEST and SC in the population analyzed. However, on average maternal effects did not show any change. A large increase in EBV accuracy after multitrait analysis was observed for SC compared to accuracy from single trait evaluation. These results suggest that incorporation of birth weight and gestation length data into calving ease evaluation can provide a tool for direct and accurate selection for reduced calving difficulty in beef cattle. However, given the high genetic correlations between BWT and CE, for both direct and maternal genetic effects, lower dystocia rates could also be achieved effectively by selection for lower BWT in situations where

CE data is not available or is difficult to obtain as is common practice. The outcome of such a strategy would be limited by the reduction in growth performance resulting from decreasing BWT selection. For this reason, genetic improvement programs should consider both dystocia and growth.

Table 6.1 Descriptive statistics, means and standard deviations of variables analyzed

Basic data summary	N				
Number of animals	69,118				
Number of records[1]	40,420				
Number of contemporary groups	1,664				
Number of sires	857				
Number of dams	24,400				
Number of dams with own record[2]	5,388				
Number of first-parity dams with record[3]	1,782				
Traits	N	Mean	SD	Min	Max
Birth weight, kg	39,759	46.54	4.79	36.29	80.74
Gestation length, d	37,663	286.48	4.93	266.00	307.75
Snell score, %	14,377	83.29	23.31	3.44	100.00

[1]Number of animals with data for any or all of the traits analyzed

[2]The dams have birth weight, gestation length, calving ease or combination of records

[3]The dams have own calving ease record as well as one heifer progeny each, with record

Table 6.2 Percent incidence of calving ease categories and the corresponding Snell scores (% unassisted calving, in brackets)

Sex	AOD	Calving ease score†				
		1	2	3	4	5
Male	2	32.26 (100)	12.21 (62)	2.65 (38.6)	1.71 (23.7)	0.76 (10.4)
	3	0.62 (92.7)	0.15 (54.7)	0.03 (31.3)	0.00 (16.4)	0.00 (3.1)
Female	2	38.42 (93.1)	8.28 (55)	1.26 (31.6)	0.41 (16.8)	0.58 (3.4)
	3	0.57 (89.6)	0.08 (51.6)	0.02 (28.2)	0.00 (13.3)	0.00 (0.0)
Totals (%)		71.87	20.72	3.96	2.12	1.34

†1 = normal or unassisted birth; 2 = assisted or easy pull birth; 3 = hard pull or mechanically assisted birth; 4 = surgical birth; 5 = mal-presentation or dead calf; Sex – sex of calf; AOD – Age of dam.

Table 6.3 Variance component and parameter estimates (± SE) for birth weight (BWT), gestation length (GEST) and percent unassisted calving (SC)

Model item [1]	BWT	GEST	SC
Variance component	(kg^2)	($days^2$)	($\%^2$)
V_p	19.68 ± 0.22	23.1 ± 0.30	428.7 ± 5.76
V_a	9.09 ± 0.71	14.28 ± 1.02	60.93 ± 10.36
$Cov_{a,m}$	-1.31 ± 0.39	-2.08 ± 0.51	-10.77 ± 6.84
V_m	2.66 ± 0.32	2.34 ± 0.37	25.76 ± 9.59
V_e	9.23 ± 0.38	8.61 ± 0.53	352.8 ± 10.14
Parameter			
h^2_a	0.46 ± 0.03	0.62 ± 0.04	0.14 ± 0.02
h^2_m	0.14 ± 0.02	0.10 ± 0.02	0.06 ± 0.02
$r_{a,m}$	- 0.27 ± 0.06	- 0.36 ± 0.06	- 0.27 ± 0.14

[1] V_p = phenotypic variance, V_a = direct genetic variance, $Cov_{a,m}$ = direct by maternal genetic covariance, V_m = maternal genetic variance, V_e = residual variance, h^2_a = direct heritability, h^2_m = maternal heritability, $r_{a,m}$ = the genetic correlation between maternal and direct genetic effects, SE = standard error.

Table 6.4 Comparison of variance component and parameter estimates (± SE) for percent unassisted calving (SC) obtained from single trait (UniSC) and multiple trait (TriSC) models

Model item [1]	TriSC	UniSC
Component	($\%^2$)	($\%^2$)
V_p	428.1 ± 5.75	424.5 ± 10.95
V_a	60.07 ± 10.25	45.68 ± 12.16
$Cov_{a,m}$	-10.52 ± 6.79	-10.87 ± 8.63
V_m	25.89 ± 9.55	22.57 ± 11.06
V_e	201.9 ± 49.08	356.2 ± 11.99
Parameter		
h^2_a	0.14 ± 0.02	0.11 ± 0.03
h^2_m	0.06 ± 0.02	0.05 ± 0.03
$r_{a,m}$	-0.27 ± 0.14	-0.34 ± 0.22

[1] V_p = phenotypic variance, V_a = direct genetic variance, $Cov_{a,m}$ = direct by maternal genetic covariance, V_m = maternal genetic variance, V_{pe} = maternal permanent environmental variance, V_e = residual variance, h^2_a = direct heritability, h^2_m = maternal heritability, $r_{a,m}$ = the genetic correlation between maternal and direct genetic effects, SE = standard error.

Table 6.5 Estimates of genetic correlations ± SE, obtained from the three-trait analysis of birth weight (BWT), gestation length (GEST) and percentage unassisted calving, (SC)

Model item [1]	BWTm	GESTd	GESTm	SCd	SCm
BWTd	-0.27 ± 0.06	0.43 ± 0.04	-0.21 ± 0.08	-0.93 ± 0.04	0.27 ± 0.12
BWTm		-0.26 ± 0.06	0.72 ± 0.07	0.15 ± 0.11	-0.68 ± 0.14
GESTd			-0.36 ± 0.06	-0.38 ± 0.08	0.18 ± 0.12
GESTm				0.01 ± 0.13	-0.49 ± 0.17
SCd					-0.27 ± 0.14

[1]BWTd = direct birth weight, BWTm = maternal birth weight, GESTd = direct gestational length, GESTm = maternal gestational length, SCd = direct percentage unassisted calving, SCm = maternal percentage unassisted calving.

Table 6.6 Estimates of residual covariance ([1]) and residual correlation ([2]), ± SE obtained for tri-variate analysis of birth weight (BWT), gestation length (GEST) and percentage unassisted calving ease, (SC)

Trait	GEST[1]	SC[1]	GEST[2]	SC[2]
BWT	0.56 ± 0.34	-15.12 ± 1.56	0.06 ± 0.04	-0.35 ± 0.05
GEST		-1.52 ± 1.66		-0.04 ± 0.04

Table 6.7 Comparison of EBV accuracy and mean EBV estimates (± SE) for EBV derived from Single trait and multiple trait analyses. Correlations (Spearman rank and Pearson) between single and multiple trait derived EBVs are also given for animals with percent unassisted calving (SC) records as well as their sires and dams.

	Sire	Dam	Animals
EBV Accuracy			
Uni-variate	0.359 ± 0.008	0.169 ± 0.001	0.436 ± 0.001
Tri-variate	0.699 ± 0.008	0.434 ± 0.001	0.678 ± 0.000
Gain (%)	95	157	56
EBV Means			
Uni-variate	0.039 ± 0.111	0.238 ± 0.011	1.289 ± 0.022
Tri-variate	0.607 ± 0.230	0.983 ± 0.031	3.962 ± 0.044
Correlations between single and multiple trait EBV			
Spearman	0.47	0.41	0.61
Pearson	0.51	0.51	0.62

Figure 6.1 Genetic trend of average direct estimated breeding value for birth weight (BWT), gestation length (GEST) and percent unassisted calving (SC) for Charolais cattle.

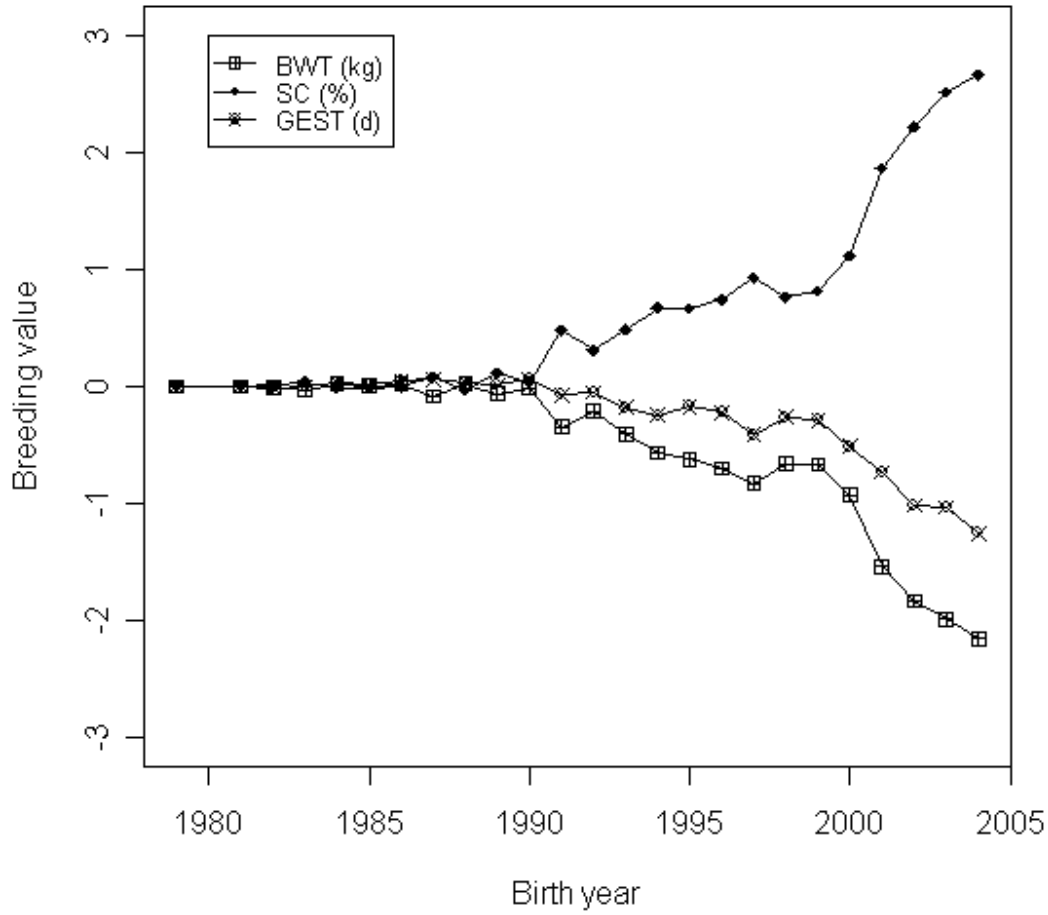
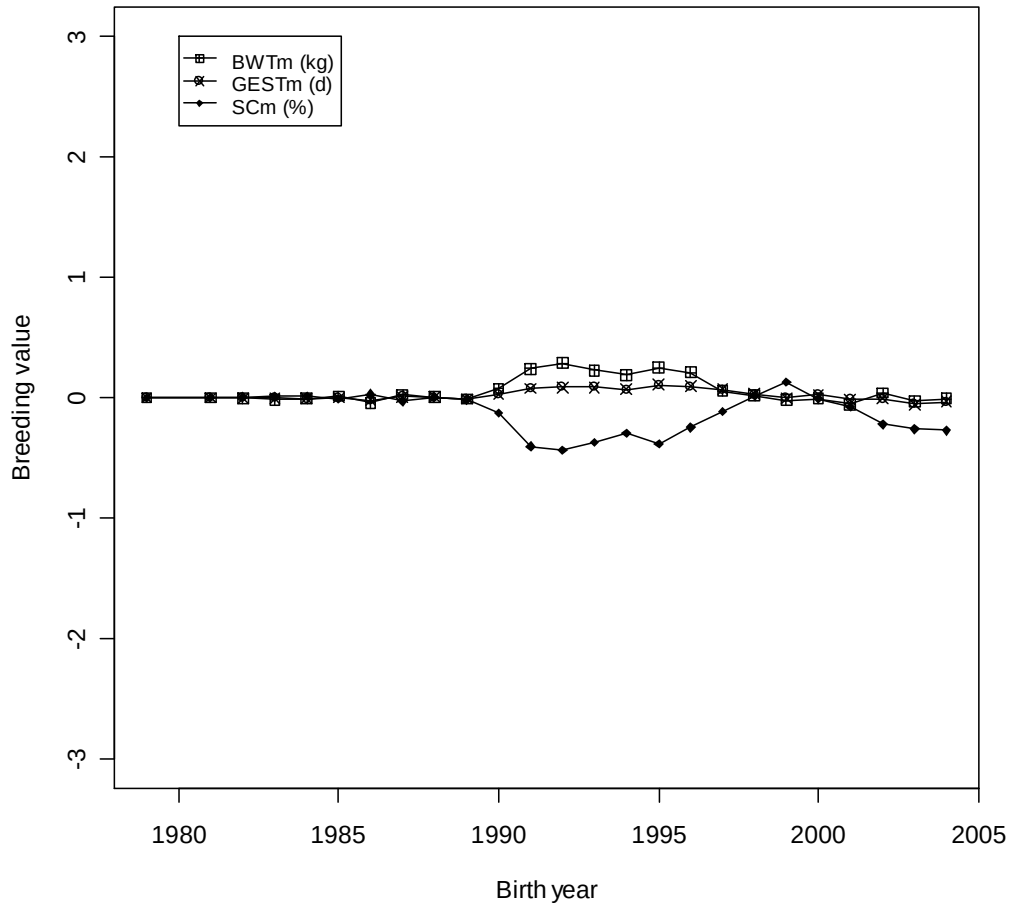


Figure 6.2 Genetic trend of average maternal estimated breeding value for birth weight (BWTm), Gestation length (GESTm) and percent unassisted calving (SCm) for Charolais cattle.



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APPENDICES

APPENDIX 1: Lists of SNPs associated with ADG, DMI and RFI

Appendix 1: Table 1. Names, chromosomal locations, minor allele frequencies and allele substitution effects for SNPs used to build marker panels using PS RR-BLUP (Chapter 3) method.

SNPID	BTA	Trait	Minor allele	Freq	Position	‡Estimate	SE
†Hapmap50890-BTA-121436	Chr24	ADG	A	0.334	28961542	0.031	0.003
rs29010392	Chr11	ADG	G	0.439	59067281	0.033	0.003
rs41576862	Chr24	ADG	C	0.12	10984429	0.002	0.007
rs41579555	Chr18	ADG	T	0.3	50059898	0.022	0.006
rs41597632	Chr10	ADG	C	0.189	62466743	-0.043	0.007
rs41601279	Chr24	ADG	A	0.2	26564151	-0.009	0.005
rs41625563	Chr7	ADG	G	0.432	91903228	0.033	0.002
rs41630325	Chr15	ADG	G	0.265	37389561	-0.008	0.001
rs41635766	Chr18	ADG	T	0.196	47346235	-0.022	0.002
rs41656065	Chr7	ADG	T	0.216	71845956	0.022	0.01
rs41658480	Chr6	ADG	G	0.433	54328469	-0.029	0.005
rs41847101	Chr17	ADG	T	0.463	66962668	-0.031	0.005
rs41894363	Chr18	ADG	T	0.177	58277805	-0.031	0.004
rs42117657	Chr27	ADG	A	0.201	21306526	-0.036	0.006
rs42913880	Chr3	ADG	T	0.209	96331875	-0.015	0.006
rs43614200	Chr10	ADG	A	0.192	13146428	-0.006	0.011
rs43709090	Chr5	ADG	A	0.19	1.2E+08	0.058	0.005

rs43727930	Chr27	ADG	T	0.111	36780954	0.076	0.006
ss105239516	Chr10	ADG	A	0.207	14071411	-0.028	0.009
ss105291171 ss117968562	Chr6	ADG	T	0.437	38729866	0.005	0.01
ss105307554 ss117968245	Chr6	ADG	A	0.414	37963147	-0.032	0.003
ss117962667	Chr3	ADG	C	0.337	43428200	0.035	0.005
ss117966992	Chr3	ADG	A	0.122	43225815	-0.042	0.008
ss117969528	Chr9	ADG	A	0.394	88157050	0.031	0.005
ss86276352 ss86336018	Chr3	ADG	A	0.473	93173991	-0.038	0.003
ss86282373	Chr24	ADG	T	0.438	26339920	0.032	0.002
ss86283682	Chr29	ADG	C	0.306	31376202	-0.049	0.003
ss86283704	Chr9	ADG	G	0.253	6415256	0.035	0.007
ss86291906	Chr2	ADG	T	0.179	64159904	0.043	0.004
ss86293533	Chr22	ADG	T	0.474	14015132	0.028	0.003
ss86296291	Chr5	ADG	T	0.355	1.23E+08	-0.031	0.004
ss86300106	Chr11	ADG	T	0.221	95815319	-0.045	0.004
ss86304896	Chr20	ADG	A	0.104	23683579	-0.059	0.008
ss86305113 ss86338143	ChrUn	ADG	G	0.453	2995350	0.034	0.006
ss86314795	Chr18	ADG	T	0.121	62373058	-0.068	0.007
ss86325631	Chr10	ADG	C	0.371	13666563	0.039	0.004
ss86327201	Chr9	ADG	A	0.05	87221264	-0.021	0.011
ss86334058	Chr28	ADG	G	0.424	45321054	0.035	0.001
ss86341174 ss86312678	Chr22	ADG	C	0.253	55890005	-0.049	0.007
rs29027007	Chr23	DMI	A	0.406	11432167	-0.021	0.023
rs41565462	Chr11	DMI	A	0.051	1.01E+08	-0.47	0.027
rs41569387	Chr11	DMI	A	0.267	70053572	-0.061	0.029

rs41572724	Chr1	DMI	A	0.056	8432955	0.33	0.051
rs41578671	Chr19	DMI	C	0.332	57511323	-0.127	0.026
rs41593516	Chr26	DMI	C	0.241	39437807	-0.3	0.035
rs41654591	Chr10	DMI	A	0.325	91420638	-0.257	0.021
rs41887389	Chr18	DMI	A	0.228	50742772	0.034	0.04
rs42029905	Chr23	DMI	A	0.444	45588817	-0.174	0.033
rs42052858	Chr24	DMI	C	0.146	64215863	-0.208	0.026
rs42215930	Chr14	DMI	T	0.299	5117434	-0.128	0.033
rs42410387	Chr6	DMI	A	0.334	1.19E+08	0.011	0.075
rs42411131	Chr6	DMI	G	0.296	1.19E+08	0.273	0.047
rs42484917	Chr14	DMI	T	0.113	56901724	0.221	0.026
rs42541659	Chr1	DMI	A	0.449	60865899	0.077	0.031
rs42630163	Chr1	DMI	T	0.142	18244760	0.302	0.022
rs42821965	Chr14	DMI	G	0.08	42462335	0.31	0.052
rs43057535	Chr1	DMI	A	0.268	1.43E+08	0.155	0.022
rs43099270	Chr1	DMI	C	0.265	4284068	-0.135	0.011
rs43362139	Chr3	DMI	G	0.191	1.14E+08	0.065	0.024
rs43458937	Chr6	DMI	C	0.428	39794334	-0.209	0.031
rs43460584	Chr6	DMI	A	0.364	41462782	-0.042	0.027
rs43585140	Chr9	DMI	C	0.156	14393905	-0.09	0.049
ss117963035	Chr2	DMI	A	0.317	1.09E+08	0.141	0.02
ss86283078	Chr3	DMI	A	0.209	1.12E+08	-0.164	0.022
ss86285204	Chr19	DMI	C	0.397	14738309	-0.257	0.031
ss86287613	Chr21	DMI	G	0.481	34754177	-0.011	0.031
ss86289527	Chr10	DMI	G	0.3	36285826	0.134	0.016

ss86298219	Chr12	DMI	C	0.457	37801938	0.125	0.022
ss86298834	Chr5	DMI	T	0.435	1.18E+08	-0.178	0.021
ss86299146	Chr13	DMI	C	0.347	53356612	-0.196	0.026
ss86302411	Chr26	DMI	C	0.47	5128409	0.065	0.026
ss86312150	Chr26	DMI	C	0.285	7796869	-0.157	0.029
ss86314057	Chr8	DMI	G	0.102	56217967	0.39	0.028
ss86321294	Chr3	DMI	A	0.441	17276446	0.176	0.033
ss86324110	Chr2	DMI	T	0.053	1.38E+08	-0.219	0.049
ss86326499	Chr24	DMI	A	0.488	33183196	0.005	0.02
ss86329667	Chr22	DMI	A	0.262	19476532	-0.2	0.033
ss86331995 ss141408536 ss86338007	Chr14	DMI	G	0.343	72796829	0.182	0.015
ss86333184	Chr13	DMI	A	0.38	24907224	-0.044	0.02
ss86333246	Chr11	DMI	T	0.048	99293872	0.294	0.04
ss86336486 ss86310850	Chr4	DMI	A	0.212	77565084	0.191	0.025
ss86337384 ss86319462	Chr10	DMI	C	0.22	16211358	-0.292	0.038
ss86340488 ss86290533	Chr24	DMI	G	0.294	13180301	-0.012	0.016
BFGL-NGS-111692	Chr21	RFI	G	0.334	42187202	-0.119	0.022
rs29027007	Chr23	RFI	A	0.406	11432167	-0.085	0.016
rs41569387	Chr11	RFI	A	0.267	70053572	-0.129	0.01
rs41589498	Chr3	RFI	T	0.177	2516633	0.199	0.018
rs41591637	Chr14	RFI	G	0.295	52474088	-0.123	0.03
rs41594287	Chr10	RFI	C	0.222	91290322	0.14	0.016
rs41615974	Chr13	RFI	G	0.281	49140747	-0.116	0.018
rs41659405	Chr1	RFI	C	0.122	39454543	-0.282	0.018
rs41907795	Chr19	RFI	A	0.344	27060121	-0.095	0.016

rs41994086	Chr16	RFI	G	0.429	52549377	0.153	0.019
rs42005069	Chr6	RFI	G	0.467	55266545	0.01	0.024
rs42076978	Chr25	RFI	A	0.293	36565740	-0.045	0.013
rs42203217	Chr14	RFI	G	0.398	58882002	-0.082	0.019
rs42218435	Chr11	RFI	A	0.095	33511438	-0.168	0.037
rs42244558	Chr5	RFI	A	0.095	1293420	-0.272	0.011
rs42364886	Chr5	RFI	G	0.217	36795401	0.126	0.013
rs42598824	Chr16	RFI	T	0.35	77735267	0.111	0.022
rs42972397	Chr9	RFI	G	0.392	90796431	-0.148	0.016
rs43009143	Chr28	RFI	C	0.342	26852434	-0.002	0.009
rs43308427	Chr2	RFI	C	0.47	60143191	-0.04	0.022
rs43389761	Chr4	RFI	G	0.277	48969929	-0.082	0.017
rs43400303	Chr4	RFI	A	0.14	63892006	-0.118	0.016
rs43557189	Chr8	RFI	C	0.256	53208327	0.189	0.022
ss105311629	Chr13	RFI	A	0.273	11334505	-0.164	0.018
ss86288579	ChrUn	RFI	A	0.127	190955	0.161	0.03
ss86291559	Chr19	RFI	A	0.254	11624568	0.138	0.021
ss86301703	Chr19	RFI	G	0.063	15791841	-0.277	0.042
ss86303188	Chr23	RFI	T	0.434	19562079	0.077	0.013
ss86305968 ss86339265	Chr2	RFI	T	0.327	24659200	0.017	0.017
ss86307289	Chr4	RFI	A	0.444	15139390	-0.079	0.018
ss86312876	Chr18	RFI	G	0.137	51665556	0.283	0.03
ss86313507	Chr29	RFI	C	0.267	8984232	0.062	0.013
ss86318987	Chr6	RFI	A	0.475	29162222	-0.088	0.007
ss86321297	Chr24	RFI	G	0.389	48150873	0.061	0.015

ss86339405 ss86315360	Chr20	RFI	A	0.299	6555724	-0.058	0.015

‡Trait units are kg/d for ADG and DMI and kg DM/d for RFI. SNPID - NCBI rs/ss SNP ID, some SNPs have multiple predicted IDs based on their sequence similarities to multiple submissions in the NCBI database; †These SNPs have no rs/ss SNP ID; BTA – Chromosome; Position – Chromosomal position (bp); Estimate – Allele substitution effect; Freq – Minor allele frequency; SE – standard error.

Appendix 1: Table 2. Names, chromosomal locations, minor allele frequencies and allele substitution effects for SNPs used to build marker panels using RR-BLUP (Chapter 4) method.

SNPID	BTA	Trait	Minor Allele	Freq	Position	‡Estimate	SE
rs29009742	Chr23	ADG RRBLUP	A	0.345	48193360	0.014	0.001
rs29009978	Chr7	ADG RRBLUP	T	0.426	80131726	0.016	0.005
rs29010006	Chr12	ADG RRBLUP	T	0.437	63065550	-0.015	0.004
rs29010083	Chr15	ADG RRBLUP	A	0.324	80779274	-0.018	0.003
rs29010392	Chr11	ADG RRBLUP	G	0.439	59067281	-0.003	0.003
rs29011971	Chr11	ADG RRBLUP	A	0.314	54363220	0.003	0.004
rs29014674	Chr11	ADG RRBLUP	T	0.334	59350664	-0.006	0.005
rs29018725	Chr5	ADG RRBLUP	T	0.431	1.19E+08	-0.02	0.004
rs29019237	Chr11	ADG RRBLUP	C	0.441	83712430	-0.007	0.007
rs29019483	Chr28	ADG RRBLUP	A	0.284	2765207	-0.002	0.003
rs29020690	Chr2	ADG RRBLUP	G	0.194	20710301	-0.005	0.005
rs29023646	Chr21	ADG RRBLUP	A	0.376	2637648	0.005	0.006
rs29025923	Chr6	ADG RRBLUP	G	0.417	23332868	-0.017	0.002
rs29026930	Chr27	ADG RRBLUP	T	0.444	30880998	-0.026	0.006
rs41255638	Chr2	ADG RRBLUP	G	0.2	7744685	-0.006	0.005
rs41568120	Chr13	ADG RRBLUP	C	0.432	1121570	0.023	0.005
rs41575911	Chr20	ADG RRBLUP	T	0.268	42162193	-0.003	0.004
rs41578313	Chr2	ADG RRBLUP	A	0.473	1.18E+08	-0.013	0.002
rs41579555	Chr18	ADG RRBLUP	T	0.3	50059898	0.025	0.003
rs41581215	Chr18	ADG RRBLUP	C	0.35	41024459	-0.012	0.004

rs41591022	Chr6	ADG RRBLUP	A	0.417	23312425	-0.017	0.002
rs41596552	Chr16	ADG RRBLUP	A	0.282	8482725	-0.013	0.005
rs41601279	Chr24	ADG RRBLUP	A	0.2	26564151	-0.01	0.003
rs41605791	Chr17	ADG RRBLUP	A	0.436	68881238	0.022	0.003
rs41610069	Chr11	ADG RRBLUP	C	0.453	43867005	0.004	0.005
rs41610664	Chr4	ADG RRBLUP	A	0.281	88046023	-0.015	0.004
rs41614062	Chr2	ADG RRBLUP	T	0.498	83013168	-0.004	0.001
rs41617180	Chr21	ADG RRBLUP	C	0.465	2488633	-0.006	0.005
rs41620111	Chr14	ADG RRBLUP	T	0.27	45628286	0.037	0.005
rs41621351	Chr6	ADG RRBLUP	T	0.417	23283248	-0.017	0.002
rs41623175	Chr16	ADG RRBLUP	G	0.297	10100317	0.029	0.003
rs41625563	Chr7	ADG RRBLUP	G	0.432	91903228	0.009	0.001
rs41628392	Chr9	ADG RRBLUP	A	0.409	7408656	0.016	0.003
rs41636993	Chr2	ADG RRBLUP	T	0.3	17551644	-0.001	0.004
rs41639125	Chr1	ADG RRBLUP	C	0.473	6783109	0.014	0.004
rs41640505	Chr2	ADG RRBLUP	A	0.409	89276549	-0.009	0.005
rs41641037	Chr17	ADG RRBLUP	C	0.304	34397253	0.005	0.005
rs41641100	Chr20	ADG RRBLUP	C	0.495	47353822	-0.013	0.004
rs41642440	Chr22	ADG RRBLUP	G	0.454	28291985	0.015	0.002
rs41648477	Chr28	ADG RRBLUP	A	0.433	5772594	-0.021	0.003
rs41656065	Chr7	ADG RRBLUP	T	0.216	71845956	0.004	0.006
rs41656975	Chr7	ADG RRBLUP	C	0.392	93869682	0.015	0.006
rs41657401	Chr7	ADG RRBLUP	G	0.483	6032638	0.021	0.002
rs41658480	Chr6	ADG RRBLUP	G	0.433	54328469	-0.024	0.004
rs41658634	Chr10	ADG RRBLUP	A	0.424	14285133	-0.015	0.002

rs41660664	Chr6	ADG RRBLUP	A	0.384	514960	0.019	0.003
rs41663389	Chr6	ADG RRBLUP	A	0.388	574157	0.006	0.002
rs41665465	Chr9	ADG RRBLUP	C	0.209	88701211	0.011	0.008
rs41666779	Chr14	ADG RRBLUP	A	0.372	53364955	-0.031	0.002
rs41681356	Chr12	ADG RRBLUP	C	0.371	84229314	0.029	0.003
rs41772088	Chr15	ADG RRBLUP	T	0.319	54045333	0.007	0.003
rs41818125	ChrUn	ADG RRBLUP	C	0.368	245878	-0.002	0.005
rs41846328	Chr17	ADG RRBLUP	T	0.381	67026840	-0.003	0.005
rs41847101	Chr17	ADG RRBLUP	T	0.463	66962668	-0.031	0.01
rs41849313	Chr28	ADG RRBLUP	C	0.421	34323647	-0.012	0.002
rs41877216	Chr18	ADG RRBLUP	T	0.264	39089580	0.015	0.003
rs41887415	Chr18	ADG RRBLUP	A	0.32	50648768	-0.016	0.002
rs41894363	Chr18	ADG RRBLUP	T	0.177	58277805	0	0.007
rs41895988	Chr19	ADG RRBLUP	C	0.49	7270527	0.015	0.004
rs41900270	Chr18	ADG RRBLUP	C	0.45	62533850	0.008	0.005
rs41931717	Chr20	ADG RRBLUP	G	0.495	6776038	-0.01	0.006
rs41968142	Chr7	ADG RRBLUP	G	0.474	82951458	0	0.007
rs42140351	Chr28	ADG RRBLUP	G	0.394	6656202	-0.019	0.007
rs42149900	Chr28	ADG RRBLUP	A	0.423	42772804	0.001	0.004
rs42230224	Chr10	ADG RRBLUP	T	0.305	29247746	0.002	0.006
rs42269671	Chr2	ADG RRBLUP	G	0.339	8696447	-0.005	0.003
rs42270183	Chr2	ADG RRBLUP	C	0.374	20504698	-0.034	0.003
rs42338999	Chr11	ADG RRBLUP	C	0.253	60503780	-0.011	0.005
rs42352144	Chr3	ADG RRBLUP	T	0.423	97572111	-0.015	0.005
rs42386845	Chr16	ADG RRBLUP	G	0.261	5805896	0.004	0.005

rs42398026	Chr13	ADG RRBLUP	T	0.473	1651486	0.015	0.004
rs42406963	Chr12	ADG RRBLUP	A	0.34	63760820	0.001	0.007
rs42425010	Chr2	ADG RRBLUP	T	0.498	1.18E+08	-0.025	0.006
rs42426466	Chr2	ADG RRBLUP	G	0.303	1.18E+08	-0.002	0.001
rs42427384	Chr2	ADG RRBLUP	G	0.307	1.18E+08	0	0.001
rs42511166	Chr13	ADG RRBLUP	C	0.372	73306761	-0.031	0.003
rs42571431	Chr16	ADG RRBLUP	T	0.441	8565508	-0.002	0.004
rs42599209	Chr16	ADG RRBLUP	G	0.402	73429897	-0.02	0.005
rs42607660	Chr9	ADG RRBLUP	T	0.47	3717780	0.003	0.006
rs42731491	Chr7	ADG RRBLUP	A	0.351	1304084	0.001	0.004
rs42808317	Chr11	ADG RRBLUP	T	0.475	58976747	-0.006	0.002
rs42922702	Chr1	ADG RRBLUP	G	0.268	92325177	-0.02	0.003
rs42995154	Chr22	ADG RRBLUP	G	0.286	9190090	0.002	0.006
rs43015221	Chr24	ADG RRBLUP	C	0.464	8151719	-0.014	0.006
rs43153060	Chr26	ADG RRBLUP	G	0.322	881994	-0.011	0.003
rs43263928	Chr1	ADG RRBLUP	T	0.198	1.25E+08	0.019	0.003
rs43272296	Chr1	ADG RRBLUP	A	0.327	1.34E+08	0.018	0.004
rs43293349	Chr2	ADG RRBLUP	A	0.213	21301376	-0.007	0.005
rs43406975	Chr4	ADG RRBLUP	C	0.426	78222615	0.02	0.005
rs43418798	Chr12	ADG RRBLUP	C	0.207	61621355	0.021	0.006
rs43494032	Chr8	ADG RRBLUP	C	0.439	31439257	0.044	0.005
rs43514144	Chr7	ADG RRBLUP	C	0.349	36645610	-0.006	0.007
rs43584717	Chr9	ADG RRBLUP	G	0.401	1326785	-0.015	0.003
rs43604507	Chr9	ADG RRBLUP	T	0.394	66401629	-0.001	0.009
rs43651804	Chr10	ADG RRBLUP	C	0.313	93336973	-0.013	0.004

rs43664272	Chr11	ADG RRBLUP	A	0.223	2896524	-0.012	0.002
rs43691104	Chr11	ADG RRBLUP	T	0.363	1.1E+08	-0.01	0.005
rs43699555	Chr12	ADG RRBLUP	C	0.45	52690850	0.012	0.003
rs43706918	Chr15	ADG RRBLUP	A	0.345	12274036	0.02	0.004
rs43709835	Chr3	ADG RRBLUP	G	0.314	21163506	0.006	0.003
ss86325009	Chr1	ADG RRBLUP	C	0.466	55091202	0.02	0.005
ss86284116	Chr1	ADG RRBLUP	T	0.478	1.48E+08	0.025	0.007
ss86325631	Chr10	ADG RRBLUP	C	0.371	13666563	0.02	0.002
ss86311219 ss86337271	Chr10	ADG RRBLUP	A	0.402	70064823	0.002	0.003
ss86299444	Chr10	ADG RRBLUP	C	0.486	77672166	-0.018	0.005
ss86331115	Chr11	ADG RRBLUP	T	0.295	12860331	0.008	0.006
ss86331582	Chr11	ADG RRBLUP	A	0.3	54511207	-0.003	0.004
ss105239679 ss86336880 ss86302477	Chr11	ADG RRBLUP	C	0.354	93023360	-0.002	0.005
ss117975021	Chr11	ADG RRBLUP	T	0.375	54437607	0.005	0.002
ss105298676	Chr11	ADG RRBLUP	C	0.395	83688144	0.008	0.005
ss86303886	Chr11	ADG RRBLUP	T	0.418	59157410	0.02	0.004
ss86332463	Chr11	ADG RRBLUP	G	0.464	1.05E+08	0.008	0.003
ss86320135	Chr11	ADG RRBLUP	C	0.489	1.1E+08	-0.033	0.003
ss86301030 ss86336908	Chr12	ADG RRBLUP	G	0.339	71219931	-0.001	0.002
ss86295321	Chr12	ADG RRBLUP	T	0.385	29147372	0.002	0.007
ss86298219	Chr12	ADG RRBLUP	C	0.457	37801938	0.03	0.003
ss86331147	Chr13	ADG RRBLUP	T	0.337	20921842	0.007	0.005
ss86338406 ss141335895	Chr13	ADG RRBLUP	T	0.426	77670942	-0.009	0.003
ss105235969	Chr14	ADG RRBLUP	C	0.284	4497878	-0.012	0.005
ss86284999 ss86339961 ss141414250	Chr14	ADG RRBLUP	G	0.397	77948993	0	0.002

ss86296210	Chr14	ADG RRBLUP	C	0.489	45681753	0.013	0.006
ss105236466	Chr14	ADG RRBLUP	G	0.499	27452257	-0.035	0.004
ss86301413	Chr15	ADG RRBLUP	A	0.335	13630002	0.014	0.005
ss86320579	Chr15	ADG RRBLUP	T	0.466	53996750	-0.019	0.004
ss86330276	Chr15	ADG RRBLUP	C	0.493	30063426	-0.011	0.003
ss86312269	Chr16	ADG RRBLUP	G	0.363	11132371	0.01	0.004
ss86327921	Chr16	ADG RRBLUP	T	0.389	46191853	-0.007	0.004
ss86274657	Chr16	ADG RRBLUP	A	0.391	54648039	-0.032	0.005
ss86314795	Chr18	ADG RRBLUP	T	0.121	62373058	-0.041	0.007
ss86291311	Chr18	ADG RRBLUP	T	0.275	18155403	0.023	0.004
ss86287366	Chr18	ADG RRBLUP	A	0.411	56410232	0.005	0.004
ss86303710	Chr18	ADG RRBLUP	C	0.455	39864747	-0.021	0.004
ss86316986 ss86338899 ss141748132	Chr19	ADG RRBLUP	T	0.45	48622410	-0.007	0.007
ss86298079	Chr19	ADG RRBLUP	T	0.467	43301158	0.032	0.005
ss117963035	Chr2	ADG RRBLUP	A	0.317	1.09E+08	0.014	0.004
ss86294644 ss86340983 ss140238761	Chr2	ADG RRBLUP	T	0.427	92455935	-0.01	0.006
ss86295987 ss86340193	Chr2	ADG RRBLUP	A	0.498	83037165	0.004	0.001
ss86299499	Chr21	ADG RRBLUP	T	0.388	2594377	-0.008	0.001
ss86308974	Chr21	ADG RRBLUP	A	0.468	34686928	-0.017	0.005
ss86322707 ss86339325	Chr21	ADG RRBLUP	C	0.483	69085027	-0.002	0.001
ss86341174 ss86312678	Chr22	ADG RRBLUP	C	0.253	55890005	-0.008	0.002
ss86312863	Chr22	ADG RRBLUP	G	0.253	55912636	-0.008	0.002
ss86330399	Chr22	ADG RRBLUP	A	0.276	8241438	0.007	0.004
ss141906455 ss86288770 ss86336754	Chr22	ADG RRBLUP	T	0.314	8170453	0.017	0.003
ss86336944 ss86300614	Chr22	ADG RRBLUP	T	0.327	60010048	0.018	0.002

ss86274456	Chr22	ADG RRBLUP	C	0.33	12663906	-0.027	0.002
ss86308836 ss86338846	Chr22	ADG RRBLUP	C	0.363	55200138	0.026	0.003
ss86307905	Chr22	ADG RRBLUP	T	0.397	5074898	0.006	0.004
ss86329969 ss86341019	Chr22	ADG RRBLUP	C	0.45	9060236	-0.006	0.003
ss86274638	Chr22	ADG RRBLUP	T	0.463	14183041	-0.021	0.004
ss86293533	Chr22	ADG RRBLUP	T	0.474	14015132	-0.006	0.002
ss86333969 ss86337890	Chr22	ADG RRBLUP	T	0.478	38450275	-0.024	0.003
ss86297894	Chr23	ADG RRBLUP	C	0.425	2859323	0.021	0.003
ss105256273	Chr24	ADG RRBLUP	T	0.291	26502604	0.001	0.004
Hapmap50890-BTA-1214	Chr24	ADG RRBLUP	A	0.334	28961542	0.017	0.005
ss86282373	Chr24	ADG RRBLUP	T	0.438	26339920	0.01	0.005
ss105276721	Chr25	ADG RRBLUP	T	0.287	36787467	0.011	0.005
ss86284697	Chr25	ADG RRBLUP	G	0.337	39561967	0.018	0.003
ss86312450	Chr25	ADG RRBLUP	C	0.423	43779571	-0.005	0.007
ss86306823	Chr26	ADG RRBLUP	A	0.293	40310048	-0.042	0.005
ss86290521 ss86338600	Chr26	ADG RRBLUP	G	0.406	1653843	0.03	0.005
ss86284923	Chr26	ADG RRBLUP	A	0.411	48311186	-0.013	0.004
ss86288380	Chr27	ADG RRBLUP	G	0.333	9980281	0.001	0.005
ss142217392	Chr27	ADG RRBLUP	T	0.433	46460863	-0.028	0.001
ss86289896	Chr28	ADG RRBLUP	A	0.402	30379675	0.006	0.003
ss86337980 ss142249816 ss86303623	Chr28	ADG RRBLUP	A	0.415	33523002	0	0.003
ss86334058	Chr28	ADG RRBLUP	G	0.424	45321054	0.017	0.006
ss86304175	Chr28	ADG RRBLUP	A	0.461	44198614	-0.013	0.006
ss86322359	Chr29	ADG RRBLUP	A	0.49	13358272	-0.04	0.003
ss117962667	Chr3	ADG RRBLUP	C	0.337	43428200	0.021	0.003

ss86332833	Chr3	ADG RRBLUP	C	0.403	95154751	0.005	0.003
ss86339531 ss140365835 ss86326482	Chr3	ADG RRBLUP	G	0.461	1.01E+08	0.003	0.003
ss86320117	Chr3	ADG RRBLUP	A	0.467	1.17E+08	0.034	0.002
ss86276352 ss86336018	Chr3	ADG RRBLUP	A	0.473	93173991	-0.031	0.004
ss86302003	Chr4	ADG RRBLUP	C	0.403	1.17E+08	-0.005	0.003
ss86324094	Chr4	ADG RRBLUP	A	0.48	1.16E+08	0.002	0.003
	Chr5	ADG RRBLUP	T	0.445	99266935	-0.029	0.003
ss86289117	Chr6	ADG RRBLUP	A	0.175	32765343	-0.009	0.003
ss140638770 ss117968523	Chr6	ADG RRBLUP	T	0.316	37852400	-0.009	0.005
ss117968717	Chr6	ADG RRBLUP	A	0.403	40096368	0.01	0.006
ss105307554 ss117968245	Chr6	ADG RRBLUP	A	0.414	37963147	-0.026	0.004
ss105291171 ss117968562	Chr6	ADG RRBLUP	T	0.437	38729866	-0.002	0.005
ss140642970 ss117968397	Chr6	ADG RRBLUP	A	0.445	42204900	-0.005	0.006
ss105300789 ss117968553	Chr6	ADG RRBLUP	A	0.458	33785060	0.006	0.008
ss105311444 ss140645091 ss117968186	Chr6	ADG RRBLUP	C	0.472	44804409	0.018	0.004
ss86293586	Chr7	ADG RRBLUP	C	0.275	71629520	0.008	0.004
ss86304564 ss86337150	Chr7	ADG RRBLUP	T	0.353	11594482	0.005	0.002
ss86318242	Chr7	ADG RRBLUP	T	0.476	6599674	0.001	0.003
ss86310493	Chr8	ADG RRBLUP	A	0.314	19235645	0.003	0.008
ss86328642	Chr8	ADG RRBLUP	G	0.316	1.16E+08	-0.027	0.007
ss86305956	Chr8	ADG RRBLUP	C	0.362	65136890	0.026	0.007
ss86341071	Chr8	ADG RRBLUP	C	0.365	90972338	0.005	0.003
ss140894649 ss86333395 ss86335572	Chr8	ADG RRBLUP	G	0.426	1.09E+08	-0.005	0.005
ss86283704	Chr9	ADG RRBLUP	G	0.253	6415256	0.009	0.002
ss86310026	Chr9	ADG RRBLUP	G	0.291	25009	0.003	0.004

ss86318845	Chr9	ADG RRBLUP	C	0.32	96255785	0.015	0.003
ss117969528	Chr9	ADG RRBLUP	A	0.394	88157050	0.017	0.002
ss86328537	Chr9	ADG RRBLUP	A	0.449	66360744	-0.016	0.004
ss105249534	ChrUn	ADG RRBLUP	C	0.369	46003	0.021	0.003
ss86305113 ss86338143	ChrUn	ADG RRBLUP	G	0.453	2995350	0.016	0.009
rs29011450	Chr28	DMI RRBLUP	A	0.423	37860813	0.024	0.004
rs29012925	Chr5	DMI RRBLUP	C	0.416	1.18E+08	-0.018	0.003
rs29014495	Chr24	DMI RRBLUP	T	0.499	33101881	0.011	0
rs29016002	Chr1	DMI RRBLUP	A	0.424	63611305	0.014	0.003
rs29016356	Chr19	DMI RRBLUP	A	0.185	35045329	-0.019	0.003
rs29018725	Chr5	DMI RRBLUP	T	0.431	1.19E+08	-0.016	0.004
rs29019483	Chr28	DMI RRBLUP	A	0.284	2765207	0.02	0.003
rs29019540	Chr1	DMI RRBLUP	A	0.334	1.15E+08	-0.019	0.006
rs29020900	Chr14	DMI RRBLUP	A	0.491	19910197	-0.013	0.003
rs29023646	Chr21	DMI RRBLUP	A	0.376	2637648	-0.012	0.004
rs29027007	Chr23	DMI RRBLUP	A	0.406	11432167	-0.018	0.004
rs29027283	Chr19	DMI RRBLUP	C	0.489	22465360	-0.012	0.005
rs41255303	Chr7	DMI RRBLUP	T	0.31	11088641	-0.028	0.004
rs41569387	Chr11	DMI RRBLUP	A	0.267	70053572	-0.019	0.004
rs41569794	Chr4	DMI RRBLUP	A	0.348	74993512	0.022	0.003
rs41571046	Chr11	DMI RRBLUP	A	0.203	1.02E+08	-0.014	0.004
rs41571862	Chr1	DMI RRBLUP	T	0.353	6219142	0.02	0.002
rs41578671	Chr19	DMI RRBLUP	C	0.332	57511323	-0.017	0.004
rs41580132	Chr24	DMI RRBLUP	T	0.369	33160416	0.009	0.002
rs41580478	Chr14	DMI RRBLUP	T	0.428	72400485	-0.02	0.003

rs41582543	Chr1	DMI RRBLUP	T	0.374	60809664	-0.008	0.006
rs41587678	Chr4	DMI RRBLUP	C	0.376	49069017	-0.017	0.005
rs41591637	Chr14	DMI RRBLUP	G	0.295	52474088	-0.033	0.003
rs41593516	Chr26	DMI RRBLUP	C	0.241	39437807	-0.029	0.002
rs41594336	Chr20	DMI RRBLUP	G	0.409	2569272	0.023	0.006
rs41595934	Chr6	DMI RRBLUP	G	0.307	35095138	-0.015	0.003
rs41596013	Chr6	DMI RRBLUP	G	0.385	45960114	0.006	0.003
rs41597443	Chr8	DMI RRBLUP	G	0.42	41664453	-0.017	0.005
rs41597632	Chr10	DMI RRBLUP	C	0.189	62466743	-0.016	0.001
rs41615197	Chr11	DMI RRBLUP	G	0.454	37412349	0.019	0.005
rs41617805	ChrUn	DMI RRBLUP	C	0.203	3459353	0.023	0.003
rs41620466	Chr19	DMI RRBLUP	A	0.36	12049383	0.005	0.003
rs41621136	Chr14	DMI RRBLUP	C	0.352	69508332	-0.018	0.003
rs41630162	Chr13	DMI RRBLUP	T	0.368	46222328	-0.024	0.003
rs41637283	Chr18	DMI RRBLUP	G	0.378	31692831	0.012	0.007
rs41638079	Chr18	DMI RRBLUP	C	0.412	37573693	0.014	0.005
rs41639611	Chr21	DMI RRBLUP	A	0.425	30670019	-0.017	0.003
rs41640212	Chr20	DMI RRBLUP	T	0.41	39860784	0.024	0.004
rs41641220	Chr25	DMI RRBLUP	A	0.374	6398911	-0.01	0.004
rs41641491	Chr19	DMI RRBLUP	C	0.333	14639908	0.013	0.002
rs41641502	Chr19	DMI RRBLUP	A	0.391	14541593	-0.023	0.003
rs41643439	Chr23	DMI RRBLUP	C	0.356	32266053	0.02	0.003
rs41645263	Chr24	DMI RRBLUP	C	0.488	24617207	0.016	0.003
rs41652463	Chr28	DMI RRBLUP	G	0.413	24176807	0.024	0.003
rs41653434	Chr7	DMI RRBLUP	G	0.443	90107228	0.02	0.002

rs41654591	Chr10	DMI RRBLUP	A	0.325	91420638	-0.028	0.003
rs41655774	Chr6	DMI RRBLUP	G	0.348	1.2E+08	-0.004	0.005
rs41658128	Chr7	DMI RRBLUP	G	0.337	11212022	-0.022	0.005
rs41658343	Chr9	DMI RRBLUP	C	0.456	77100499	-0.011	0.004
rs41658480	Chr6	DMI RRBLUP	G	0.433	54328469	-0.021	0.002
rs41658634	Chr10	DMI RRBLUP	A	0.424	14285133	-0.009	0.003
rs41665047	Chr10	DMI RRBLUP	T	0.472	62410140	-0.01	0.004
rs41666531	Chr26	DMI RRBLUP	C	0.482	39417271	-0.031	0.002
rs41666779	Chr14	DMI RRBLUP	A	0.372	53364955	-0.017	0.005
rs41667842	Chr12	DMI RRBLUP	C	0.34	80998850	-0.029	0.002
rs41696831	Chr13	DMI RRBLUP	G	0.463	48392938	-0.02	0.004
rs41826110	Chr16	DMI RRBLUP	T	0.265	69249251	-0.02	0.003
rs41872004	Chr18	DMI RRBLUP	G	0.499	32630275	-0.027	0.004
rs41874204	Chr18	DMI RRBLUP	T	0.408	37401684	0.014	0.006
rs41887389	Chr18	DMI RRBLUP	A	0.228	50742772	-0.011	0.005
rs41913775	Chr14	DMI RRBLUP	T	0.334	45588041	0.021	0.003
rs41936397	Chr20	DMI RRBLUP	G	0.213	13064471	0.022	0.001
rs41976011	Chr21	DMI RRBLUP	A	0.291	18331255	-0.009	0.005
rs42010591	Chr22	DMI RRBLUP	G	0.299	46831728	0.021	0.003
rs42029905	Chr23	DMI RRBLUP	A	0.444	45588817	-0.026	0.005
rs42095651	Chr26	DMI RRBLUP	A	0.299	31528736	-0.014	0.003
rs42113305	Chr7	DMI RRBLUP	T	0.461	1.06E+08	-0.015	0.003
rs42205322	ChrUn	DMI RRBLUP	T	0.415	28470	0.026	0.004
rs42211818	Chr2	DMI RRBLUP	T	0.306	41147382	-0.009	0.001
rs42215845	Chr14	DMI RRBLUP	G	0.293	5139498	-0.022	0.002

rs42215930	Chr14	DMI RRBLUP	T	0.299	5117434	-0.023	0.002
rs42244571	Chr5	DMI RRBLUP	T	0.482	1237389	0.026	0.003
rs42267353	Chr8	DMI RRBLUP	T	0.489	27772306	-0.015	0.005
rs42340315	Chr13	DMI RRBLUP	A	0.414	49042803	-0.018	0.003
rs42410387	Chr6	DMI RRBLUP	A	0.334	1.19E+08	0.023	0.008
rs42411131	Chr6	DMI RRBLUP	G	0.296	1.19E+08	0.028	0.002
rs42541659	Chr1	DMI RRBLUP	A	0.449	60865899	0.011	0.003
rs42609685	Chr24	DMI RRBLUP	T	0.467	29594856	0.016	0.002
rs42686095	Chr25	DMI RRBLUP	A	0.383	22968554	0.022	0.003
rs42761380	Chr24	DMI RRBLUP	G	0.453	29658911	-0.016	0.003
rs42846886	Chr14	DMI RRBLUP	A	0.206	20420772	0.016	0.003
rs42848382	Chr28	DMI RRBLUP	C	0.457	35051073	-0.017	0.002
rs42972397	Chr9	DMI RRBLUP	G	0.392	90796431	-0.026	0.001
rs43057535	Chr1	DMI RRBLUP	A	0.268	1.43E+08	0.016	0.003
rs43066203	Chr1	DMI RRBLUP	T	0.268	1.43E+08	0.016	0.003
rs43099270	Chr1	DMI RRBLUP	C	0.265	4284068	-0.02	0.003
rs43157783	Chr5	DMI RRBLUP	A	0.333	2731741	0.026	0.001
rs43235365	Chr1	DMI RRBLUP	T	0.41	67801352	-0.016	0.003
rs43281624	Chr1	DMI RRBLUP	G	0.496	1.44E+08	0.02	0.002
rs43288647	Chr7	DMI RRBLUP	A	0.436	1782962	-0.014	0.001
rs43308752	Chr17	DMI RRBLUP	A	0.308	30075837	-0.003	0.003
rs43367746	Chr3	DMI RRBLUP	G	0.423	1.11E+08	-0.006	0.005
rs43368994	Chr3	DMI RRBLUP	T	0.336	1.11E+08	-0.008	0.002
rs43404908	Chr4	DMI RRBLUP	C	0.427	78161176	0.025	0.002
rs43406975	Chr4	DMI RRBLUP	C	0.426	78222615	0.024	0.002

rs43458937	Chr6	DMI RRBLUP	C	0.428	39794334	-0.036	0.005
rs43460584	Chr6	DMI RRBLUP	A	0.364	41462782	-0.016	0.007
rs43486526	Chr6	DMI RRBLUP	A	0.231	1.18E+08	0.011	0.003
rs43488797	Chr6	DMI RRBLUP	A	0.247	1.19E+08	0.021	0.002
rs43528584	Chr7	DMI RRBLUP	G	0.412	87975144	0.026	0.003
rs43620039	Chr10	DMI RRBLUP	A	0.496	13936704	-0.014	0.003
rs43646790	Chr10	DMI RRBLUP	T	0.395	91160685	0.015	0.004
rs43659115	Chr11	DMI RRBLUP	C	0.417	2119843	-0.022	0.001
rs43691423	Chr12	DMI RRBLUP	G	0.333	47745184	0.019	0.002
rs43707936	Chr3	DMI RRBLUP	G	0.403	4233402	0.02	0.005
rs43708498	Chr17	DMI RRBLUP	A	0.339	30117923	-0.002	0.003
rs43712212	Chr3	DMI RRBLUP	T	0.461	1.07E+08	-0.014	0.002
rs43712305	Chr3	DMI RRBLUP	C	0.432	51468870	0.016	0.002
rs43732439	ChrUn	DMI RRBLUP	G	0.305	572298	0.025	0.003
ss86305181	Chr1	DMI RRBLUP	A	0.276	55117570	-0.019	0.002
ss86322201	Chr1	DMI RRBLUP	C	0.419	1.47E+08	-0.033	0.003
ss86337384 ss86319462	Chr10	DMI RRBLUP	C	0.22	16211358	-0.027	0.003
ss86289527	Chr10	DMI RRBLUP	G	0.3	36285826	0.022	0.003
ss86325631	Chr10	DMI RRBLUP	C	0.371	13666563	0.009	0.004
ss86323690	Chr10	DMI RRBLUP	A	0.42	55467759	0.007	0.005
ss86333253	Chr11	DMI RRBLUP	C	0.297	2016951	-0.013	0.004
ss86295624	Chr11	DMI RRBLUP	C	0.393	98973737	0.015	0.006
ss86333925	Chr11	DMI RRBLUP	C	0.427	99663236	0.029	0.005
ss86336850	Chr11	DMI RRBLUP	A	0.475	69550821	0.023	0.005
ss86319906	Chr11	DMI RRBLUP	T	0.495	98890768	0.012	0.004

ss86300073	Chr12	DMI RRBLUP	G	0.369	64166117	-0.025	0.004
ss86298219	Chr12	DMI RRBLUP	C	0.457	37801938	0.023	0.004
ss86299146	Chr13	DMI RRBLUP	C	0.347	53356612	-0.017	0.003
ss86333184	Chr13	DMI RRBLUP	A	0.38	24907224	-0.012	0.004
ss141276965 ss86341012 ss86322947	Chr13	DMI RRBLUP	T	0.404	13138591	-0.024	0.004
ss86327363	Chr13	DMI RRBLUP	C	0.428	23104022	0.01	0.006
ss86308829	Chr13	DMI RRBLUP	C	0.483	28137385	-0.011	0.004
ss86331995 ss141408536 ss86338007	Chr14	DMI RRBLUP	G	0.343	72796829	0.026	0.003
ss86321835 ss86340640	Chr14	DMI RRBLUP	A	0.398	46758531	-0.025	0.003
ss141404526 ss86340426 ss86329284	Chr14	DMI RRBLUP	T	0.414	68219827	-0.025	0.002
ss105250812	Chr14	DMI RRBLUP	A	0.421	72289416	0.02	0.001
ss86300618	Chr14	DMI RRBLUP	A	0.446	68157431	0.016	0.002
ss105235808	Chr14	DMI RRBLUP	A	0.479	6339015	0.014	0.003
ss86312269	Chr16	DMI RRBLUP	G	0.363	11132371	0.033	0.002
ss86325758	Chr17	DMI RRBLUP	C	0.438	38831747	0.01	0.004
ss117965187	Chr19	DMI RRBLUP	C	0.276	11913008	0.002	0.004
ss86340116	Chr19	DMI RRBLUP	C	0.305	15624481	0.019	0.003
ss86282748	Chr19	DMI RRBLUP	G	0.333	14371695	-0.019	0.002
ss86322196	Chr19	DMI RRBLUP	A	0.343	12105345	0.006	0.003
ss117965228	Chr19	DMI RRBLUP	C	0.385	10216561	0.01	0.001
ss86285204	Chr19	DMI RRBLUP	C	0.397	14738309	-0.032	0.002
ss86340252	Chr19	DMI RRBLUP	G	0.409	58653826	0.019	0.002
ss86319269	Chr19	DMI RRBLUP	A	0.453	27858989	-0.025	0.001
ss86287664	Chr2	DMI RRBLUP	T	0.284	65812460	-0.02	0.001
ss117963035	Chr2	DMI RRBLUP	A	0.317	1.09E+08	0.023	0.004

ss86274327 ss86341382 ss140200326	Chr2	DMI RRBLUP	G	0.469	40959608	-0.005	0.002
ss86302454 ss86341326	Chr2	DMI RRBLUP	T	0.484	67968260	-0.01	0.002
ss86291859	Chr21	DMI RRBLUP	C	0.246	28089897	0.023	0.004
ss86327696	Chr21	DMI RRBLUP	C	0.334	24163903	0.017	0.005
ss86299499	Chr21	DMI RRBLUP	T	0.388	2594377	-0.01	0.005
ss86297678 ss86336600	Chr21	DMI RRBLUP	A	0.446	65672197	0.017	0.002
ss86287613	Chr21	DMI RRBLUP	G	0.481	34754177	-0.019	0.006
ss86328277	Chr22	DMI RRBLUP	C	0.407	43786348	0.013	0.004
ss86335893 ss86295729 ss141929725	Chr22	DMI RRBLUP	T	0.47	36030388	-0.013	0.004
ss105256273	Chr24	DMI RRBLUP	T	0.291	26502604	-0.015	0.002
ss86340488 ss86290533	Chr24	DMI RRBLUP	G	0.294	13180301	-0.017	0.005
ss86282373	Chr24	DMI RRBLUP	T	0.438	26339920	0.026	0.002
ss86326499	Chr24	DMI RRBLUP	A	0.488	33183196	-0.01	0.001
ss86284580	Chr25	DMI RRBLUP	T	0.288	40999193	-0.013	0.002
ss86286856	Chr25	DMI RRBLUP	T	0.33	43328712	-0.019	0.001
ss142084607 ss86285940 ss86336419	Chr25	DMI RRBLUP	T	0.445	9035401	0.014	0.002
ss86291919	Chr26	DMI RRBLUP	A	0.171	13563199	0.008	0.005
ss86312150	Chr26	DMI RRBLUP	C	0.285	7796869	-0.019	0.003
ss86306823	Chr26	DMI RRBLUP	A	0.293	40310048	-0.033	0.004
ss86297201	Chr26	DMI RRBLUP	A	0.388	12543004	-0.018	0.003
ss86302411	Chr26	DMI RRBLUP	C	0.47	5128409	0.013	0.004
ss86278429	Chr26	DMI RRBLUP	A	0.497	7433501	-0.015	0.003
ss86295367	Chr28	DMI RRBLUP	A	0.416	1185260	-0.015	0.002
ss86338981 ss86316321	Chr28	DMI RRBLUP	G	0.444	3252260	-0.021	0.004
ss86283078	Chr3	DMI RRBLUP	A	0.209	1.12E+08	-0.007	0.004

ss86334691	Chr3	DMI RRBLUP	A	0.233	1.23E+08	-0.024	0.003
ss86336295 ss86332960	Chr3	DMI RRBLUP	C	0.242	1.2E+08	-0.016	0.002
ss86300695	Chr3	DMI RRBLUP	T	0.371	1.15E+08	-0.014	0.002
ss117962856	Chr3	DMI RRBLUP	T	0.38	22068686	0.012	0.003
ss86339363 ss86311787	Chr3	DMI RRBLUP	T	0.433	1.11E+08	0.006	0.006
ss86321294	Chr3	DMI RRBLUP	A	0.441	17276446	0.027	0.001
ss86288485	Chr3	DMI RRBLUP	C	0.46	46800080	-0.014	0.003
ss86314903	Chr4	DMI RRBLUP	T	0.26	86175679	-0.018	0.002
ss86296136	Chr4	DMI RRBLUP	G	0.346	71778598	-0.019	0.003
ss86291547	Chr4	DMI RRBLUP	T	0.348	77858119	-0.019	0.002
ss86340969 ss86319210	Chr4	DMI RRBLUP	A	0.376	40447359	-0.007	0.004
ss140433225 ss117975221	Chr4	DMI RRBLUP	A	0.377	49699919	0.017	0.004
ss86306854	Chr4	DMI RRBLUP	T	0.44	1.02E+08	-0.001	0.002
ss86298460	Chr4	DMI RRBLUP	C	0.5	1.01E+08	0.007	0.002
ss86336111	Chr5	DMI RRBLUP	G	0.322	1.23E+08	0.014	0.004
ss86286524	Chr5	DMI RRBLUP	A	0.325	1.18E+08	0.01	0.002
ss86332091	Chr5	DMI RRBLUP	T	0.331	1.15E+08	0.023	0.002
ss86298834	Chr5	DMI RRBLUP	T	0.435	1.18E+08	-0.015	0.002
ss140599049	Chr5	DMI RRBLUP	C	0.464	1.19E+08	0.017	0.002
ss117968078 ss105300915	Chr6	DMI RRBLUP	A	0.248	37096525	-0.021	0.003
ss105311575 ss117968559	Chr6	DMI RRBLUP	G	0.414	40151936	0.019	0.006
ss105291171 ss117968562	Chr6	DMI RRBLUP	T	0.437	38729866	0.023	0.001
ss140642970 ss117968397	Chr6	DMI RRBLUP	A	0.445	42204900	-0.009	0.003
ss86329848	Chr6	DMI RRBLUP	A	0.447	31783985	-0.015	0.004
ss105300789 ss117968553	Chr6	DMI RRBLUP	A	0.458	33785060	-0.015	0.002

ss117968721	Chr6	DMI RRBLUP	T	0.458	33761327	-0.015	0.003
ss140743800 ss86337403 ss86275837	Chr7	DMI RRBLUP	A	0.442	34102145	0.017	0.003
ss86312018	Chr8	DMI RRBLUP	A	0.48	53765346	0.021	0.003
ss86277885	Chr9	DMI RRBLUP	C	0.345	54247543	0.023	0.005
ss86290757	Chr9	DMI RRBLUP	T	0.407	1.05E+08	0.019	0.002
rs29011393	Chr6	RFI RRBLUP	A	0.317	29139241	0.026	0.001
rs29015159	Chr2	RFI RRBLUP	C	0.444	92075538	0.01	0.005
rs29015265	Chr4	RFI RRBLUP	T	0.402	66897419	-0.025	0.003
rs29018213	Chr20	RFI RRBLUP	G	0.371	72686898	-0.025	0.004
rs29019540	Chr1	RFI RRBLUP	A	0.334	1.15E+08	-0.015	0.007
rs29020900	Chr14	RFI RRBLUP	A	0.491	19910197	-0.007	0.001
rs29021889	Chr6	RFI RRBLUP	T	0.311	49334857	-0.006	0.003
rs29022067	Chr17	RFI RRBLUP	G	0.372	31309718	-0.029	0.003
rs29022883	Chr4	RFI RRBLUP	A	0.293	51115714	0.006	0.003
rs29024293	Chr2	RFI RRBLUP	T	0.242	60249495	-0.014	0.003
rs29027007	Chr23	RFI RRBLUP	A	0.406	11432167	-0.017	0.005
rs41566885	Chr27	RFI RRBLUP	C	0.421	37370739	-0.017	0.004
rs41569318	Chr25	RFI RRBLUP	A	0.425	23069380	-0.007	0.003
rs41569387	Chr11	RFI RRBLUP	A	0.267	70053572	-0.025	0.005
rs41570453	Chr6	RFI RRBLUP	A	0.417	22616875	0.023	0.003
rs41573624	Chr6	RFI RRBLUP	C	0.281	22359286	-0.034	0.003
rs41576649	Chr10	RFI RRBLUP	A	0.489	96508076	-0.004	0.003
rs41579492	Chr14	RFI RRBLUP	C	0.423	58838436	-0.013	0.004
rs41579807	Chr19	RFI RRBLUP	G	0.258	14667205	-0.011	0.004
rs41580123	Chr14	RFI RRBLUP	C	0.493	62673287	0.025	0.003

rs41580478	Chr14	RFI RRBLUP	T	0.428	72400485	-0.034	0.004
rs41584022	Chr24	RFI RRBLUP	G	0.478	33074041	0.008	0.004
rs41587222	Chr23	RFI RRBLUP	G	0.496	22815029	-0.015	0.007
rs41587678	Chr4	RFI RRBLUP	C	0.376	49069017	-0.018	0.004
rs41588707	Chr4	RFI RRBLUP	G	0.153	63995739	-0.012	0.005
rs41589112	Chr8	RFI RRBLUP	A	0.458	49801064	-0.013	0.003
rs41589498	Chr3	RFI RRBLUP	T	0.177	2516633	0.034	0.002
rs41590720	Chr4	RFI RRBLUP	G	0.231	21506496	0.01	0.007
rs41591637	Chr14	RFI RRBLUP	G	0.295	52474088	-0.04	0.005
rs41593516	Chr26	RFI RRBLUP	C	0.241	39437807	-0.034	0.004
rs41593661	Chr5	RFI RRBLUP	A	0.493	1.06E+08	0.013	0.005
rs41594287	Chr10	RFI RRBLUP	C	0.222	91290322	0.021	0.002
rs41596511	Chr7	RFI RRBLUP	A	0.483	99649982	-0.019	0.004
rs41599754	Chr4	RFI RRBLUP	A	0.457	50360661	0.009	0.003
rs41600388	Chr19	RFI RRBLUP	C	0.48	14562521	0.003	0.001
rs41615197	Chr11	RFI RRBLUP	G	0.454	37412349	0.026	0.005
rs41615974	Chr13	RFI RRBLUP	G	0.281	49140747	-0.022	0.004
rs41618669	Chr1	RFI RRBLUP	A	0.335	1.58E+08	0.012	0.004
rs41628306	Chr13	RFI RRBLUP	C	0.262	39406173	0.029	0.003
rs41630507	Chr19	RFI RRBLUP	A	0.371	12362294	0.019	0.003
rs41636768	Chr18	RFI RRBLUP	T	0.437	55150035	-0.036	0.004
rs41637289	Chr18	RFI RRBLUP	G	0.318	31419763	-0.011	0.005
rs41641502	Chr19	RFI RRBLUP	A	0.391	14541593	-0.025	0.004
rs41641505	Chr19	RFI RRBLUP	G	0.294	14463447	0.017	0.002
rs41643757	Chr21	RFI RRBLUP	C	0.379	47625363	0.021	0.002

rs41644507	Chr22	RFI RRBLUP	T	0.391	50130591	-0.003	0.003
rs41645263	Chr24	RFI RRBLUP	C	0.488	24617207	0.014	0.005
rs41649876	Chr6	RFI RRBLUP	C	0.496	27831792	0.028	0.006
rs41652468	Chr28	RFI RRBLUP	G	0.275	23668737	-0.022	0.003
rs41655825	Chr6	RFI RRBLUP	A	0.486	1.17E+08	0.033	0.003
rs41657910	Chr11	RFI RRBLUP	G	0.296	33989537	0.031	0.004
rs41657913	Chr11	RFI RRBLUP	G	0.464	34105348	-0.012	0.008
rs41658343	Chr9	RFI RRBLUP	C	0.456	77100499	-0.008	0.004
rs41663853	Chr28	RFI RRBLUP	C	0.413	14379998	0.028	0.003
rs41665964	Chr5	RFI RRBLUP	G	0.453	58236173	0.007	0.004
rs41667842	Chr12	RFI RRBLUP	C	0.34	80998850	-0.029	0.005
rs41703327	Chr21	RFI RRBLUP	A	0.322	42104742	-0.022	0.004
rs41723352	Chr3	RFI RRBLUP	A	0.498	1.27E+08	0.008	0.003
rs41789740	Chr16	RFI RRBLUP	G	0.338	52438	-0.023	0.005
rs41831100	Chr16	RFI RRBLUP	C	0.483	75536974	-0.003	0.004
rs41872004	Chr18	RFI RRBLUP	G	0.499	32630275	-0.02	0.005
rs41907795	Chr19	RFI RRBLUP	A	0.344	27060121	-0.024	0.005
rs41968651	Chr21	RFI RRBLUP	A	0.388	18429868	-0.018	0.007
rs41994086	Chr16	RFI RRBLUP	G	0.429	52549377	0.032	0.004
rs42005069	Chr6	RFI RRBLUP	G	0.467	55266545	0.009	0.008
rs42067726	Chr25	RFI RRBLUP	T	0.486	32183153	0.005	0.005
rs42068538	Chr25	RFI RRBLUP	G	0.469	31892337	0.011	0.001
rs42076978	Chr25	RFI RRBLUP	A	0.293	36565740	0	0.002
rs42142693	Chr28	RFI RRBLUP	G	0.242	24107627	0.034	0.005
rs42145142	Chr28	RFI RRBLUP	G	0.392	25286084	0.032	0.003

rs42153608	Chr28	RFI RRBLUP	C	0.301	39481034	0.025	0.004
rs42203217	Chr14	RFI RRBLUP	G	0.398	58882002	-0.022	0.003
rs42205322	ChrUn	RFI RRBLUP	T	0.415	28470	0.026	0.005
rs42218359	Chr14	RFI RRBLUP	C	0.496	5668165	-0.022	0.003
rs42229148	Chr3	RFI RRBLUP	T	0.337	79800923	0.024	0.005
rs42267353	Chr8	RFI RRBLUP	T	0.489	27772306	-0.012	0.004
rs42316404	Chr17	RFI RRBLUP	A	0.433	8899286	0.034	0.008
rs42364886	Chr5	RFI RRBLUP	G	0.217	36795401	0.03	0.003
rs42410387	Chr6	RFI RRBLUP	A	0.334	1.19E+08	0.021	0.004
rs42411131	Chr6	RFI RRBLUP	G	0.296	1.19E+08	0.025	0.004
rs42425117	Chr16	RFI RRBLUP	C	0.411	74900509	-0.009	0.002
rs42450575	Chr4	RFI RRBLUP	T	0.329	76239483	0.003	0.003
rs42474272	Chr14	RFI RRBLUP	G	0.483	25455256	0.021	0.005
rs42517435	Chr29	RFI RRBLUP	T	0.389	24455280	-0.023	0.004
rs42598824	Chr16	RFI RRBLUP	T	0.35	77735267	0.016	0.002
rs42600007	Chr16	RFI RRBLUP	G	0.492	77819152	0.036	0.003
rs42611064	Chr5	RFI RRBLUP	C	0.415	44176108	-0.011	0.004
rs42625829	Chr11	RFI RRBLUP	C	0.372	10237050	0.02	0.004
rs42653268	Chr10	RFI RRBLUP	C	0.219	1.03E+08	-0.032	0.002
rs42669983	Chr4	RFI RRBLUP	A	0.371	76748642	-0.009	0.004
rs42746836	Chr7	RFI RRBLUP	C	0.433	2310381	-0.009	0.005
rs42746858	Chr7	RFI RRBLUP	T	0.471	2287322	0.014	0.003
rs42756348	Chr4	RFI RRBLUP	A	0.351	49674071	-0.019	0.003
rs42771121	Chr13	RFI RRBLUP	G	0.421	51699788	-0.023	0.005
rs42848382	Chr28	RFI RRBLUP	C	0.457	35051073	-0.016	0.003

rs42883957	Chr2	RFI RRBLUP	G	0.447	56721815	-0.008	0.006
rs42894216	Chr20	RFI RRBLUP	C	0.411	74161665	0.012	0.004
rs42915745	Chr7	RFI RRBLUP	T	0.469	1.04E+08	0.021	0.004
rs42972397	Chr9	RFI RRBLUP	G	0.392	90796431	-0.031	0.003
rs42975505	Chr3	RFI RRBLUP	T	0.369	6606822	0.007	0.007
rs43007076	Chr6	RFI RRBLUP	T	0.356	479837	0.011	0.007
rs43095753	Chr2	RFI RRBLUP	T	0.395	30197476	0.025	0.002
rs43101847	Chr14	RFI RRBLUP	T	0.378	4302229	0.013	0.003
rs43127117	Chr8	RFI RRBLUP	C	0.458	49775558	-0.013	0.003
rs43161947	Chr8	RFI RRBLUP	T	0.401	37257077	0.022	0.006
rs43197278	Chr2	RFI RRBLUP	G	0.489	1.35E+08	0.018	0.004
rs43235106	Chr1	RFI RRBLUP	G	0.417	65560287	0.03	0.004
rs43283301	Chr1	RFI RRBLUP	A	0.366	1.6E+08	-0.01	0.003
rs43288647	Chr7	RFI RRBLUP	A	0.436	1782962	-0.011	0.003
rs43301566	Chr2	RFI RRBLUP	G	0.415	28418145	0.006	0.004
rs43308427	Chr2	RFI RRBLUP	C	0.47	60143191	-0.011	0.005
rs43328895	Chr2	RFI RRBLUP	A	0.479	1.35E+08	-0.018	0.002
rs43350479	Chr3	RFI RRBLUP	A	0.457	87291654	-0.024	0.007
rs43368589	Chr3	RFI RRBLUP	C	0.392	1.23E+08	-0.024	0.006
rs43370810	Chr3	RFI RRBLUP	T	0.423	1.26E+08	-0.012	0.003
rs43388052	Chr4	RFI RRBLUP	G	0.469	39490595	-0.009	0.004
rs43389711	Chr4	RFI RRBLUP	A	0.407	46392808	0.002	0.003
rs43389761	Chr4	RFI RRBLUP	G	0.277	48969929	-0.009	0.004
rs43390906	Chr4	RFI RRBLUP	G	0.406	46325575	0.006	0.003
rs43404908	Chr4	RFI RRBLUP	C	0.427	78161176	0.02	0.003

rs43406975	Chr4	RFI RRBLUP	C	0.426	78222615	0.017	0.003
rs43466020	Chr6	RFI RRBLUP	C	0.302	49361007	-0.015	0.004
rs43499539	Chr7	RFI RRBLUP	A	0.262	5854636	0.019	0.003
rs43557189	Chr8	RFI RRBLUP	C	0.256	53208327	0.032	0.005
rs43578762	Chr8	RFI RRBLUP	C	0.275	1.05E+08	-0.007	0.004
rs43604365	Chr9	RFI RRBLUP	C	0.44	52502821	0.017	0.008
rs43604391	Chr9	RFI RRBLUP	C	0.44	52475302	0.015	0.008
rs43712212	Chr3	RFI RRBLUP	T	0.461	1.07E+08	-0.01	0.005
ss86322201	Chr1	RFI RRBLUP	C	0.419	1.47E+08	-0.04	0.003
ss86310901	Chr10	RFI RRBLUP	A	0.342	2377496	-0.02	0.001
ss86279757 ss86336164 ss140991997	Chr10	RFI RRBLUP	G	0.369	2403281	-0.015	0.001
	Chr10	RFI RRBLUP	G	0.442	92987293	0.01	0.005
ss86310828	Chr10	RFI RRBLUP	C	0.469	99916215	-0.012	0.005
ss86317647	Chr11	RFI RRBLUP	A	0.36	74657887	-0.014	0.001
ss86300073	Chr12	RFI RRBLUP	G	0.369	64166117	-0.021	0.007
ss86314443	Chr13	RFI RRBLUP	G	0.272	53855395	-0.025	0.006
ss105311629	Chr13	RFI RRBLUP	A	0.273	11334505	-0.027	0.005
ss86283788	Chr13	RFI RRBLUP	C	0.323	11404442	-0.039	0.003
ss86299146	Chr13	RFI RRBLUP	C	0.347	53356612	-0.016	0.006
ss141276965 ss86341012 ss86322947	Chr13	RFI RRBLUP	T	0.404	13138591	-0.019	0.003
ss86308829	Chr13	RFI RRBLUP	C	0.483	28137385	-0.003	0.005
ss86331995 ss141408536 ss86338007	Chr14	RFI RRBLUP	G	0.343	72796829	0.036	0.003
ss86283706	Chr14	RFI RRBLUP	A	0.343	67656472	-0.009	0.001
ss105250812	Chr14	RFI RRBLUP	A	0.421	72289416	0.017	0.005
ss86295552	Chr15	RFI RRBLUP	C	0.456	64898228	-0.022	0.004

ss86291074	Chr16	RFI RRBLUP	T	0.354	75069607	-0.023	0.003
ss86297871	Chr16	RFI RRBLUP	G	0.367	75470851	0.01	0.003
ss86326352	Chr16	RFI RRBLUP	T	0.434	33318456	0.029	0.004
ss86301273	Chr18	RFI RRBLUP	C	0.392	64189447	-0.027	0.002
ss86320018	Chr18	RFI RRBLUP	C	0.483	4219281	0.009	0.004
ss86291559	Chr19	RFI RRBLUP	A	0.254	11624568	0.025	0.003
ss86282748	Chr19	RFI RRBLUP	G	0.333	14371695	-0.011	0.005
ss86277601	Chr19	RFI RRBLUP	C	0.364	57387665	-0.018	0.005
ss86285204	Chr19	RFI RRBLUP	C	0.397	14738309	-0.035	0.003
ss86305968 ss86339265	Chr2	RFI RRBLUP	T	0.327	24659200	0.006	0.004
ss86334438	Chr2	RFI RRBLUP	A	0.408	1.23E+08	-0.019	0.003
ss86324899	Chr2	RFI RRBLUP	T	0.434	28387865	-0.003	0.004
ss86339405 ss86315360	Chr20	RFI RRBLUP	A	0.299	6555724	-0.02	0.003
	Chr21	RFI RRBLUP	G	0.334	42187202	-0.02	0.006
ss86294045	Chr21	RFI RRBLUP	G	0.412	45207089	-0.022	0.005
ss86284478	Chr21	RFI RRBLUP	T	0.452	47689910	-0.013	0.003
ss105256889	Chr21	RFI RRBLUP	T	0.469	44671099	-0.024	0.006
ss141991350	Chr23	RFI RRBLUP	G	0.187	30661700	0.017	0.005
ss86311521	Chr23	RFI RRBLUP	C	0.372	13526733	0.019	0.007
ss86303188	Chr23	RFI RRBLUP	T	0.434	19562079	0.01	0.001
ss86274038	Chr24	RFI RRBLUP	A	0.389	45908516	0.035	0.003
ss86321297	Chr24	RFI RRBLUP	G	0.389	48150873	0.01	0.004
ss86291523	Chr24	RFI RRBLUP	C	0.408	49258254	-0.025	0.003
ss86329651 ss86341529	Chr24	RFI RRBLUP	T	0.419	48186558	0.009	0.002
ss86326499	Chr24	RFI RRBLUP	A	0.488	33183196	0.001	0.001

ss86288518	Chr25	RFI RRBLUP	C	0.369	36525574	0.012	0.004
ss105292021	Chr25	RFI RRBLUP	A	0.425	31925031	0.008	0.002
ss86291919	Chr26	RFI RRBLUP	A	0.171	13563199	0.007	0.006
ss86278429	Chr26	RFI RRBLUP	A	0.497	7433501	-0.029	0.005
ss86274681	Chr27	RFI RRBLUP	T	0.209	38778633	0.016	0.002
ss86309215	Chr27	RFI RRBLUP	A	0.374	37915598	-0.027	0.003
ss86293700	Chr28	RFI RRBLUP	T	0.372	10275788	-0.009	0.003
ss86305683	Chr3	RFI RRBLUP	A	0.496	1.27E+08	-0.015	0.004
ss86287884	Chr4	RFI RRBLUP	T	0.333	53654310	0.007	0.004
ss86296136	Chr4	RFI RRBLUP	G	0.346	71778598	-0.015	0.004
ss140433225 ss117975221	Chr4	RFI RRBLUP	A	0.377	49699919	0.01	0.003
ss86319491	Chr4	RFI RRBLUP	T	0.42	68200162	0.018	0.005
ss86307289	Chr4	RFI RRBLUP	A	0.444	15139390	-0.021	0.003
ss86298460	Chr4	RFI RRBLUP	T	0.5	1.01E+08	0.011	0.003
ss117967712	Chr5	RFI RRBLUP	C	0.398	64455406	0.007	0.004
ss117968730 ss105291872	Chr6	RFI RRBLUP	A	0.276	38756335	-0.008	0.003
ss105307554 ss117968245	Chr6	RFI RRBLUP	A	0.414	37963147	0.014	0.006
ss86296895	Chr6	RFI RRBLUP	T	0.442	20609814	0.028	0.005
ss140641941 ss117968124 ss105291235	Chr6	RFI RRBLUP	C	0.458	41373555	-0.002	0.005
ss140705000 ss86289221 ss86341119	Chr6	RFI RRBLUP	C	0.468	1.13E+08	-0.021	0.004
ss86318987	Chr6	RFI RRBLUP	A	0.475	29162222	-0.021	0.002
ss86296735	Chr7	RFI RRBLUP	A	0.44	90661452	-0.004	0.004
ss86311845 ss86338661	Chr7	RFI RRBLUP	T	0.5	94060138	0.014	0.007
ss86335482 ss86314126	Chr8	RFI RRBLUP	A	0.411	1.05E+08	0.012	0.005
ss86285282	Chr8	RFI RRBLUP	T	0.446	65785346	0.019	0.004

ss86312018	Chr8	RFI RRBLUP	A	0.48	53765346	0.025	0.002
ss86288121	Chr9	RFI RRBLUP	T	0.339	45590253	0.022	0.006
ss86339067 ss86292090	Chr9	RFI RRBLUP	T	0.391	8132199	0.017	0.004
ss86288579	ChrUn	RFI RRBLUP	A	0.127	190955	0.03	0.007
ss117968619	ChrUn	RFI RRBLUP	A	0.493	645904	-0.019	0.003

[‡]Trait units are kg/d for ADG and DMI and kg DM/d for RFI. Trait units are kg/d for ADG and DMI and kg DM/d for RFI. SNPID - NCBI rs/ss SNP ID, some SNPs have multiple predicted IDs based on their sequence similarities to multiple submissions in the NCBI database; [†]These SNPs have no rs/ss SNP ID; BTA – Chromosome; Estimate – Allele substitution effect; Position – Chromosomal position (bp); Freq – Minor allele frequency; SE – standard error.

Appendix 1: Table 3. Names, chromosomal locations, minor allele frequencies and allele substitution effects for SNPs used to build marker panels using BayesB (Chapter 4) method.

SNPID	BTA	Trait	Minor Allele	Freq	Position	‡Estimate	SE
rs43699555	Chr12	ADG	C	0.450	52690850	0.037	0.002
rs43692387	Chr12	ADG	G	0.296	10051336	0.020	0.008
rs43679745	Chr28	ADG	G	0.346	3327704	0.026	0.008
rs43671345	Chr11	ADG	C	0.490	23187875	0.023	0.005
rs43657649	Chr11	ADG	T	0.282	8262880	-0.031	0.006
rs43514144	Chr7	ADG	C	0.349	36645610	-0.019	0.008
rs43457984	Chr6	ADG	T	0.255	44870027	-0.028	0.003
rs43454260	Chr6	ADG	T	0.475	4594143	-0.009	0.005
rs43405710	Chr4	ADG	C	0.165	80106017	0.012	0.007
rs43343756	Chr3	ADG	T	0.058	80317931	-0.019	0.008
rs43338539	Chr6	ADG	C	0.448	89838827	0.024	0.004
rs43315236	Chr2	ADG	T	0.242	1.39E+08	-0.013	0.002

rs43293349	Chr2	ADG	A	0.213	21301376	-0.015	0.007
rs43263928	Chr1	ADG	T	0.198	1.25E+08	0.035	0.008
rs43210840	Chr1	ADG	T	0.363	5395581	0.006	0.006
rs43155744	Chr20	ADG	A	0.105	52142008	-0.048	0.011
rs42995154	Chr22	ADG	G	0.286	9190090	0.021	0.009
rs42940694	Chr14	ADG	C	0.172	17780218	-0.017	0.010
rs42919109	Chr4	ADG	C	0.424	1.18E+08	-0.019	0.010
rs42821712	Chr15	ADG	A	0.194	73429015	0.023	0.008
rs42779999	Chr14	ADG	T	0.173	55992026	-0.023	0.005
rs42724681	Chr4	ADG	T	0.051	37908643	-0.020	0.010
rs42682890	Chr3	ADG	T	0.152	1.21E+08	-0.021	0.008
rs42623264	Chr7	ADG	T	0.466	2030863	0.033	0.007
rs42571431	Chr16	ADG	T	0.441	8565508	0.009	0.006
rs42555873	Chr6	ADG	G	0.426	93850919	0.023	0.004
rs42553298	Chr26	ADG	A	0.398	29806662	-0.019	0.009
rs42463478	Chr26	ADG	G	0.365	31980788	0.008	0.007

rs42454677	Chr4	ADG	A	0.093	37617190	-0.028	0.011
rs42430657	Chr2	ADG	T	0.062	1.13E+08	0.045	0.005
rs42409733	Chr17	ADG	G	0.187	43903430	-0.015	0.005
rs42384304	Chr1	ADG	G	0.316	1.43E+08	-0.006	0.004
rs42345023	Chr4	ADG	T	0.161	26787861	0.006	0.002
rs42331193	Chr15	ADG	G	0.242	61202071	0.019	0.005
rs42322946	Chr1	ADG	A	0.339	1.12E+08	-0.011	0.009
rs42287574	Chr7	ADG	C	0.400	31326395	-0.027	0.004
rs42243754	Chr20	ADG	T	0.383	13445531	0.012	0.008
rs42214703	Chr11	ADG	A	0.230	33877081	0.006	0.009
rs42149900	Chr28	ADG	A	0.423	42772804	-0.008	0.005
rs42136181	Chr28	ADG	T	0.469	13976932	-0.006	0.003
rs42096848	Chr26	ADG	T	0.084	33442529	-0.012	0.006
rs42078604	Chr10	ADG	A	0.079	27431249	-0.004	0.011
rs42036451	Chr23	ADG	A	0.412	51829563	-0.025	0.003
rs41974043	Chr21	ADG	T	0.291	22950530	0.001	0.007

rs41931717	Chr20	ADG	G	0.495	6776038	-0.029	0.008
rs41929051	Chr19	ADG	A	0.305	58330995	0.004	0.005
rs41847776	Chr17	ADG	G	0.230	66994795	0.012	0.006
rs41833066	Chr17	ADG	T	0.052	2341971	-0.007	0.016
rs41772088	Chr15	ADG	T	0.319	54045333	0.013	0.006
rs41767926	Chr15	ADG	T	0.266	47461242	-0.032	0.005
rs41742877	Chr14	ADG	A	0.079	45009927	0.019	0.006
rs41707481	Chr13	ADG	C	0.123	71746495	0.012	0.005
rs41681356	Chr12	ADG	C	0.371	84229314	0.058	0.007
rs41673273	Chr12	ADG	A	0.128	66147671	-0.012	0.013
rs41667026	Chr12	ADG	A	0.396	66650688	-0.005	0.003
rs41666366	Chr14	ADG	C	0.330	39940208	0.009	0.002
rs41665465	Chr9	ADG	C	0.209	88701211	0.001	0.009
rs41664019	Chr2	ADG	A	0.190	84004688	-0.001	0.004
rs41663389	Chr6	ADG	A	0.388	574157	0.020	0.007
rs41658480	Chr6	ADG	G	0.433	54328469	-0.041	0.007

rs41656301	Chr5	ADG	T	0.351	12059218	-0.027	0.008
rs41651635	Chr4	ADG	C	0.469	21807442	0.022	0.005
rs41650870	Chr5	ADG	C	0.320	4008641	0.015	0.004
rs41642440	Chr22	ADG	G	0.454	28291985	0.013	0.004
rs41638872	Chr1	ADG	G	0.279	6410343	-0.024	0.006
rs41630141	Chr19	ADG	G	0.111	3388338	0.002	0.009
rs41628655	Chr2	ADG	G	0.495	11060396	0.014	0.004
rs41621351	Chr6	ADG	T	0.417	23283248	-0.033	0.008
rs41619612	Chr20	ADG	T	0.303	12990038	-0.020	0.004
rs41617949	Chr16	ADG	A	0.392	4594441	-0.033	0.008
rs41615193	Chr17	ADG	C	0.128	38879124	0.015	0.011
rs41613877	Chr1	ADG	C	0.153	54386907	0.009	0.005
rs41612879	Chr11	ADG	A	0.354	73554365	-0.014	0.003
rs41607284	Chr19	ADG	A	0.262	36872529	-0.026	0.008
rs41606992	Chr7	ADG	G	0.166	44983241	0.001	0.007
rs41603577	Chr1	ADG	A	0.174	6914655	-0.007	0.011

rs41597632	Chr10	ADG	C	0.189	62466743	-0.015	0.010
rs41596552	Chr16	ADG	A	0.282	8482725	-0.028	0.011
rs41592540	Chr3	ADG	A	0.460	89047394	0.008	0.009
rs41591478	Chr4	ADG	A	0.071	83032965	-0.024	0.016
rs41589985	Chr6	ADG	A	0.244	1.05E+08	-0.023	0.004
rs41588730	Chr4	ADG	G	0.152	15919194	0.007	0.006
rs41585993	Chr22	ADG	A	0.161	57400935	-0.026	0.003
rs41581215	Chr18	ADG	C	0.350	41024459	-0.026	0.005
rs41579865	Chr2	ADG	G	0.227	1.24E+08	-0.001	0.006
rs41579094	Chr1	ADG	T	0.216	72224767	0.010	0.010
rs41578721	Chr1	ADG	C	0.490	1.08E+08	0.016	0.004
rs41578313	Chr2	ADG	A	0.473	1.18E+08	-0.043	0.005
rs41578200	Chr1	ADG	G	0.107	1.22E+08	-0.042	0.007
rs41575037	Chr14	ADG	A	0.123	14806128	-0.022	0.008
rs41574019	Chr1	ADG	T	0.172	55206940	-0.025	0.008
rs41573413	Chr9	ADG	G	0.363	7324515	0.031	0.003

rs41571503	Chr5	ADG	T	0.411	4627083	0.014	0.003
rs41571293	Chr2	ADG	G	0.145	13295994	-0.023	0.008
rs41569794	Chr4	ADG	A	0.348	74993512	0.024	0.006
rs41566876	Chr15	ADG	G	0.194	50542101	0.005	0.007
rs41255638	Chr2	ADG	G	0.200	7744685	-0.053	0.005
rs29026610	Chr27	ADG	G	0.047	36843395	0.021	0.014
rs29024165	Chr1	ADG	A	0.220	8748046	0.010	0.007
rs29023646	Chr21	ADG	A	0.376	2637648	-0.010	0.004
rs29022416	Chr28	ADG	A	0.123	1653077	0.005	0.013
rs29021604	Chr25	ADG	G	0.310	23490959	0.013	0.005
rs29019899	Chr10	ADG	A	0.422	52197725	0.003	0.009
rs29019237	Chr11	ADG	C	0.441	83712430	-0.013	0.006
rs29018725	Chr5	ADG	T	0.431	1.19E+08	0.002	0.005
rs29018202	Chr5	ADG	A	0.266	88210499	-0.011	0.005
rs29013548	Chr6	ADG	T	0.207	56074790	-0.022	0.006
rs29012951	Chr3	ADG	T	0.195	65181703	-0.025	0.006

rs29010006	Chr12	ADG	T	0.437	63065550	-0.019	0.008
ss105235969	Chr14	ADG	C	0.284	4497878	-0.029	0.007
ss105238445	Chr1	ADG	A	0.377	40407178	0.001	0.003
ss105246072	Chr16	ADG	A	0.493	11770065	0.029	0.004
ss105256273	Chr24	ADG	T	0.291	26502604	-0.029	0.004
ss105261392	Chr2	ADG	C	0.079	31965973	-0.038	0.008
ss105301297 ss117968486	Chr6	ADG	A	0.143	54118747	-0.048	0.009
ss105307554 ss117968245	Chr6	ADG	A	0.414	37963147	-0.034	0.009
ss117962901	Chr15	ADG	T	0.127	77605914	-0.031	0.011
ss117969528	Chr9	ADG	A	0.394	88157050	0.024	0.007
ss117972668	Chr20	ADG	A	0.145	66278762	-0.035	0.005
ss140599049	Chr5	ADG	C	0.464	1.19E+08	0.024	0.008
ss140894649 ss86333395 ss86335572	Chr8	ADG	G	0.426	1.09E+08	-0.012	0.009
ss140965634 ss86328186 ss86336072	Chr9	ADG	G	0.407	82757568	-0.048	0.004
ss141518308	Chr16	ADG	A	0.429	23342316	-0.003	0.009
ss141661973 ss86306109 ss86337121	Chr18	ADG	C	0.321	24685411	0.028	0.011

ss86273787	Chr11	ADG	C	0.268	95214925	-0.018	0.008
ss86274256	Chr4	ADG	A	0.106	1.21E+08	0.018	0.010
ss86274328	Chr3	ADG	A	0.467	53882751	0.000	0.005
ss86274638	Chr22	ADG	T	0.463	14183041	-0.040	0.005
ss86274798	Chr3	ADG	T	0.119	11315999	0.005	0.007
ss86280264	Chr8	ADG	G	0.336	355812	-0.009	0.001
ss86284643	Chr17	ADG	A	0.180	72324382	0.024	0.009
ss86285720	Chr16	ADG	C	0.415	28736622	0.007	0.004
ss86287837 ss86339738	Chr13	ADG	G	0.383	74225430	0.015	0.008
ss86287995	Chr7	ADG	T	0.143	25676801	-0.032	0.009
ss86288744	Chr8	ADG	A	0.115	21337906	0.041	0.012
ss86289117	Chr6	ADG	A	0.175	32765343	-0.011	0.003
ss86289359	Chr26	ADG	A	0.081	44210363	0.019	0.015
ss86289749	Chr15	ADG	T	0.435	43818027	0.020	0.006
ss86290205	Chr3	ADG	T	0.075	8198278	0.001	0.005
ss86290901	Chr8	ADG	C	0.106	8154063	-0.006	0.004

ss86292117	Chr8	ADG	G	0.117	11432925	0.003	0.006
ss86293022	Chr5	ADG	T	0.102	70326991	-0.012	0.007
ss86293616	Chr21	ADG	A	0.245	58864403	0.013	0.002
ss86294356	Chr3	ADG	T	0.272	1.05E+08	0.015	0.010
ss86294473	Chr28	ADG	C	0.180	7271662	0.012	0.003
ss86295170	Chr6	ADG	C	0.165	1.09E+08	-0.013	0.016
ss86295518	Chr28	ADG	G	0.104	22361775	0.022	0.012
ss86297248	Chr4	ADG	C	0.157	1.18E+08	-0.010	0.008
ss86299430	Chr3	ADG	G	0.258	1.1E+08	0.011	0.001
ss86300519	Chr2	ADG	A	0.333	1.34E+08	-0.010	0.008
ss86303886	Chr11	ADG	T	0.418	59157410	0.023	0.004
ss86304300	Chr4	ADG	G	0.411	1.21E+08	-0.046	0.003
ss86305525	Chr13	ADG	G	0.280	74965592	0.017	0.004
ss86306989	ChrUn	ADG	C	0.129	228689	-0.023	0.005
ss86307635	Chr25	ADG	C	0.193	2219666	0.039	0.007
ss86308454	Chr8	ADG	G	0.160	1.11E+08	-0.035	0.005

ss86308458	Chr19	ADG	C	0.152	55940162	-0.020	0.007
ss86308974	Chr21	ADG	A	0.468	34686928	-0.021	0.005
ss86310143	Chr21	ADG	T	0.346	13421297	0.024	0.003
ss86311196	Chr22	ADG	A	0.264	28500663	0.031	0.011
ss86311308	Chr21	ADG	C	0.084	18864883	-0.012	0.009
ss86311376	Chr6	ADG	T	0.195	43378454	-0.017	0.013
ss86311555	Chr17	ADG	A	0.215	65658383	0.005	0.004
ss86312849	Chr21	ADG	G	0.415	67306717	-0.048	0.005
ss86313014	Chr9	ADG	C	0.124	55121684	0.028	0.008
ss86314403	Chr24	ADG	T	0.253	61421413	0.001	0.006
ss86314795	Chr18	ADG	T	0.121	62373058	-0.063	0.003
ss86315800 ss86341659	Chr7	ADG	T	0.406	88123861	0.011	0.009
ss86316677	Chr18	ADG	C	0.227	558096	-0.001	0.009
ss86316707	Chr8	ADG	T	0.446	45275580	-0.016	0.005
ss86318054	Chr8	ADG	T	0.371	71955582	0.008	0.005
ss86320010 ss86339925	Chr19	ADG	C	0.292	22061928	0.000	0.003

ss86320135	Chr11	ADG	C	0.489	1.1E+08	-0.050	0.006
ss86320583	Chr13	ADG	C	0.399	72616346	0.010	0.003
ss86321151	Chr8	ADG	C	0.100	87368038	-0.059	0.006
ss86321326	Chr2	ADG	G	0.207	1.33E+08	-0.006	0.005
ss86321848	Chr25	ADG	C	0.201	31572104	0.035	0.008
ss86324718	Chr17	ADG	A	0.466	67152339	0.029	0.005
ss86325159	Chr24	ADG	T	0.092	24519728	0.014	0.008
ss86325467	ChrUn	ADG	C	0.471	775474	-0.014	0.005
ss86326514	Chr1	ADG	T	0.431	6747617	-0.018	0.008
ss86326932	Chr21	ADG	T	0.294	50811545	0.011	0.003
ss86327362	Chr13	ADG	C	0.164	20884653	-0.009	0.012
ss86328721	ChrUn	ADG	A	0.270	68578	0.015	0.006
ss86329969 ss86341019	Chr22	ADG	C	0.450	9060236	-0.020	0.006
ss86331488	Chr5	ADG	G	0.375	79052209	0.003	0.007
ss86332609	Chr11	ADG	A	0.108	1.04E+08	0.040	0.009
ss86335492	Chr24	ADG	T	0.127	64469669	0.011	0.007

ss86335494 ss86324637	Chr14	ADG	G	0.283	60480179	-0.020	0.004
ss86339066	Chr1	ADG	C	0.477	77994925	0.033	0.003
ss86339080 ss86321562	Chr3	ADG	C	0.363	35899934	0.008	0.006
ss86339282 ss86279966	Chr4	ADG	A	0.167	15942260	0.055	0.012
ss86339613	Chr9	ADG	G	0.159	2757960	0.005	0.016
ss86340327	Chr1	ADG	G	0.154	1.44E+08	0.005	0.004
ss86340488 ss86290533	Chr24	ADG	G	0.294	13180301	-0.014	0.006
ss86340544	Chr1	ADG	A	0.246	1.2E+08	0.008	0.007
ss86341174 ss86312678	Chr22	ADG	C	0.253	55890005	-0.039	0.004
ss86341347	Chr20	ADG	T	0.231	6305174	-0.014	0.007
ss86341614 ss140240646 ss86335177	Chr2	ADG	A	0.255	94230524	-0.003	0.005
BTA-80441-no-rs	Chr7	ADG	G	0.447	1.03E+08	-0.004	0.004
rs43736191	Chr14	DMI	C	0.088	58481107	0.031	0.008
rs43732439	ChrUn	DMI	G	0.305	572298	0.065	0.008
rs43708441	Chr15	DMI	T	0.392	19129877	0.026	0.011
rs43707936	Chr3	DMI	G	0.403	4233402	0.033	0.004

rs43656295	Chr11	DMI	C	0.415	1380874	0.016	0.006
rs43650985	Chr10	DMI	T	0.384	93464033	0.023	0.008
rs43646790	Chr10	DMI	T	0.395	91160685	0.046	0.013
rs43632233	Chr10	DMI	G	0.456	50697851	0.000	0.006
rs43631525	Chr10	DMI	A	0.226	55618423	0.043	0.018
rs43609676	Chr9	DMI	A	0.386	92020866	0.064	0.012
rs43551782	Chr8	DMI	A	0.299	53829682	0.006	0.010
rs43538446	Chr14	DMI	A	0.343	50317494	0.021	0.007
rs43486149	Chr6	DMI	T	0.384	1.1E+08	-0.023	0.009
rs43460584	Chr6	DMI	A	0.364	41462782	-0.021	0.017
rs43458937	Chr6	DMI	C	0.428	39794334	-0.200	0.040
rs43448222	Chr6	DMI	A	0.062	6904027	0.010	0.003
rs43417449	ChrUn	DMI	T	0.161	57507	0.004	0.008
rs43404908	Chr4	DMI	C	0.427	78161176	0.100	0.008
rs43389761	Chr4	DMI	G	0.277	48969929	-0.030	0.012
rs43363397	Chr3	DMI	C	0.044	1.14E+08	0.026	0.010

rs43351271	Chr3	DMI	G	0.181	90315653	0.049	0.016
rs43347342	Chr3	DMI	A	0.481	74781903	0.006	0.006
rs43333482	Chr27	DMI	A	0.170	25339303	0.018	0.011
rs43266806	Chr1	DMI	G	0.432	1.14E+08	0.000	0.010
rs43231384	Chr1	DMI	G	0.411	43053682	-0.026	0.014
rs43230383	Chr7	DMI	A	0.059	46197724	0.008	0.016
rs43192154	Chr24	DMI	T	0.155	8249290	0.013	0.012
rs43138491	Chr14	DMI	C	0.405	56769638	0.043	0.007
rs43068911	Chr24	DMI	G	0.486	1749526	-0.026	0.008
rs43066203	Chr1	DMI	T	0.268	1.43E+08	0.047	0.013
rs42976268	Chr15	DMI	T	0.495	68999619	0.010	0.009
rs42935030	Chr11	DMI	G	0.244	3507795	-0.035	0.018
rs42931535	Chr26	DMI	C	0.418	41451573	0.049	0.012
rs42846536	Chr26	DMI	G	0.366	1201611	0.051	0.005
rs42843551	Chr18	DMI	C	0.394	56812287	0.027	0.014
rs42822981	Chr29	DMI	T	0.391	43183857	-0.010	0.009

rs42804772	Chr15	DMI	A	0.434	4130261	0.017	0.011
rs42761380	Chr24	DMI	G	0.453	29658911	-0.045	0.013
rs42657029	Chr3	DMI	C	0.235	5270356	-0.043	0.010
rs42598849	Chr22	DMI	G	0.495	43581839	0.036	0.010
rs42581544	Chr6	DMI	T	0.258	92434963	-0.030	0.019
rs42436495	Chr6	DMI	G	0.499	65770568	0.017	0.010
rs42413754	Chr10	DMI	C	0.340	38806659	0.021	0.008
rs42410387	Chr6	DMI	A	0.334	1.19E+08	0.067	0.027
rs42385835	Chr17	DMI	A	0.117	33241876	-0.032	0.020
rs42299674	Chr13	DMI	G	0.198	1024645	-0.066	0.030
rs42255170	ChrUn	DMI	G	0.408	98208	-0.067	0.021
rs42244558	Chr5	DMI	A	0.095	1293420	-0.066	0.012
rs42186402	Chr29	DMI	T	0.487	42112878	-0.010	0.012
rs42186052	Chr29	DMI	T	0.272	39044755	0.073	0.012
rs42142693	Chr28	DMI	G	0.242	24107627	0.066	0.010
rs42096562	Chr26	DMI	A	0.076	26325359	-0.050	0.029

rs42095651	Chr26	DMI	A	0.299	31528736	-0.035	0.009
rs42069458	Chr25	DMI	T	0.091	33414127	0.001	0.004
rs42029905	Chr23	DMI	A	0.444	45588817	-0.078	0.012
rs42002618	Chr22	DMI	A	0.306	22393278	-0.063	0.016
rs41999849	Chr22	DMI	G	0.420	14313538	0.034	0.015
rs41981646	Chr21	DMI	G	0.492	40782607	-0.030	0.012
rs41979341	Chr21	DMI	T	0.346	38142840	0.070	0.022
rs41749553	Chr15	DMI	T	0.470	6805538	-0.055	0.009
rs41712508	Chr13	DMI	A	0.374	78203199	0.038	0.007
rs41698238	Chr13	DMI	C	0.278	46655289	-0.010	0.010
rs41669831	Chr24	DMI	T	0.103	41411977	-0.029	0.012
rs41663665	Chr16	DMI	G	0.172	26984024	0.000	0.008
rs41658128	Chr7	DMI	G	0.337	11212022	-0.052	0.014
rs41657913	Chr11	DMI	G	0.464	34105348	-0.032	0.011
rs41654781	Chr5	DMI	T	0.275	26118923	0.052	0.018
rs41654591	Chr10	DMI	A	0.325	91420638	-0.094	0.009

rs41642566	Chr20	DMI	T	0.435	65280292	0.037	0.012
rs41641550	Chr22	DMI	T	0.453	25108520	-0.028	0.008
rs41641502	Chr19	DMI	A	0.391	14541593	-0.123	0.007
rs41640891	Chr22	DMI	T	0.282	22353504	0.010	0.005
rs41634228	Chr16	DMI	A	0.365	71332974	-0.092	0.013
rs41634115	Chr13	DMI	A	0.163	11858077	0.071	0.010
rs41634033	Chr13	DMI	T	0.495	77245638	-0.011	0.004
rs41628306	Chr13	DMI	C	0.262	39406173	0.092	0.016
rs41624066	Chr13	DMI	C	0.268	70718467	-0.037	0.010
rs41619108	Chr17	DMI	G	0.195	39291020	-0.043	0.014
rs41617449	Chr22	DMI	A	0.416	8025065	-0.007	0.005
rs41616927	Chr20	DMI	G	0.169	29368688	-0.043	0.009
rs41614172	Chr11	DMI	A	0.085	92304437	-0.037	0.008
rs41603148	Chr14	DMI	G	0.386	61543942	-0.028	0.021
rs41593516	Chr26	DMI	C	0.241	39437807	-0.164	0.029
rs41591637	Chr14	DMI	G	0.295	52474088	-0.088	0.012

rs41586807	Chr28	DMI	C	0.224	13044356	-0.086	0.013
rs41585925	Chr3	DMI	C	0.383	1.19E+08	0.023	0.005
rs41584106	Chr26	DMI	A	0.291	12208280	0.020	0.008
rs41583332	Chr21	DMI	A	0.272	24520032	0.055	0.012
rs41579376	Chr1	DMI	A	0.236	71357245	0.000	0.004
rs41576460	Chr15	DMI	T	0.293	69954719	-0.073	0.012
rs41573907	Chr8	DMI	A	0.132	5056570	0.032	0.007
rs41573752	Chr15	DMI	A	0.426	61095348	0.066	0.008
rs41573352	Chr2	DMI	T	0.184	96505129	0.010	0.013
rs41573085	Chr8	DMI	T	0.450	27651741	-0.053	0.021
rs41571909	Chr19	DMI	T	0.159	29774305	-0.061	0.012
rs41567895	Chr12	DMI	T	0.457	42177429	-0.008	0.008
rs41566731	Chr9	DMI	C	0.308	71767226	0.073	0.024
rs41566668	Chr6	DMI	A	0.242	1.13E+08	-0.011	0.008
rs41257771	Chr1	DMI	A	0.099	95616571	-0.006	0.014
rs41255303	Chr7	DMI	T	0.310	11088641	-0.086	0.016

rs29027617	Chr20	DMI	A	0.117	25738312	0.029	0.022
rs29027283	Chr19	DMI	C	0.489	22465360	-0.047	0.026
rs29026478	Chr10	DMI	A	0.440	49890208	-0.059	0.010
rs29026129	Chr11	DMI	A	0.500	5205392	-0.003	0.010
rs29026096	Chr17	DMI	T	0.466	7042994	0.019	0.009
rs29024751	Chr9	DMI	A	0.403	2289236	-0.042	0.009
rs29024600	Chr14	DMI	T	0.093	35796168	0.003	0.013
rs29022067	Chr17	DMI	G	0.372	31309718	-0.037	0.014
rs29021346	Chr18	DMI	A	0.238	23275745	-0.021	0.004
rs29020548	Chr25	DMI	A	0.279	39809717	0.026	0.010
rs29019654	Chr3	DMI	C	0.168	86441965	0.006	0.010
rs29014495	Chr24	DMI	T	0.499	33101881	0.054	0.011
rs29014373	Chr23	DMI	G	0.362	22188607	-0.042	0.010
rs29013548	Chr6	DMI	T	0.207	56074790	0.043	0.012
rs29012925	Chr5	DMI	C	0.416	1.18E+08	-0.087	0.008
rs29012211	Chr4	DMI	C	0.223	65611733	0.060	0.007

ss105238867	Chr1	DMI	C	0.082	1.49E+08	-0.032	0.011
ss105241200	Chr1	DMI	T	0.282	29675490	0.047	0.008
ss105241761	Chr11	DMI	A	0.212	71221315	-0.033	0.008
ss105255461	Chr20	DMI	A	0.176	30128561	-0.042	0.010
ss105263670	Chr16	DMI	T	0.171	3324217	-0.009	0.009
ss105265024	Chr25	DMI	C	0.465	12107898	0.047	0.011
ss105268923	Chr25	DMI	T	0.342	38570263	-0.067	0.013
ss105311575 ss117968559	Chr6	DMI	G	0.414	40151936	0.031	0.014
ss117962856	Chr3	DMI	T	0.380	22068686	0.015	0.016
ss117963675	Chr3	DMI	G	0.435	1758975	-0.020	0.013
ss117966959	Chr3	DMI	C	0.213	76469248	-0.050	0.006
ss117968721	Chr6	DMI	T	0.458	33761327	-0.026	0.006
ss117971272	Chr14	DMI	G	0.400	25031801	0.005	0.015
ss117972526	Chr19	DMI	T	0.466	11338007	0.017	0.006
ss140253345 ss86328775 ss86339957	Chr2	DMI	A	0.348	1.09E+08	-0.010	0.004
ss142238292 ss86304589 ss86340705	Chr28	DMI	T	0.224	21591645	0.107	0.042

ss86274681	Chr27	DMI	T	0.209	38778633	0.034	0.012
ss86274954	Chr11	DMI	A	0.459	83979734	-0.038	0.011
ss86284580	Chr25	DMI	T	0.288	40999193	-0.048	0.015
ss86284631	Chr9	DMI	T	0.484	7546236	0.104	0.019
ss86285509	Chr17	DMI	T	0.168	12274582	0.019	0.012
ss86285886	Chr21	DMI	A	0.338	61168707	0.065	0.005
ss86286498	Chr25	DMI	T	0.485	31668919	-0.094	0.022
ss86287003	ChrUn	DMI	C	0.192	34356	-0.044	0.012
ss86287290	Chr29	DMI	T	0.154	50032867	-0.003	0.011
ss86287613	Chr21	DMI	G	0.481	34754177	-0.030	0.017
ss86289929	Chr21	DMI	G	0.489	18472447	-0.023	0.009
ss86290858	Chr1	DMI	T	0.283	1.3E+08	0.035	0.006
ss86291231	Chr15	DMI	T	0.208	73366906	0.025	0.017
ss86292046	Chr6	DMI	C	0.295	1.21E+08	-0.044	0.012
ss86293562	Chr1	DMI	G	0.200	24797856	0.001	0.011
ss86293796	Chr5	DMI	A	0.227	1.16E+08	0.049	0.016

ss86295351	Chr15	DMI	G	0.310	61349657	-0.045	0.010
ss86295367	Chr28	DMI	A	0.416	1185260	-0.040	0.014
ss86295521	Chr1	DMI	G	0.410	1.34E+08	-0.037	0.013
ss86295570	Chr12	DMI	T	0.296	11485922	-0.026	0.009
ss86296197	Chr10	DMI	A	0.365	67569885	-0.002	0.010
ss86296210	Chr14	DMI	C	0.489	45681753	0.055	0.012
ss86297114	Chr19	DMI	G	0.458	58447837	-0.012	0.006
ss86297371 ss86335612	Chr10	DMI	T	0.382	9801558	0.068	0.017
ss86297977	Chr19	DMI	A	0.156	56094794	-0.001	0.007
ss86298219	Chr12	DMI	C	0.457	37801938	0.068	0.014
ss86299499	Chr21	DMI	T	0.388	2594377	-0.049	0.016
ss86300695	Chr3	DMI	T	0.371	1.15E+08	-0.035	0.006
ss86300698	Chr14	DMI	C	0.259	63626440	0.022	0.012
ss86301441	Chr2	DMI	T	0.486	67981464	0.029	0.006
ss86301567	Chr3	DMI	T	0.334	1.13E+08	-0.018	0.013
ss86301748	Chr10	DMI	T	0.163	89125552	-0.057	0.009

ss86304613	Chr25	DMI	G	0.322	34258184	0.033	0.007
ss86309292	Chr1	DMI	C	0.207	1.37E+08	0.028	0.013
ss86312318	Chr14	DMI	A	0.365	741867	-0.018	0.009
ss86313678 ss86338332	ChrUn	DMI	T	0.056	113374	-0.042	0.008
ss86314027	Chr3	DMI	C	0.412	1.19E+08	-0.027	0.014
ss86314743	Chr14	DMI	A	0.212	12749386	-0.037	0.013
ss86315831	Chr29	DMI	G	0.159	7301394	0.019	0.007
ss86315942	Chr20	DMI	G	0.492	18542320	0.074	0.011
ss86316937	Chr21	DMI	G	0.264	65869305	-0.051	0.018
ss86317533	Chr7	DMI	T	0.335	39673757	0.022	0.008
ss86318343	Chr3	DMI	A	0.320	1.16E+08	0.006	0.006
ss86319906	Chr11	DMI	T	0.495	98890768	0.022	0.008
ss86320161	Chr21	DMI	A	0.206	60785856	0.017	0.010
ss86322196	Chr19	DMI	A	0.343	12105345	0.043	0.013
ss86322201	Chr1	DMI	C	0.419	1.47E+08	-0.137	0.017
ss86322344	Chr10	DMI	G	0.067	29755801	-0.028	0.026

ss86325151	Chr3	DMI	G	0.082	1.09E+08	0.032	0.007
ss86325370	Chr16	DMI	T	0.186	40159031	-0.019	0.022
ss86325390	Chr21	DMI	A	0.363	65440924	0.019	0.016
ss86325631	Chr10	DMI	C	0.371	13666563	0.059	0.033
ss86326539	Chr2	DMI	C	0.197	63860450	-0.029	0.022
ss86328134	Chr10	DMI	A	0.272	7588559	-0.085	0.016
ss86333122	ChrUn	DMI	G	0.298	154211	-0.021	0.012
ss86333925	Chr11	DMI	C	0.427	99663236	0.077	0.016
ss86334496	Chr11	DMI	G	0.449	3030076	0.012	0.011
ss86335118	Chr6	DMI	T	0.268	6995395	0.030	0.013
ss86335942 ss86294357 ss141839036	Chr21	DMI	G	0.418	989878	-0.037	0.007
ss86336579 ss141275756 ss86321211	Chr13	DMI	G	0.298	11654669	-0.013	0.010
ss86337384 ss86319462	Chr10	DMI	C	0.220	16211358	-0.103	0.013
ss86338759 ss86333470	Chr2	DMI	G	0.478	77544443	-0.001	0.007
ss86339682 ss86284681 ss141524398	Chr16	DMI	A	0.176	29943324	0.023	0.012
ss86339980 ss86289656	Chr5	DMI	A	0.146	25667586	-0.076	0.016

ss86340101 ss86327218	Chr26	DMI	A	0.223	4791900	0.054	0.012
ss86340188	Chr7	DMI	C	0.226	1.06E+08	-0.025	0.009
ss86340914	Chr12	DMI	T	0.342	10388746	-0.040	0.020
BTA-67183-no-rs	Chr10	DMI	C	0.298	41694453	-0.024	0.015
rs43703976	Chr19	RFI	A	0.180	20361224	-0.018	0.014
rs43604391	Chr9	RFI	C	0.440	52475302	0.021	0.018
rs43604365	Chr9	RFI	C	0.440	52502821	0.032	0.008
rs43599152	Chr9	RFI	C	0.207	57318410	0.014	0.008
rs43593442	Chr9	RFI	C	0.147	23270144	0.001	0.011
rs43554522	Chr8	RFI	T	0.498	47162094	-0.033	0.010
rs43503728	Chr7	RFI	G	0.168	18276028	-0.061	0.016
rs43486526	Chr6	RFI	A	0.231	1.18E+08	0.054	0.021
rs43458640	Chr6	RFI	C	0.196	39159587	-0.033	0.010
rs43420802	Chr4	RFI	A	0.284	1.18E+08	0.024	0.006
rs43389761	Chr4	RFI	G	0.277	48969929	-0.010	0.009
rs43389711	Chr4	RFI	A	0.407	46392808	0.007	0.013

rs43351692	Chr3	RFI	T	0.206	92572144	0.032	0.014
rs43316439	Chr12	RFI	T	0.432	7979158	-0.008	0.008
rs43258007	ChrUn	RFI	G	0.408	1066036	0.031	0.008
rs43242760	Chr1	RFI	A	0.444	63134248	0.022	0.007
rs43233558	Chr1	RFI	C	0.383	52217228	0.025	0.009
rs43099931	Chr29	RFI	C	0.306	20184591	-0.020	0.016
rs43055872	Chr19	RFI	A	0.116	39320627	-0.010	0.012
rs43046262	Chr21	RFI	A	0.158	49891547	0.051	0.008
rs42934127	Chr6	RFI	G	0.168	50149885	-0.026	0.017
rs42803833	Chr4	RFI	A	0.054	82708005	-0.059	0.014
rs42771121	Chr13	RFI	G	0.421	51699788	-0.051	0.016
rs42756258	Chr6	RFI	G	0.342	22112069	0.016	0.010
rs42711594	Chr8	RFI	A	0.380	82809414	-0.032	0.015
rs42619441	Chr7	RFI	T	0.105	39932580	-0.010	0.015
rs42568101	Chr9	RFI	C	0.236	31783414	0.002	0.009
rs42468541	Chr24	RFI	G	0.195	37456528	-0.019	0.014

rs42431948	Chr2	RFI	T	0.311	1.13E+08	0.056	0.009
rs42425010	Chr2	RFI	T	0.498	1.18E+08	0.019	0.009
rs42374771	Chr26	RFI	A	0.274	12578304	0.013	0.006
rs42369003	ChrUn	RFI	A	0.202	279239	0.015	0.014
rs42324388	Chr1	RFI	T	0.095	1.12E+08	-0.063	0.017
rs42316404	Chr17	RFI	A	0.433	8899286	0.116	0.026
rs42256240	Chr12	RFI	G	0.340	8549943	-0.064	0.018
rs42228344	Chr4	RFI	G	0.080	54932963	-0.018	0.010
rs42142693	Chr28	RFI	G	0.242	24107627	0.106	0.018
rs42093810	Chr26	RFI	G	0.190	20122895	0.094	0.013
rs42068538	Chr25	RFI	G	0.469	31892337	0.054	0.009
rs42042322	Chr24	RFI	T	0.203	3915836	-0.080	0.017
rs42005069	Chr6	RFI	G	0.467	55266545	0.016	0.016
rs41906295	Chr17	RFI	A	0.460	45764457	0.001	0.005
rs41848648	Chr17	RFI	G	0.409	66227782	-0.051	0.008
rs41800681	Chr16	RFI	T	0.250	34841192	-0.060	0.008

rs41773923	Chr15	RFI	G	0.485	56639348	-0.046	0.011
rs41767484	Chr15	RFI	A	0.205	51708727	0.049	0.015
rs41751493	Chr15	RFI	G	0.273	6708079	0.045	0.004
rs41728184	ChrUn	RFI	C	0.126	1172550	-0.048	0.014
rs41678672	Chr3	RFI	G	0.361	99728783	0.003	0.006
rs41670179	Chr7	RFI	C	0.151	79426025	-0.060	0.016
rs41663519	Chr9	RFI	C	0.437	78442558	0.026	0.018
rs41659569	Chr8	RFI	C	0.421	38510343	0.105	0.021
rs41659405	Chr1	RFI	C	0.122	39454543	-0.070	0.018
rs41655604	Chr10	RFI	A	0.142	97143918	0.016	0.013
rs41655005	Chr6	RFI	G	0.368	86434938	-0.035	0.006
rs41649876	Chr6	RFI	C	0.496	27831792	0.043	0.014
rs41647379	Chr27	RFI	A	0.049	35673921	0.069	0.017
rs41641502	Chr19	RFI	A	0.391	14541593	-0.033	0.003
rs41630820	Chr1	RFI	G	0.409	61523007	0.025	0.010
rs41630175	Chr10	RFI	G	0.321	96474580	-0.029	0.007

rs41628306	Chr13	RFI	C	0.262	39406173	0.066	0.016
rs41626174	Chr16	RFI	T	0.368	30203519	0.028	0.006
rs41621937	Chr29	RFI	C	0.454	5476041	0.042	0.011
rs41618893	Chr9	RFI	G	0.115	17693535	0.006	0.011
rs41611784	Chr7	RFI	G	0.489	54695094	-0.056	0.006
rs41604269	Chr2	RFI	A	0.210	28746310	0.021	0.009
rs41599754	Chr4	RFI	A	0.457	50360661	0.022	0.010
rs41591637	Chr14	RFI	G	0.295	52474088	-0.082	0.016
rs41589498	Chr3	RFI	T	0.177	2516633	0.115	0.016
rs41588707	Chr4	RFI	G	0.153	63995739	-0.022	0.012
rs41588503	Chr10	RFI	T	0.412	41672044	-0.033	0.015
rs41587678	Chr4	RFI	C	0.376	49069017	-0.034	0.005
rs41587222	Chr23	RFI	G	0.496	22815029	-0.016	0.012
rs41586992	Chr29	RFI	T	0.486	9156230	-0.032	0.002
rs41585017	Chr29	RFI	T	0.079	33632380	0.006	0.011
rs41583408	Chr21	RFI	T	0.307	35468395	0.051	0.005

rs41573624	Chr6	RFI	C	0.281	22359286	-0.041	0.009
rs41568944	Chr4	RFI	A	0.389	17446529	-0.018	0.008
rs41568388	Chr15	RFI	G	0.357	37885743	-0.013	0.005
rs41255303	Chr7	RFI	T	0.310	11088641	-0.077	0.016
rs29027600	Chr10	RFI	C	0.166	1288073	-0.058	0.008
rs29027193	Chr10	RFI	T	0.414	50600523	-0.016	0.010
rs29027007	Chr23	RFI	A	0.406	11432167	-0.043	0.013
rs29026804	Chr12	RFI	A	0.093	13588884	-0.063	0.019
rs29026607	Chr5	RFI	T	0.307	59756374	0.023	0.014
rs29025355	Chr4	RFI	A	0.177	53136031	0.002	0.011
rs29024039	Chr27	RFI	A	0.415	45906983	-0.044	0.013
rs29023017	Chr8	RFI	C	0.095	33663651	0.002	0.015
rs29022883	Chr4	RFI	A	0.293	51115714	0.015	0.014
rs29022289	Chr1	RFI	A	0.294	1.26E+08	-0.039	0.004
rs29022067	Chr17	RFI	G	0.372	31309718	-0.038	0.007
rs29020690	Chr2	RFI	G	0.194	20710301	0.022	0.009

rs29020548	Chr25	RFI	A	0.279	39809717	0.057	0.013
rs29018633	Chr2	RFI	T	0.475	38241365	0.034	0.009
rs29015935	Chr12	RFI	A	0.213	16810706	0.104	0.009
rs29011976	Chr3	RFI	C	0.467	41842787	0.032	0.004
rs29011393	Chr6	RFI	A	0.317	29139241	0.070	0.016
rs29009770	Chr4	RFI	G	0.057	52897683	0.016	0.010
ss105237713	Chr13	RFI	C	0.313	27853489	-0.006	0.011
ss105240423	Chr12	RFI	T	0.052	65687891	0.027	0.010
ss105263599	Chr24	RFI	A	0.091	56895558	-0.046	0.020
ss105275774 ss117973754	Chr25	RFI	C	0.308	32242634	-0.011	0.010
ss105296554 ss117971073 ss141343771	Chr14	RFI	T	0.336	835054	0.071	0.013
ss117969846	Chr10	RFI	C	0.308	70096968	-0.072	0.015
ss117971462 ss141351932 ss105247221	Chr14	RFI	A	0.212	7102015	0.057	0.014
ss140641916 ss117968758 ss105293497	Chr6	RFI	T	0.281	41300911	-0.011	0.014
ss140641941 ss117968124 ss105291235	Chr6	RFI	C	0.458	41373555	0.001	0.007
ss141276965 ss86341012 ss86322947	Chr13	RFI	T	0.404	13138591	-0.044	0.008

ss141654962 ss86318202 ss86337113	Chr18	RFI	G	0.304	16418383	0.034	0.005
ss86274038	Chr24	RFI	A	0.389	45908516	0.092	0.010
ss86274502	Chr11	RFI	T	0.333	64698301	0.002	0.009
ss86274681	Chr27	RFI	T	0.209	38778633	0.026	0.015
ss86274799	Chr27	RFI	T	0.434	2553132	-0.049	0.016
ss86277601	Chr19	RFI	C	0.364	57387665	-0.032	0.012
ss86278327	Chr18	RFI	A	0.402	32661190	-0.009	0.019
ss86278429	Chr26	RFI	A	0.497	7433501	-0.080	0.006
ss86282947	Chr10	RFI	T	0.208	9688343	-0.036	0.012
ss86283450	Chr6	RFI	T	0.085	93993832	-0.007	0.015
ss86283706	Chr14	RFI	A	0.343	67656472	-0.010	0.013
ss86283959	Chr2	RFI	G	0.171	33159312	0.046	0.012
ss86284635	Chr1	RFI	G	0.340	1.43E+08	0.030	0.012
ss86285204	Chr19	RFI	C	0.397	14738309	-0.104	0.007
ss86286174	Chr4	RFI	G	0.328	55361039	-0.011	0.012
ss86287003	ChrUn	RFI	C	0.192	34356	-0.041	0.012

ss86287290	Chr29	RFI	T	0.154	50032867	-0.047	0.005
ss86287613	Chr21	RFI	G	0.481	34754177	-0.026	0.015
ss86287884	Chr4	RFI	T	0.333	53654310	0.017	0.014
ss86288114	Chr23	RFI	G	0.320	22348553	-0.019	0.010
ss86288579	ChrUn	RFI	A	0.127	190955	0.096	0.042
ss86289209 ss86337363	Chr18	RFI	G	0.489	51920265	0.043	0.014
ss86289465 ss86335977	Chr3	RFI	C	0.328	1.07E+08	-0.006	0.010
ss86289800	Chr5	RFI	G	0.299	1.13E+08	0.034	0.009
ss86290591	Chr23	RFI	T	0.381	28542478	0.050	0.010
ss86290923	Chr15	RFI	T	0.053	82561727	-0.002	0.006
ss86291559	Chr19	RFI	A	0.254	11624568	0.077	0.011
ss86291696	Chr3	RFI	T	0.108	1.24E+08	0.011	0.011
ss86292530	Chr11	RFI	C	0.466	1.01E+08	-0.023	0.009
ss86293317	Chr29	RFI	T	0.140	51337489	0.013	0.004
ss86293365	Chr3	RFI	C	0.103	1.15E+08	0.020	0.004
ss86293732	Chr19	RFI	G	0.332	41582575	0.029	0.010

ss86294905	Chr4	RFI	G	0.317	10640830	0.061	0.011
ss86295428	Chr16	RFI	G	0.390	68396075	0.046	0.006
ss86295552	Chr15	RFI	C	0.456	64898228	-0.048	0.009
ss86297076	Chr25	RFI	G	0.376	5941852	-0.010	0.004
ss86297137	Chr10	RFI	C	0.224	93529041	0.040	0.010
ss86298248 ss86339367	Chr22	RFI	T	0.472	10663506	0.024	0.007
ss86298358	Chr25	RFI	C	0.402	43857883	0.056	0.017
ss86298927	Chr23	RFI	C	0.183	11372374	0.006	0.013
ss86299733	Chr2	RFI	T	0.125	1.18E+08	-0.014	0.006
ss86300073	Chr12	RFI	G	0.369	64166117	-0.037	0.014
ss86300114	Chr27	RFI	G	0.486	37207203	-0.055	0.013
ss86300928	Chr7	RFI	C	0.350	15139569	0.014	0.009
ss86301478	Chr26	RFI	T	0.123	8823038	-0.044	0.010
ss86303837	Chr8	RFI	A	0.156	51629723	-0.037	0.005
ss86304164	Chr3	RFI	A	0.051	11564218	-0.015	0.015
ss86304584 ss86341507	Chr15	RFI	A	0.253	2131573	0.020	0.009

ss86305154	Chr21	RFI	A	0.231	42880291	0.038	0.008
ss86305968 ss86339265	Chr2	RFI	T	0.327	24659200	0.030	0.017
ss86306850	Chr28	RFI	G	0.372	31975015	-0.004	0.009
ss86307289	Chr4	RFI	A	0.444	15139390	-0.074	0.014
ss86308963	Chr21	RFI	C	0.446	45390100	0.025	0.012
ss86309185	Chr11	RFI	A	0.298	63600222	0.098	0.022
ss86310186 ss141371469 ss86340738	Chr14	RFI	A	0.206	26357416	0.019	0.013
ss86310231	Chr16	RFI	A	0.383	199083	-0.053	0.017
ss86310257	Chr9	RFI	T	0.122	1.08E+08	0.018	0.005
ss86310909	Chr22	RFI	A	0.110	12615481	0.030	0.007
ss86311521	Chr23	RFI	C	0.372	13526733	0.045	0.015
ss86312018	Chr8	RFI	A	0.480	53765346	0.046	0.007
ss86312226	Chr5	RFI	A	0.207	59720693	-0.007	0.023
ss86313043	Chr7	RFI	A	0.192	68862105	0.037	0.004
ss86314972	Chr15	RFI	G	0.353	19397001	0.015	0.007
ss86315341	Chr20	RFI	C	0.059	60770765	-0.027	0.005

ss86316536	Chr29	RFI	A	0.276	6274933	0.005	0.006
ss86319413	Chr12	RFI	A	0.495	9278019	-0.002	0.008
ss86320103	Chr8	RFI	A	0.317	63915440	-0.039	0.005
ss86321699	Chr21	RFI	T	0.203	68713804	0.048	0.013
ss86321886	Chr4	RFI	A	0.068	16789206	-0.039	0.008
ss86322201	Chr1	RFI	C	0.419	1.47E+08	-0.078	0.013
ss86322706	Chr11	RFI	T	0.187	71866424	-0.035	0.008
ss86323205	Chr29	RFI	A	0.198	49862474	0.001	0.011
ss86325469	Chr17	RFI	A	0.080	41289530	0.039	0.013
ss86328652	Chr10	RFI	G	0.408	1.01E+08	0.005	0.008
ss86328853	Chr13	RFI	T	0.343	72889173	0.025	0.018
ss86329750	Chr20	RFI	A	0.109	74688816	0.000	0.009
ss86329753	Chr6	RFI	A	0.206	78603001	0.000	0.009
ss86330098	Chr19	RFI	C	0.263	63846755	-0.003	0.007
ss86330353	Chr25	RFI	T	0.313	22906651	0.006	0.007
ss86331995 ss141408536 ss86338007	Chr14	RFI	G	0.343	72796829	0.077	0.014

ss86332387	Chr4	RFI	T	0.477	78358391	0.022	0.010
ss86334240	Chr23	RFI	T	0.369	43527388	0.028	0.007
ss86335969	Chr3	RFI	T	0.229	1.07E+08	-0.039	0.011
ss86336055 ss86274178	Chr6	RFI	C	0.381	75618287	0.068	0.008
ss86337928 ss86332405	Chr5	RFI	G	0.431	25225409	0.034	0.007
ss86339405 ss86315360	Chr20	RFI	A	0.299	6555724	-0.027	0.007
ss86341015 ss86276181	Chr23	RFI	G	0.300	34680594	0.039	0.003
ss86341174 ss86312678	Chr22	RFI	C	0.253	55890005	0.069	0.009
ss86341521	Chr11	RFI	G	0.317	7704236	-0.013	0.010
Hapmap44010-BTA-115749	Chr4	RFI	T	0.165	94330791	0.044	0.013
BFGL-NGS-111692	Chr21	RFI	G	0.334	42187202	-0.040	0.014
BTA-114348-no-rs	Chr26	RFI	A	0.434	14634622	0.012	0.009

[‡]Trait units are kg/d for ADG and DMI and kg DM/d for RFI. SNPID - NCBI rs/ss SNP ID, some SNPs have multiple predicted IDs based on their sequence similarities to multiple submissions in the NCBI database; [†]These SNPs have no rs/ss SNP ID; BTA – Chromosome; Position – Chromosomal position (bp); Estimate – Allele substitution effect; Freq – Minor allele frequency; SE – standard error.

APPENDIX 2: Names for SNPs located within annotated genes and associated with ADG, DMI and RFI

SNPID	BTA	Position	Panel	Gene
ss117962667	3	43428200	ADG	collagen, type XI, alpha 1
ss117966992	3	43225815	ADG	collagen, type XI, alpha 1
ss105307554	6	37963147	ADG	leucine aminopeptidase 3
rs41656065	7	71845956	ADG	transposon-derived Buster3 transposase-like
ss105239516	10	14071411	ADG	similar to IQ motif containing H
rs41597632	10	62466743	ADG	oxysterol binding protein-like 3
rs43614200	10	13146428	ADG	mitogen-activated protein kinase kinase 1
rs41630325	15	37389561	ADG	spondin 1, extracellular matrix protein
ss86304896	20	23683579	ADG	GC-rich promoter binding protein 1
ss86341174	22	55890005	ADG	ATPase, Ca++ transporting, plasma membrane 4
rs41601279	24	26564151	ADG	UDP-Gal
rs42117657	27	21306526	ADG	microtubule associated tumor suppressor 1
rs41574019	1	55206940	ADG	myosin, heavy chain 15

SNPID	BTA	Position	Panel	Gene
rs41638872	1	6410343	ADG	ubiquitin specific peptidase 16
rs41578313	2	118264371	ADG	similar to KIAA1486 protein
rs43293349	2	21301376	ADG	metaxin 2
ss105307554	6	37963147	ADG	leucine aminopeptidase 3
rs42555873	6	93850919	ADG	USO1 homolog, vesicle docking protein (yeast)
rs43454260	6	4594143	ADG	PR domain containing 5
ss140894649	8	108961258	ADG	similar to Deafness, autosomal recessive 31
ss86308454	8	111309164	ADG	astrotactin 2
ss86313014	9	55121684	ADG	kelch-like 32 (Drosophila)
ss86320135	11	109899269	ADG	WD repeat domain 85
rs42214703	11	33877081	ADG	neurexin 1
rs41667026	12	66650688	ADG	glypican 6
rs43699555	12	52690850	ADG	MYC binding protein 2
rs41707481	13	71746495	ADG	protein tyrosine phosphatase, receptor type, T

SNPID	BTA	Position	Panel	Gene
rs41742877	14	45009927	ADG	eukaryotic translation initiation factor 3, subunit H
rs41581215	18	41024459	ADG	teashirt zinc finger homeobox 3
rs42243754	20	13445531	ADG	similar to microtubule associated serine/threonine kinase family member 4
ss86341174	22	55890005	ADG	ATPase, Ca++ transporting, plasma membrane 4
ss86335492	24	64469669	ADG	similar to serine (or cysteine) proteinase inhibitor, clade B (ovalbumin)
ss86289359	26	44210363	ADG	carboxypeptidase X (M14 family), member 2
ss117963035	2	108854240	DMI	insulin-like growth factor binding protein 5
rs43362139	3	113663829	DMI	microtubule-actin crosslinking factor 1
rs42410387	6	119038391	DMI	Wolf-Hirschhorn syndrome candidate 2
rs42411131	6	119003189	DMI	Wolf-Hirschhorn syndrome candidate 1
rs43460584	6	41462782	DMI	Kv channel interacting protein 4
ss86314057	8	56217967	DMI	guanine nucleotide binding protein (G protein), q polypeptide

SNPID	BTA	Position	Panel	Gene
rs41654591	10	91420638	DMI	serine palmitoyltransferase, long chain base subunit 2
rs41569387	11	70053572	DMI	annexin A4
ss86333184	13	24907224	DMI	hypothetical LOC513129
rs42484917	14	56901724	DMI	similar to Zinc finger protein ZFPM2 (Zinc finger protein multitype 2) (F
rs41887389	18	50742772	DMI	similar to Protein capicua homolog
ss86287613	21	34754177	DMI	lysyl oxidase-like 1
ss86329667	22	19476532	DMI	glutamate receptor, metabotropic 7
rs42029905	23	45588817	DMI	similar to 52 kDa repressor of the inhibitor of the protein kinase (p58IP
rs42052858	24	64215863	DMI	hypothetical protein LOC100141140
ss86302411	26	5128409	DMI	protocadherin-related 15
ss86312150	26	7796869	DMI	protein kinase, cGMP-dependent, type I
rs43266806	1	114096269	DMI	guanine monphosphate synthetase
ss86301441	2	67981464	DMI	NCK-associated protein 5
rs43389761	4	48969929	DMI	similar to Cadherin-like protein 28

SNPID	BTA	Position	Panel	Gene
rs42244558	5	1293420	DMI	similar to THAP domain containing, apoptosis associated protein 2
rs42410387	6	119038391	DMI	Wolf-Hirschhorn syndrome candidate 2
rs43631525	10	55618423	DMI	protogenin homolog (Gallus gallus)
ss86319906	11	98890768	DMI	G protein-coupled receptor 144
rs42002618	22	22393278	DMI	inositol 1,4,5-triphosphate receptor, type 1
rs42029905	23	45588817	DMI	similar to 52 kDa repressor of the inhibitor of the protein kinase (p58IP
rs41669831	24	41411977	DMI	Rho GTPase activating protein 28
ss86284580	25	40999193	DMI	Ras association and DIL domains
rs42142693	28	24107627	DMI	solute carrier family 25 (mitochondrial carrier; Graves disease autoantig
ss86315831	29	7301394	DMI	glutamate receptor, metabotropic 5
ss86305968 ss86339265	2	24659200	RFI	Rap guanine nucleotide exchange factor (GEF) 4
rs41589498	3	2516633	RFI	immunoglobulin-like domain containing receptor 2

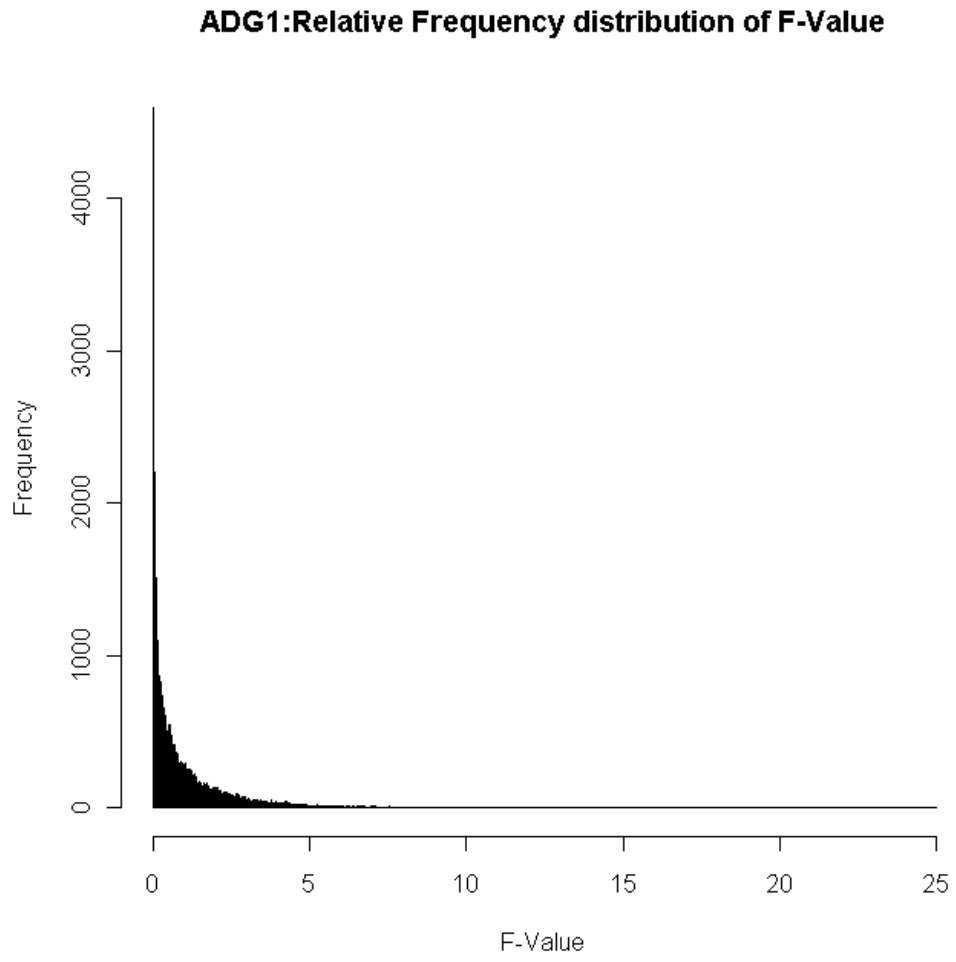
SNPID	BTA	Position	Panel	Gene
rs43389761	4	48969929	RFI	similar to Cadherin-like protein 28
rs42244558	5	1293420	RFI	similar to THAP domain containing, apoptosis associated protein 2
rs43557189	8	53208327	RFI	transient receptor potential cation channel, subfamily M, member 6
rs42972397	9	90796431	RFI	iodotyrosine deiodinase
rs41569387	11	70053572	RFI	annexin A4
ss105311629	13	11334505	RFI	USP6 N-terminal like
rs41994086	16	52549377	RFI	ring finger and CCCH-type zinc finger domains 1
BFGL-NGS-111692[†]	21	42187202	RFI	sec1 family domain containing 1
ss86321297	24	48150873	RFI	ST8 alpha-N-acetyl-neuraminide alpha-2,8-sialyltransferase 5
ss86293365	3	115359337	RFI	EPH receptor A10
rs29011976	3	41842787	RFI	similar to ATPase, H+ transporting, lysosomal accessory protein 2
rs41589498	3	2516633	RFI	immunoglobulin-like domain containing receptor 2

SNPID	BTA	Position	Panel	Gene
rs41587678	4	49069017	RFI	synaptophysin-like 1
rs43389761	4	48969929	RFI	similar to Cadherin-like protein 28
ss86313043	7	68862105	RFI	similar to ichthyin protein
rs43604365	9	52502821	RFI	ubiquitin specific peptidase 45
rs43604391	9	52475302	RFI	ubiquitin specific peptidase 45
ss86309185	11	63600222	RFI	similar to CG17657 CG17657-PA
rs42771121	13	51699788	RFI	ring finger protein 24
ss86295428	16	68396075	RFI	ribosomal protein S6 kinase, 52kDa, polypeptide 1
rs29022067	17	31309718	RFI	progesterone receptor membrane component 2
BFGL-NGS-111692[†]	21	42187202	RFI	sec1 family domain containing 1
rs42068538	25	31892337	RFI	autism susceptibility candidate 2
ss86300114	27	37207203	RFI	ADAM metallopeptidase domain 18
rs29024039	27	45906983	RFI	ubiquitin-conjugating enzyme E2E 2 (UBC4/5 homolog, yeast)
rs42142693	28	24107627	RFI	solute carrier family 25 (mitochondrial

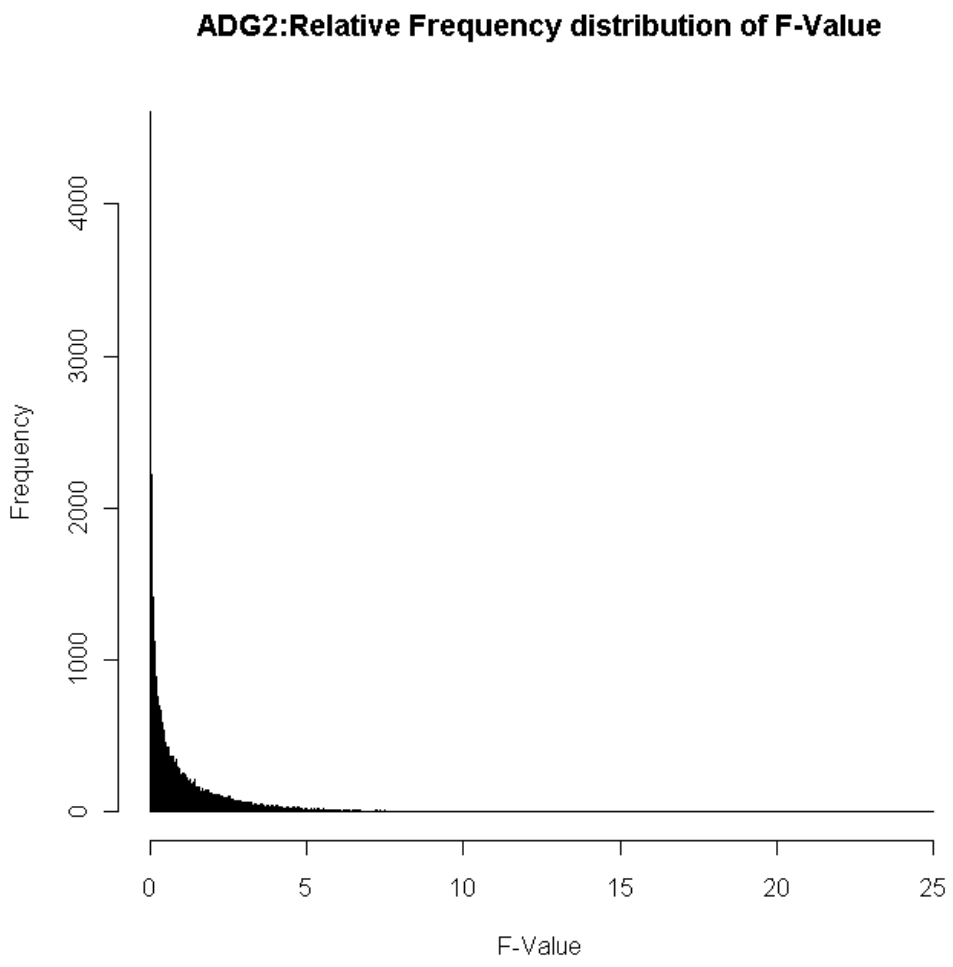
SNPID	BTA	Position	Panel	Gene
				carrier; Graves disease autoantig

SNPID - NCBI rs/ssSNP ID; †These SNPs have no rs/ss ID; BTA – Chromosome; Position – Chromosomal position (bp); MA Minor allele; MAF – Minor allele frequency. Panel – Designate either RR-BLUP panels from Chapter 3 or B panels from Chapter 4.

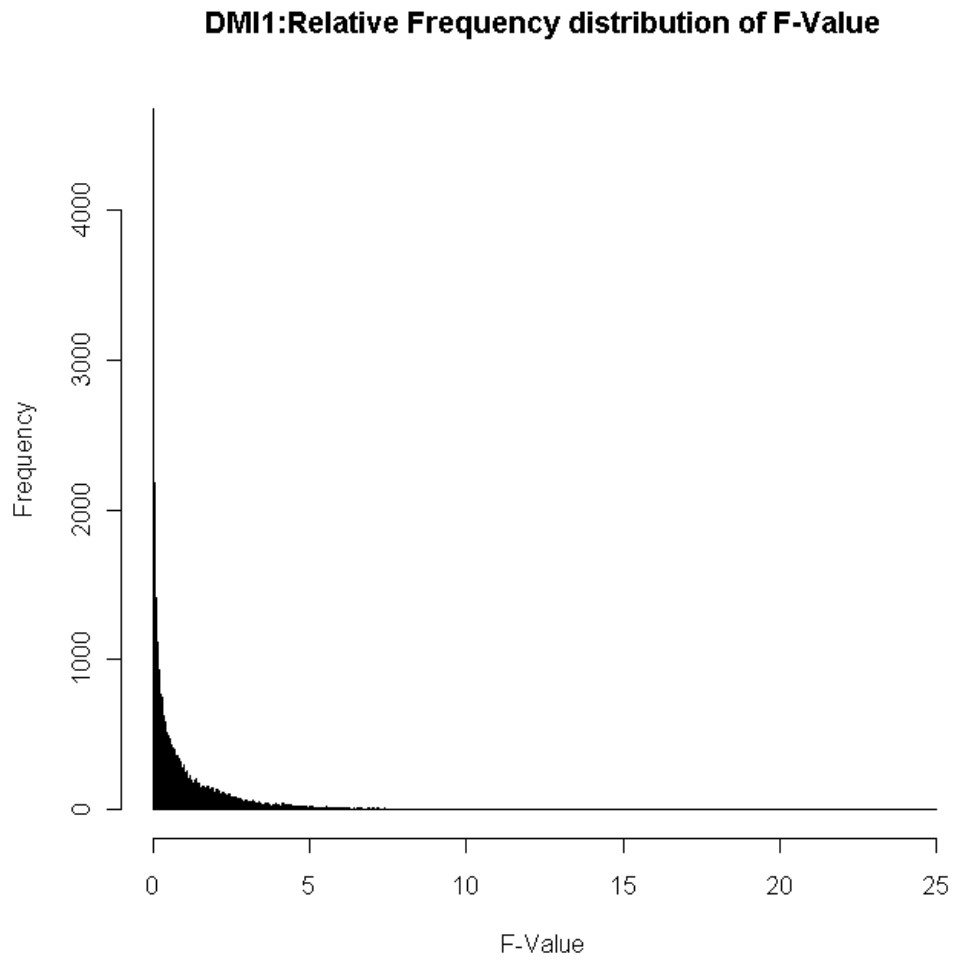
APPENDIX 3: Relative frequency distribution of F values for Single marker regression analysis in splits 1 and 2 of the Chapter 3 analysis



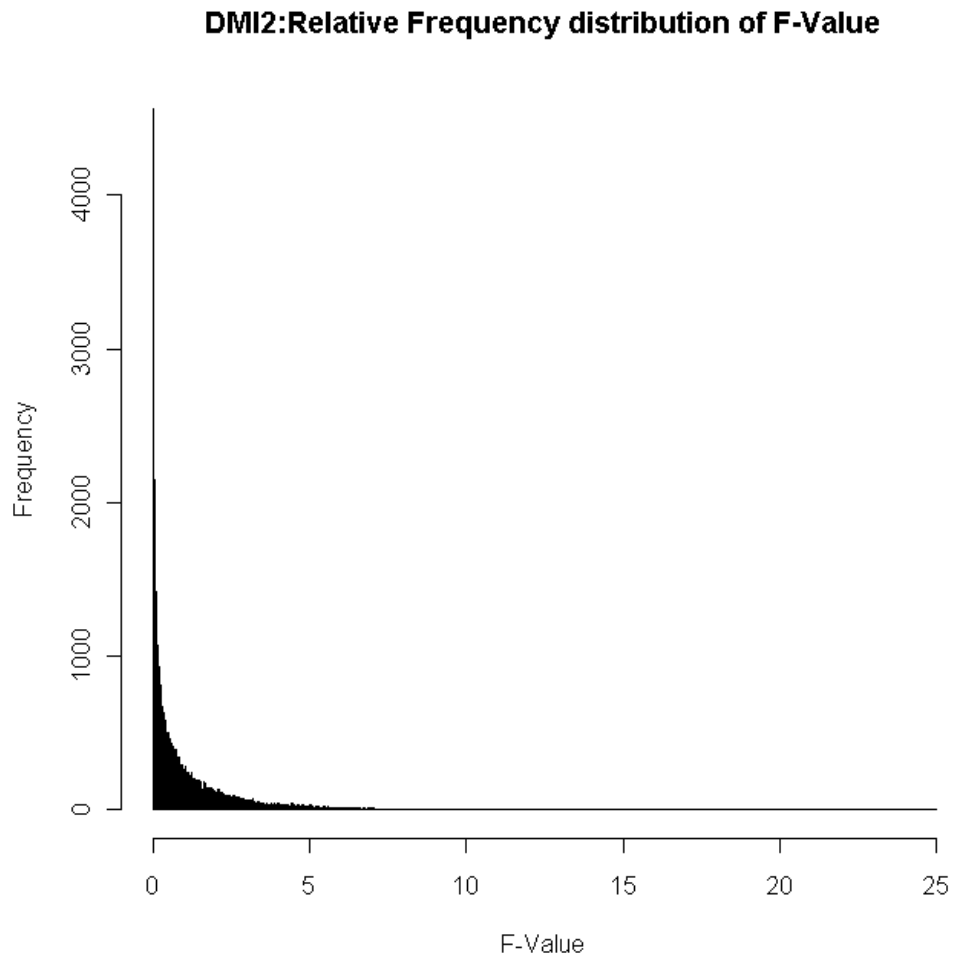
Appendix 3: Figure 1: Distribution of F-Values for Single marker regression analysis of Average daily gain (ADG) in Split 1



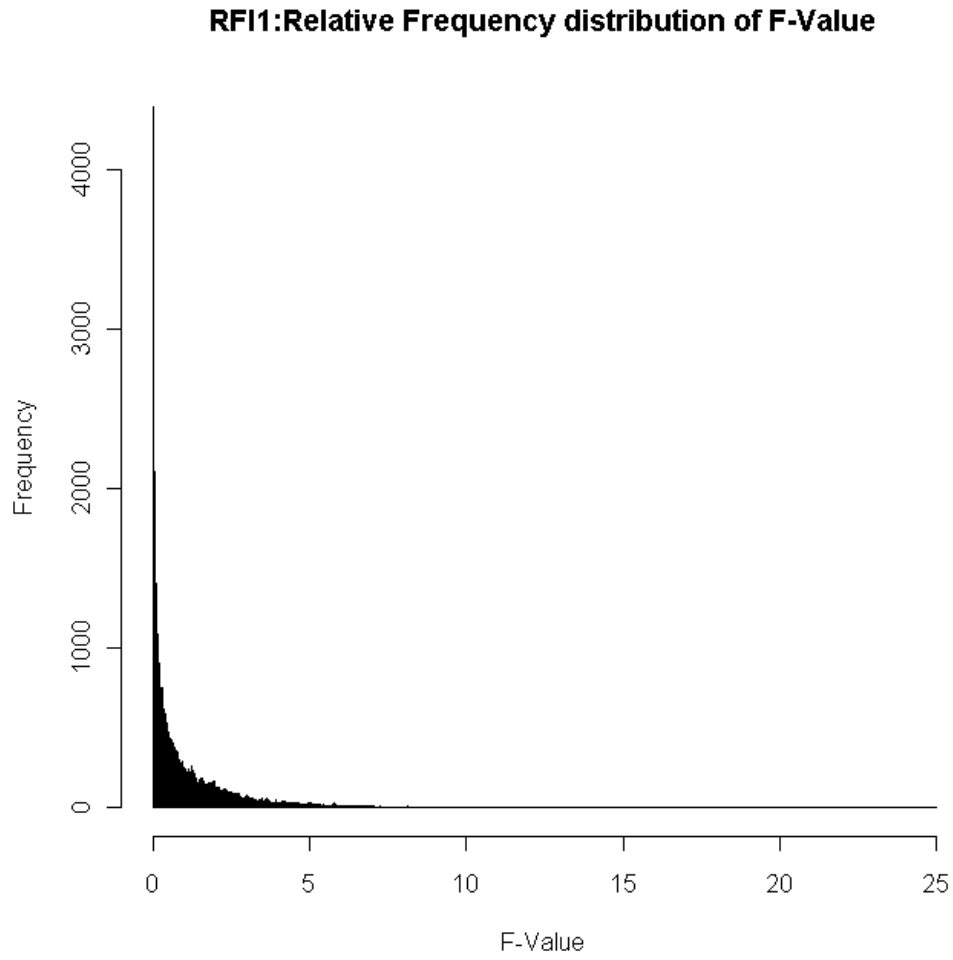
Appendix 3: Figure 2: Distribution of F-Values for Single marker regression analysis of Average daily gain (ADG) in Split 2



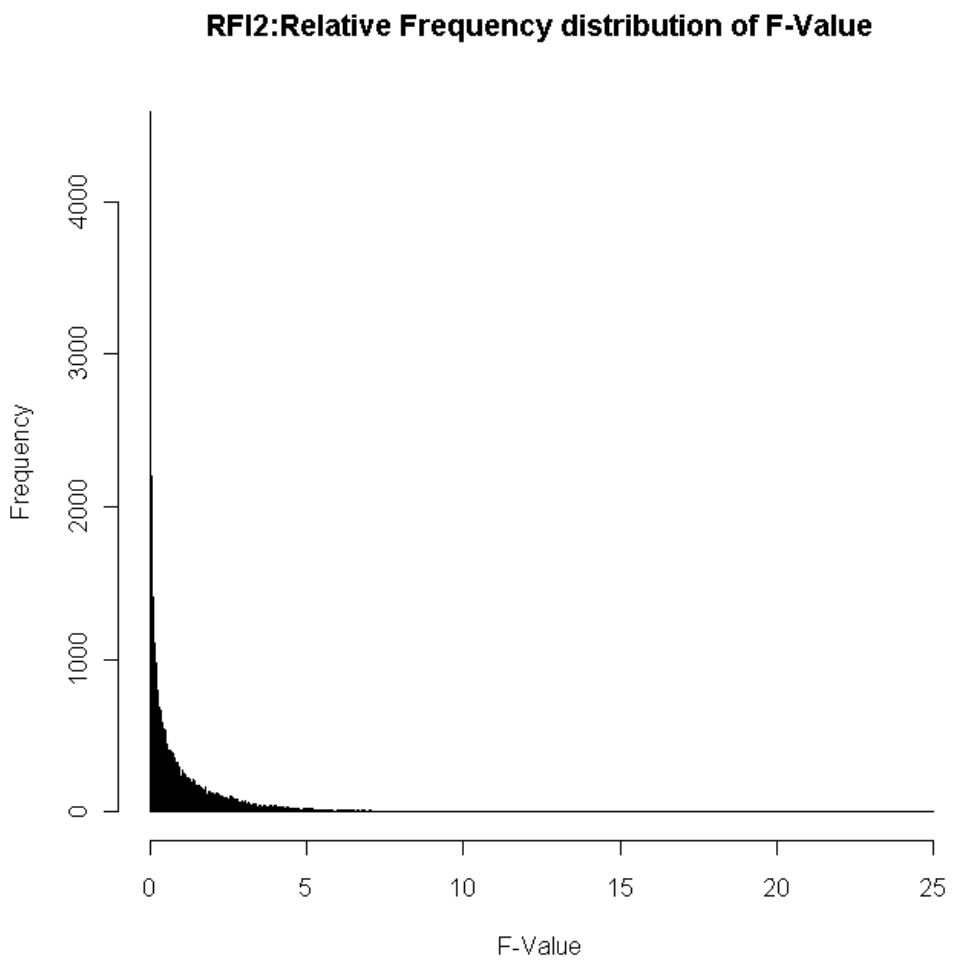
Appendix 3: Figure 3: Distribution of F-Values for Single marker regression analysis of dry matter intake (DMI) in Split 1



Appendix 3: Figure 4: Distribution of F-Values for Single marker regression analysis of dry matter intake (DMI) in Split 2



Appendix 3: Figure 5: Distribution of F-Values for Single marker regression analysis of residual feed intake (RFI) in Split 1



Appendix 3: Figure 6: Distribution of F-Values for Single marker regression analysis of residual feed intake (RFI) in Split 2

APPENDIX 4: Variance Component Estimation

Appendix 4: Table 1. Estimates of variance components obtained in the 5 replicates of the training data using the BLUP pre-selection method used in Chapter 3.

		Replicate					
†Trait	Parameter	1	2	3	4	5	Average
ADG	GenVar	0.001	0.022	0.027	0.000	0.024	0.015
	ResVar	0.071	0.055	0.052	0.074	0.048	0.060
	GenVar + SNP	0.005	0.053	0.056	0.005	0.010	0.026
	ResVar + SNP	0.037	0.046	0.052	0.052	0.043	0.046
	SNP variance	0.035	0.009	0.000	0.022	0.005	0.014
DMI	GenVar	0.662	0.938	0.960	0.576	0.842	0.796
	ResVar	1.114	0.940	1.023	1.240	0.824	1.028
	GenVar + SNP	0.000	0.823	0.646	0.094	0.380	0.389
	ResVar + SNP	0.855	0.579	0.725	1.172	0.804	0.827
	SNP variance	0.260	0.361	0.298	0.068	0.021	0.201
RFI	GenVar	0.124	0.228	0.283	0.432	0.418	0.297
	ResVar	0.682	0.567	0.536	0.479	0.374	0.528
	GenVar + SNP	0.130	0.265	0.321	0.311	0.169	0.239
	ResVar + SNP	0.354	0.385	0.328	0.371	0.410	0.370
	SNP variance	0.328	0.182	0.208	0.108	-0.036	0.158

†Trait units are kg/d for ADG and DMI and kg DM/d for RFI. ADG – Average daily gain; DMI – Dry matter intake; RFI – residual feed intake; GenVar – Genetic variance; ResVar – Residual variance; GenVar + SNP – Genetic variance when SNPs are included in the model as fixed effects; ResVar + SNP – Residual variance when SNPs are included in the model as fixed effects; SNP variance –variance attributed to SNPs as the difference between ResVar and ResVar + SNP

Appendix 4: Table 2. Estimates of variance components for ADG, DMI and RFI obtained in the 5 replicates of the training data with the RR-BLUP method used in Chapter 4.

		Replicate					
†Trait	Parameter	1	2	3	4	5	Average
ADG	ResVar	0.004 ± 0.003	0.021 ± 0.003	0.021 ± 0.003	0.021 ± 0.003	0.023 ± 0.004	0.018 ± 0.003
	GenVar	0.012 ± 0.004	0.005 ± 0.003	0.006 ± 0.004	0.006 ± 0.004	0.004 ± 0.005	0.006 ± 0.004
	SNPVar	0.036 ± 0.001	0.036 ± 0.002	0.038 ± 0.002	0.038 ± 0.002	0.030 ± 0.002	0.035 ± 0.002
DMI	ResVar	0.725 ± 0.088	0.720 ± 0.247	0.954 ± 0.220	1.040 ± 0.121	0.702 ± 0.177	0.828 ± 0.171
	GenVar	0.111 ± 0.095	0.734 ± 0.331	0.481 ± 0.228	0.193 ± 0.148	0.524 ± 0.226	0.408 ± 0.206
	SNPVar	0.069 ± 0.005	0.034 ± 0.005	0.032 ± 0.004	0.035 ± 0.003	0.034 ± 0.004	0.041 ± 0.004
RFI	ResVar	0.306 ± 0.025	0.349 ± 0.062	0.339 ± 0.118	0.385 ± 0.121	0.320 ± 0.090	0.340 ± 0.083
	GenVar	0.022 ± 0.025	0.166 ± 0.067	0.153 ± 0.137	0.200 ± 0.125	0.164 ± 0.106	0.141 ± 0.092
	SNPVar	0.067 ± 0.004	0.045 ± 0.004	0.044 ± 0.006	0.042 ± 0.008	0.046 ± 0.006	0.049 ± 0.006

†Trait units are kg/d for ADG and DMI and kg DM/d for RFI. ADG – Average daily gain; DMI – Dry matter intake; RFI – residual feed intake; GenVar – Genetic variance; ResVar – Residual variance; GenVar + SNP – Genetic variance when SNPs are included in the model as fixed effects; ResVar + SNP – Residual variance when SNPs are included in the model as fixed effects; SNP variance –variance attributed to SNPs as the difference between ResVar and ResVar + SNP

Appendix 4: Table 3. Estimates of variance components for ADG, DMI and RFI obtained in the 5 replicates of the training data with the B method used in Chapter 4.

		Replicate					
†Trait	Parameter	1	2	3	4	5	Average
ADG	ResVar	0.017 ± 0.005	0.020 ± 0.010	0.023 ± 0.013	0.031 ± 0.009	0.019 ± 0.009	0.022 ± 0.009
	GenVar	0.007 ± 0.006	0.031 ± 0.015	0.026 ± 0.016	0.016 ± 0.010	0.023 ± 0.012	0.021 ± 0.012
	SNPVar	0.081 ± 0.006	0.083 ± 0.012	0.102 ± 0.012	0.096 ± 0.008	0.088 ± 0.010	0.090 ± 0.009
DMI	ResVar	0.582 ± 0.150	0.662 ± 0.151	0.720 ± 0.120	0.870 ± 0.244	0.771 ± 0.174	0.720 ± 0.184
	GenVar	0.143 ± 0.169	0.596 ± 0.163	0.564 ± 0.210	0.326 ± 0.234	0.289 ± 0.180	0.384 ± 0.191
	SNPVar	0.599 ± 0.081	0.523 ± 0.064	0.483 ± 0.043	0.507 ± 0.096	0.492 ± 0.049	0.521 ± 0.067
RFI	ResVar	0.247 ± 0.033	0.274 ± 0.076	0.193 ± 0.119	0.188 ± 0.097	0.198 ± 0.107	0.220 ± 0.086
	GenVar	0.048 ± 0.034	0.242 ± 0.085	0.339 ± 0.174	0.362 ± 0.126	0.310 ± 0.142	0.260 ± 0.112
	SNPVar	0.410 ± 0.049	0.364 ± 0.046	0.360 ± 0.039	0.390 ± 0.035	0.321 ± 0.041	0.369 ± 0.042

†Trait units are kg/d for ADG and DMI and kg DM/d for RFI. ADG – Average daily gain; DMI – Dry matter intake; RFI – residual feed intake; GenVar – Genetic variance; ResVar – Residual variance; GenVar + SNP – Genetic variance when SNPs are included in the model as fixed effects; ResVar + SNP – Residual variance when SNPs are included in the model as fixed effects; SNP variance –variance attributed to SNPs as the difference between ResVar and ResVar + SNP